

CHAPTER 4

Diet Selection and Feeding Site Location

4.1. Introduction

The timing and length of feeding bouts of kangaroos and wallabies discussed in Chapter 3 form only a part of the strategy of 'dining out'; animals must also decide where to dine and what to select from the menu (Bunnell and Gillingham, 1985). Selection decisions are made according to energetic and nutrient needs of the forager, the risks the forager must take to meet those needs and the distribution of food items (and predators) in the environment. A forager's energetic needs are determined primarily by its body size, and then by a number of other factors including its age, sex, reproductive state and body condition. Thus animals are constrained to make certain foraging decisions on the basis of their species, sex etc. but they may also make decisions to gain additional benefits from foraging, above those required for survival, which can be directed into growth and reproduction.

The foraging strategy of a species will have been broadly defined through evolution by the species' size and therefore its metabolic requirements, gut capacity and mouthparts. Metabolic rate scales to body weight to the 0.75 power (Kleiber, 1975) such that small animals have proportionately higher metabolic demands than large animals, but large animals have higher absolute energy requirements (Bell, 1970; Jarman, 1974). Proportionately larger intakes are not possible for small animals because gut capacity is a constant proportion of body weight (Parra, 1978), so small animals must select a higher quality diet (Janis, 1976). The high intakes required by large animals cannot be supported by the low biomasses of good quality feed, so large animals must have digestive adaptations to cope with the intake of large quantities of food of low digestibility (Hofmann and Stewart, 1972; Janis, 1976). Herbivores are thought to be constrained to a range of foods on a particular fibre curve of biomass on fibre content, on which the lower limits (low fibre levels) are determined by abundance and the upper limits by digestive capacity (Demment and Van Soest, 1985). In this way body size has

been considered a possible mechanism determining inter-specific differences in diet (Bell, 1970; Jarman, 1974; Janis, 1976; Demment and Van Soest, 1985). Relationships between body size, diet, habitat selection and anti-predator strategies have been demonstrated for a number of groups of related mammals which differ in body size: antelopes (Jarman, 1974); ungulates (Geist, 1974); primates (Clutton-Brock and Harvey, 1977).

Macropodids exhibit a wide range of body sizes in which eastern grey kangaroos are towards the large end of the scale and red-necked wallabies are somewhere in the middle. The group also occupies a wide range of niches and the relationships between body size, foraging behaviour and habitat choice demonstrated for antelopes by Jarman (1974) appear to hold true for macropodids as well (Kaufmann, 1974a; Jarman, 1984; Norbury *et al.*, in press). At Wallaby Creek the eastern grey kangaroo and red-necked wallaby, which differ greatly in size, live sympatrically, on semi-improved pasture (parts of which bear little relation to their natural habitat). In this Chapter I examine whether kangaroos and wallabies utilize different components of the habitat at Wallaby Creek and if they do, whether the differences constitute an ecological separation of the species that can be explained by selection pressures of the past.

The body size difference between the sexes in sexually dimorphic species has also been suggested as a potential cause for differences between the sexes in diet and habitat use. Large males may be less tolerant of low plant biomass because of their higher absolute energy requirements (Staines *et al.*, 1982; Clutton-Brock *et al.*, 1987). Differences in the diets and habitat use of the sexes have been reported in a number of groups of animals, including macropods (Johnson and Bayliss, 1981; Taylor, 1984); primates (Boinski, 1988), and ungulates (Clutton-Brock *et al.*, 1987). For some species the high energetic requirements of heavily lactating females may lead them to forage away from other females or males, where they can meet their nutritional needs (Jarman, 1983; Johnson and Bayliss, 1981; Boinski, 1988). For some highly social ungulate species, ecological separation between the sexes results from dominant males keeping other males away from females or territorial behaviour in one sex and not the other (Jarman 1983).

Differences in body size of the two sexes may also affect their relative risk from predation; large male kangaroos and wallabies possess weapons which they use in intra-male competition (Jarman, 1983), but there are many anecdotes of males using them in defence when being attacked by dogs or humans. Female macropods with large pouch-young may be particularly vulnerable to predation because the burden of carrying a large young in the pouch may slow their movement during flight from a predator (Jaremovic, 1984). If sufficiently harassed a female may eject her young from the pouch and continue moving (Robertshaw and Harden, 1985). Dingo predation has a significant impact on the survival of young-at-foot of both species at Wallaby Creek, especially in

the early stages after the young has permanently left the pouch (Stuart-Dick, 1987; Stuart-Dick and Higginbottom, in press). Juvenile survival is very important to the reproductive success of both males and females. However, parental care is a male may sire many young in one season so the loss of one would have less of an impact on his reproductive success than the loss of a young to a female. It seems likely that females will be more wary of predators than males because they are less likely to escape an attack and their young are very vulnerable. Ecological separation of the sexes may therefore, arise from females selecting 'safer' places to feed.

The degree of sexual dimorphism in both species changes considerably with age; male and female newly emergent pouch-young are very similar in size and weight but as they get older males become progressively larger than females. Whilst adult females kangaroos, like of most species, eventually stop growing, male kangaroos show the potential to continue growing throughout adult life (Jarman, 1983). For eastern grey kangaroos the ratio by weight of females to males is about 0.7:1 at the time of females sexual maturity but can reach almost 0.5:1 by the age of 8 years (*ibid*). The difference in body size of male and female red-necked wallabies at full maturity is of the same order (Johnson, 1985). Given the large difference in body size between the sexes of both species we might expect differences between them in their choice of diet and/or feeding site location; especially when comparing the older, larger adult males with females. However, eastern grey kangaroos and red-necked wallabies live in open membership, mixed-sex groups (Southwell 1984b, Jarman and Southwell, 1986; Johnson 1989a) and the possibilities for sexual segregation may be limited in these species.

I have mentioned the importance^{of} the risk of predation in the selection of feeding sites. The relative importance of food quality and safety to an individual forager will affect that forager's assessment of patch quality and its likelihood of feeding there (Newman and Caraco, 1987). A foraging tactic which simultaneously maximises food intake and safety (or other important demands) will be precluded when these factors impose conflicting demands on the animal, such as the highest quality food patches also being the most risky (Sih, 1980). Many species have been shown to alter their habitat or patch choice in relation to differing predation risks and the relative rewards of foraging (fish: Sih, 1980; Holbrook and Schmitt, 1988; caribou: Ferguson *et al.*, 1988; squirrels: Newman and Caraco 1987).

The dingo is the main predator of kangaroos and wallabies at Wallaby Creek, with the wedge-tailed eagle being a lesser threat. Although vegetation cover will probably interfere with the searching abilities of aerial predators, it is less clear whether cover would provide protection from terrestrial predators. Jarman (1974) has suggested that the method used by herbivores to try and escape predation is related to their body size. Those species which are able to outrun their attacker may well benefit from being in open habitat because they will have a clear view of the environment when searching for

predators. Those animals, which group together with others to increase their efficiency of surveillance, may also benefit from open habitat because they can see, and respond to, the alarm behaviour of others in the group more easily. Jarman and Sinclair (1979) suggest that the risk of predators being hidden in tall grass prevents impala from feeding in certain areas where the grass is taller than a critical height. Smaller species, which rely on crypsis to avoid being spotted, are likely to benefit from being able to shelter amongst cover vegetation. I should emphasize that the degree to which vegetation provides cover depends on the animals size, so habitat that appears open to a large kangaroo may provide cover for a smaller wallaby. In this chapter I will examine the effect of the availability of cover on the distribution of kangaroos and wallabies.

Although much of the study site at Wallaby Creek has been cleared and sown to improved pasture, one regular change its environment that kangaroos and wallabies have evolved with is fire. Fire has been an important part of the Australian ecosystem since before the arrival of man. Aboriginal man utilized some herbivores' preferences for new plant growth after fire to attract game (Gill 1975), yet they also saw the need to preserve some habitat as refuge for animals, and their burning patterns produced a mosaic of recently burnt and unburnt patches for this purpose. The prescribed burning of some parts of the study site each year allowed me to look at the species' uses of burnt patches, and how that use changed over time since burning.

Following on from the previous discussion there are a number of particular predictions I will consider in this chapter in relation to feeding site selection and diet selection:

- 1) Wallabies, because of their small size, have higher relative metabolic requirements and therefore feed on a higher quality diet.
- 2) Wallabies, because of their smaller body size, are more vulnerable to predators and must feed in less exposed sites than kangaroos.
- 3) Females have better quality diets because of the high nutrient and energy requirements of reproduction.
- 4) Females are more vulnerable to predation because of their smaller size and because they are encumbered by pouch-young or accompanying young-at-foot. They should therefore feed in safer locations than males, unless they can gain more benefit from being in a group.
- 5) Feeding site choice is made on the basis of the best quality food available in the patch.

- 6) Other considerations such as vulnerability to predation or potential rates of intake may conflict with patch choice made on the basis of food quality alone, leading to animals feeding in 'sub-optimal' sites.
- 7) Kangaroos and wallabies change their use of areas after burning. Because of the availability of new plant shoots they use the burnt areas more for feeding but because dense undergrowth is removed by fire they use burnt areas less for resting.
- 8) Kangaroos and wallabies will alter their habitat use with time of day according to their prevailing activity, and environmental conditions such as temperature and light.

4.2 Methods

4.2.1 Sources of data used in this chapter

The data for this chapter on diet selection and micro-habitat location come from five sources:

- 1) Monthly searches conducted between August 1987 and February 1988 provided information on the selection of feeding and resting sites by both species.
- 2) The 15-minute continuous watches of kangaroos and wallabies, carried out between January 1986 and July 1987, provided data on the sward components that animals used for foraging (see Chapter 2 for details of methods and schedules).
- 3) Collection of kangaroo and wallaby faecal pellets and their subsequent microscopic analysis provided estimates of the contribution of various monocot and dicot species to the diet.
- 4) "Cafeteria trials" conducted with five captive eastern grey kangaroos investigated dietary preference in the absence of confounding environmental factors such as proximity to, or provision of, cover and risk of predation.
- 5) Vegetation data, providing information on the availability of different grass species, cover types and ground-sward types, came from two vegetation surveys carried out by K.Higginbottom in September 1985 and February 1986.

In June or July of each year a proportion of the study area was burnt. Assessments of diets and feeding-patch choices before and after burning events looked at the response of kangaroos and wallabies to burning of their habitat, both in their choice of feeding sites and their selection of plants and plant parts in those sites. The animals' relative preferences for burnt areas over unburnt ones are compared using estimates of the area that was burnt in July of 1987.

4.2.2 Data collection and analyses from searches

Between August 1987 and February 1988 the eleven blocks defined in section 2.4.2 were searched regularly to record changing patterns of distribution and patch choice of kangaroos and wallabies following a fire.

In the months August, September, December and February blocks were searched in each of four time periods: morning, 0-3 hours after first light (T1 and T2); midday, from then until three hours before dark (T3); afternoon, from three hours before dark to dark (T4 and T5); and evening, 1.5 to 3 hours after dark (T6). The time between dusk and 1.5 hours after dusk was not sampled. All blocks were searched in the afternoon and morning in every month but a few evening searches were not completed. These missing searches have been accounted for in the data analyses by analysing the time periods separately or by including the number of searches of each block in the calculations of density of animals per hectare.

A search consisted of walking a set route around the block and recording all kangaroos and wallabies seen *en route*. Records were made of each animal's identity, population class, group size and grid location. If the group was spread over two adjacent blocks only the animals seen in the block were recorded for the search but the animals in the adjoining block were included in the recorded group size. I recorded details of each site where an animal was sighted, including: whether the animal was in the shade if the sun was shining; whether the animal was on a burnt area or not; the dominant cover species in the vegetation patch; the dominant ground species in the patch; and the proportion of dead plant matter in the sward. A patch is defined as an area of 1m² surrounding the animal. The animal's activity was classed into broad categories of feeding, being alert, grooming and moving. If the animal was feeding I recorded which component of the vegetation it was feeding on i.e. tussock grass, blady grass, shrubs, inter-tussock sward, burnt tussock grass, or burnt blady grass.

Each block search took from 0.5 to 3 hours to complete. Blocks were searched in pairs, except for block 5 which was roughly twice the size of other blocks. T2 sometimes included the start of a resting period and T4 sometimes included the end of a resting period, so block pairs were searched in the same order in the morning and afternoon to balance out active and less active periods. The order was reversed in consecutive months. The blocks were of varying size because their boundaries were chosen to separate different vegetation types rather than to enclose similar sized areas. Where comparisons were to be made of densities of animals on different vegetation types the 1-ha grid squares or 0.25-ha grid squares were used as the units of area. Allocating each grid square to a block allowed me to account for unequal numbers of searches per grid square.

The data were recorded directly onto data sheets, with one record per animal, and then transferred onto a computer. The data set allowed comparisons between two seasons, four time periods, two species and in some cases sexes or population classes. The original data set was used to construct frequency tables which were subsequently analysed by fitting log-linear models. If no suitable model was found for three or four-way comparisons the data were split, and two-way comparisons were made using the least likelihood ratio statistic (G) (BMDP statistical software). Analyses of variance were used to compare factors affecting estimates of proportions (e.g. proportion of dead vegetation in a patch) but were only used when the conditions of homogenous variances and normality were satisfied. The Brown-Forsythe analysis of variance was used when the condition of normality was satisfied and that of homogenous variances was not (BMDP statistical software).

4.2.3 Data collection and analyses for the vegetation surveys

In order to look at the preferences in diet and feeding-site selection I required information on the availability of the different grass species and feeding-site types. K.Higginbottom carried out a number of surveys of the vegetation in the study site, by looking at the composition of a representative sub-set of the 210 1-ha grid cells that made up the study area. The vegetation surveys were all carried out within my 114 ha study area. The most comprehensive survey took place in September 1985, when approximately 74 1-ha cells were surveyed, and February 1986, when approximately 64 1-ha cells were surveyed. I have used data from these surveys for my winter and summer estimates of vegetation availability. The surveys were based on 0.25-ha cells (4 within each 1-ha grid cell), and in each of these cells 25 0.25-m² quadrats were laid in five rows of five i.e. approximately 10 m apart. The proportions of each cover type were estimated in units of 0.1, adding to a total of 1.0, as were the proportions of each ground vegetation species or type.

The data were analysed on an individual quadrat basis, and on a 0.25-ha basis by calculating the mean of the proportions of cover provided by plant species in the 25 quadrats for each cell. The data set for winter 1985 includes 6450 individual quadrats in 258 0.25-ha grid cells, and the summer 1986 set includes 7450 quadrats in 298 grid cells. When comparing the availability of different grass species with the proportions found in the diets (section 4.3.) I have calculated proportions from the individual quadrats. The feeding sites were classified by the dominant ground species in the sward surrounding the recorded animal i.e. an area larger than a quadrat. I therefore classified each 0.25-ha grid cell according to its most dominant ground species from the mean proportions of each species in the 25 quadrats. The frequencies that different ground species were the dominant in a grid square were used to calculate the availability of different site types. I should note that the availability figures used are based on the whole study site. Since most animals occupied home ranges which individually only covered a part of the study site, the availability will not be a measure of what was actually available to each animal. I did not have time to calculate the availabilities of grasses and vegetation types in each home range, data which would have been necessary to calculate the strict preferences of each individual.

4.3 Results

4.3.1 Use of burnt areas

The number of kangaroos and wallabies using burnt areas was calculated from the records which noted whether the animal sighted was standing on a burnt patch or not. Burnt areas with small proportions of tussock grasses or blady grass were indistinguishable from unburnt areas by December 1987 and the remaining burnt areas were no longer distinguishable from unburnt ones by January or February. Thus the proportion of recognizably burnt areas declined from November 1987 onwards.

Frequency tables of season x species x burnt were calculated for each time period. Time periods were not combined because animals used different areas depending on whether they were active or resting e.g. newly burnt areas provided very little cover and were not often used for resting. Table 4.1 gives percentages, of all sightings of kangaroos and wallabies, of animals seen on burnt areas in each time period, in winter (August to October) and summer (December to February). Log-linear models were fitted to the original frequency data within each time period to look at the relationship between use of burnt areas, species (eastern grey kangaroo or red-necked wallaby) and season. In the morning and midday time periods no model fitted the data so the least-likelihood ratio test was used to compare the species in each time period in each season (Sokal and Rohlf 1981).

In each time period and in both seasons, a greater percentage of the kangaroos seen were found on burnt areas compared to wallabies. Only in the midday period, in summer, was the difference not significant. The species difference in use of burnt areas was supported by the log-linear analyses; in both the afternoon and evening the interaction between use of burnt areas and species was included in the best fitting model for the three-way analysis.

The interaction between burnt and season was also included in the best fitting model of the afternoon data. Unlike other time periods, there was a greater percentage of kangaroos on burnt areas in the afternoon in summer than in winter. The unexpectedly low proportion of kangaroos using burnt areas in the afternoon will be explored further in section 4.3.4.

Table 4.1. The percentages, of all sightings of kangaroos (EGK) and wallabies (RNW), of animals seen on burnt areas in late winter and summer, in each of four time periods. Least-likelihood ratio tests compare the species within time periods and seasons. Log-linear models were fitted to the data classified by season(M), species(S) and burnt(B). A non-significant result ($p>0.05$) for test-of-fit of log-linear models means that the model does fit the data. The time periods (T1-T4) are described in section 4.2.2.

Season	Species	T1	T2	T3	T4
Winter	EGK	74.2	46.7	32.0	63.4
	n	325	137	344	164
	RNW	25.2	8.5	16.0	35.2
	n	188	47	213	91
G tests: use of burnt areas vs species (EGK or RNW)					
G		117.9	25.7	18.2	18.9
d.f.		1	1	1	1
p		<0.0001	<0.0001	<0.0001	0.0001
Summer	EGK	39.4	33.3	54.6	66.7
	n	345	162	306	99
	RNW	29.7	24.0	25.0	35.1
	n	192	50	172	74
G tests: use of burnt areas vs species (EGK or RNW)					
G		5.1	1.6	40.5	17.8
d.f.		1	1	1	1
p		<0.02	n.s.	<0.0001	<0.0001
Log-linear models for three-way analysis: season(M) x species(S) x burnt(B)					
model		no fit	no fit	BS, BM	M, BS
G				2.00	2.47
d.f.				2	3
p				0.37	0.48

In order to see if kangaroos and wallabies preferred or rejected burnt areas, or used them as would be expected from the proportion of the study area that was burnt, I calculated preference indices for the use of burnt areas. The index was a simple ratio of the percentage of animals seen on burnt areas divided by the proportion of the study site that was burnt. The index, based on that used by Petrides (1975), centres around 1.0, with values less than 1.0 indicating a rejection and greater than 1.0 indicating preference for the measured resource. Of 456 0.25-ha grid cells, 178 (40%) were burnt in July 1987. I did not map the proportion of the searched area that still appeared to be burnt in the

summer but, as I have noted, from December onwards more of the burnt area became indistinguishable from the unburnt areas. I have therefore, not calculated preference indices for summer because a 40% availability of burnt areas would be an overestimate and animals were recorded only as being on patches that still appeared to be burnt. Table 4.2 presents preference indices for kangaroos and wallabies in each time period in winter.

Table 4.2 Indices of the preference of kangaroos and wallabies for burnt areas over unburnt areas in winter. The index is the ratio of the percentage of animals seen on burnt areas divided by the proportion of the searched area that was burnt. The time periods (T1-T4) are described in section 4.2.2.

	Preference indices			
	T1	T2	T3	T4
kangaroos	1.8	1.2	0.8	1.6
n	325	137	344	164
wallabies	0.6	0.2	0.4	0.9
n	188	47	213	91

Kangaroos showed a strong preference for burnt areas in the morning and evening, and little preference in the middle of the day and the afternoon. Wallabies rejected burnt areas in each time period except at night, and showed the strongest rejection in the middle of the day when they were resting. In the above analysis I compared the preferences of kangaroos and wallabies for areas that still looked burnt. However, the grasses in burnt areas may still have provided higher quality vegetation after the time at which I was able to detect an area as burnt. I therefore calculated the densities of kangaroos and wallabies, per hectare of burnt and unburnt ground, in each of the seven months after the burn took place. Each 0.25-ha hectare grid square was classified as burnt or unburnt in August 1988 and the density of each species in each cell was calculated as the number of animals seen in a 0.25-ha grid divided by the number of times the grid cell was searched. A mean density for burned and unburned areas was calculated from the burned and unburned cell means respectively. The density was multiplied by four to give a density per hectare. Only grid cells in blocks 1,2,3,4,7,8,9,11 were included in the analyses since some evening searches of blocks 5,6 and 10 were missing. This left 258 unburnt cells and 145 burnt cells for comparison.

Figures 4.1a and b show changes in densities of kangaroos and wallabies with month since burning, on burnt and unburnt areas. Note that in this case areas classified as burnt remain so until the end of the seven months. The density of kangaroos on burnt grid cells was at peak in the second month after burning, showed a sharp decline in the following month and then a slow increase until month 6 after burning when density fell below that

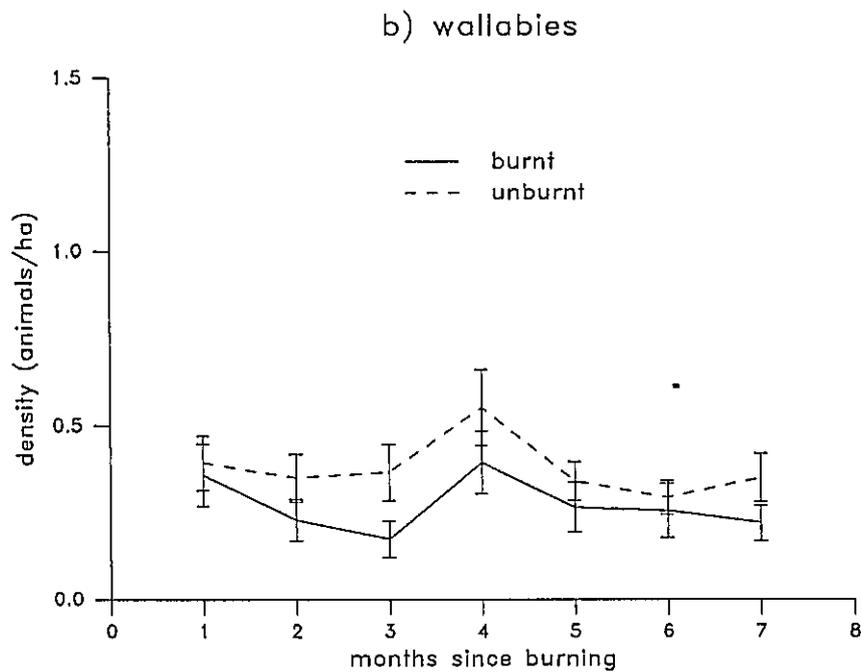
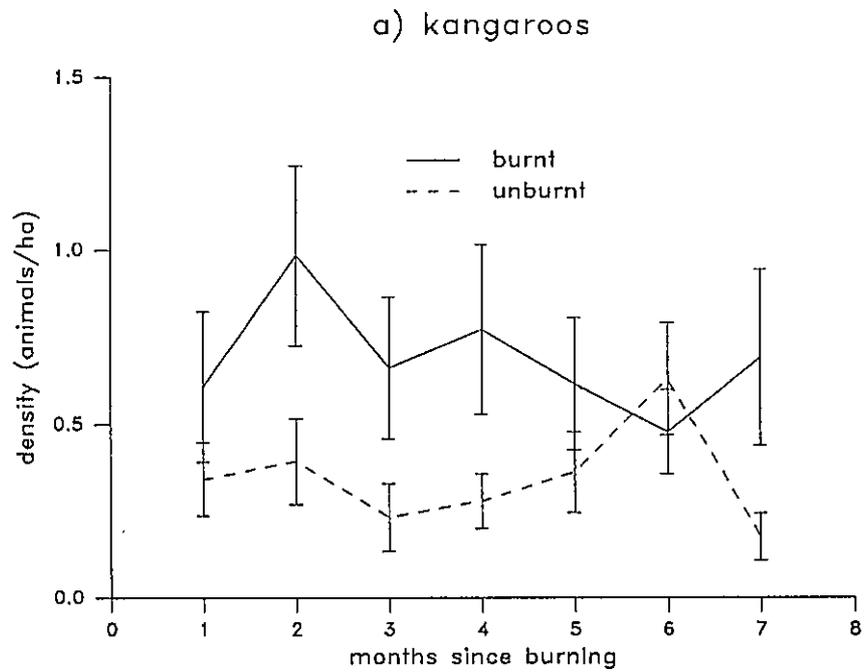


Figure 4.1 Density (\pm s.e.m.) (animals per hectare) of a) kangaroos and b) wallabies on burnt and unburnt areas in each month, for seven months following the burning of pasture in July 1987. Density is based on the number of sightings of kangaroos and wallabies on burnt and unburnt 0.25-ha grid cells.

on unburnt areas for the first time. Wallabies showed a much smaller response to burning, with densities on burnt and unburnt grid cells remaining very similar over the seven months. Unlike the kangaroos, mean densities of wallabies were always lower on burnt grid cells than on unburnt ones.

The density data did not satisfy Levene's test for equal variances and could not be improved by simple transformation so the Brown-Forsythe statistic, which does not assume equal variances, was computed for the analyses of variance table (BMDP statistical software). Table 4.3 gives the results of the two-way AOVs for each species, with month and burnt as grouping factors.

Table 4.3. Two-way AOV table comparing the densities of kangaroos and wallabies on burnt and unburnt grid cells, using the Brown-Forsythe statistic for groups with unequal variances. Degrees of freedom are $g-1$, f where g is the number of groups and f is the Satterthwaite statistic.

Species	Source	d.f	F	p
Kangaroos	month	6,1361	0.51	0.801
	burnt	1,1358	13.81	0.0002
	month x burnt	6,1361	1.07	0.379
Wallabies	month	6,2191	2.07	0.054
	burnt	1,2189	7.43	0.006
	month x burnt	6,2191	0.34	0.916

The densities of kangaroos and wallabies did not differ significantly over the seven months, but did differ between burnt and unburnt cells; densities of kangaroos were higher on burnt cells than unburnt ones but wallaby densities were the reverse. There was no significant interaction between month and burn for either species. When the months August to October were combined for winter, and December to February for summer, there was no difference between the densities of kangaroos or wallabies in winter and summer (kangaroos: $df=1,1361$; $F=0.20$; $p=0.652$ wallabies: $df=1,2161$; $F=0.37$; $p=0.544$), or any interaction between season and burnt.

Changes in the nitrogen content of the major grass species over the seven month period following the burn in July 1987 are given in Figure 4.2. Tussock-forming grasses and blady grass were greatly affected by fire, with old and dead leaves being removed by fire leaving very little green leaf. These species have, therefore, been referred to as burnt whilst the matt-forming grasses, which were hardly affected by fire, are referred to as unburnt. Unfortunately, the samples from September 1987 were lost but data from previous years showed a decline in quality of blady grass and swamp foxtail from August onwards (other burns also taking place in late July). There was a dramatic decline in the

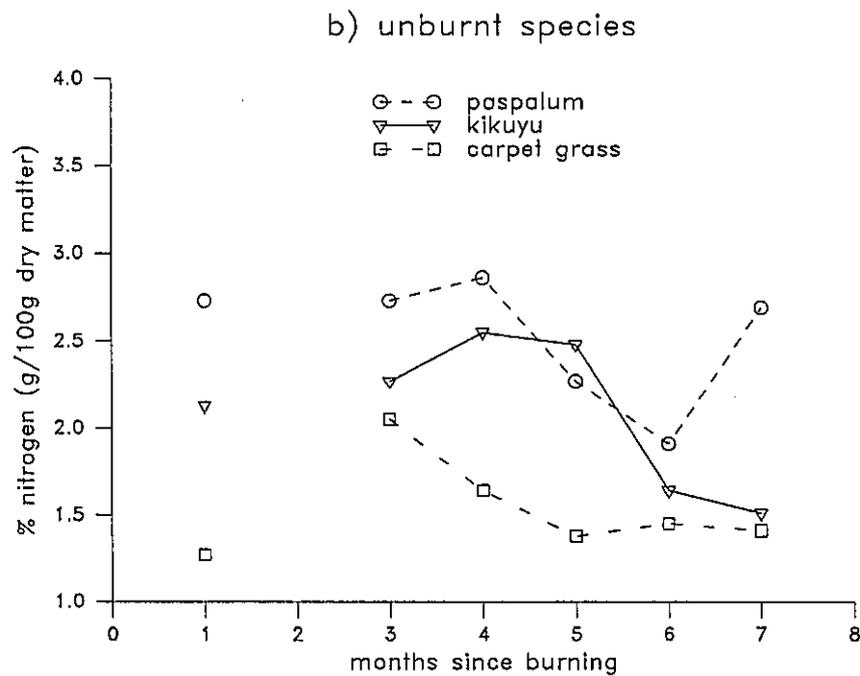
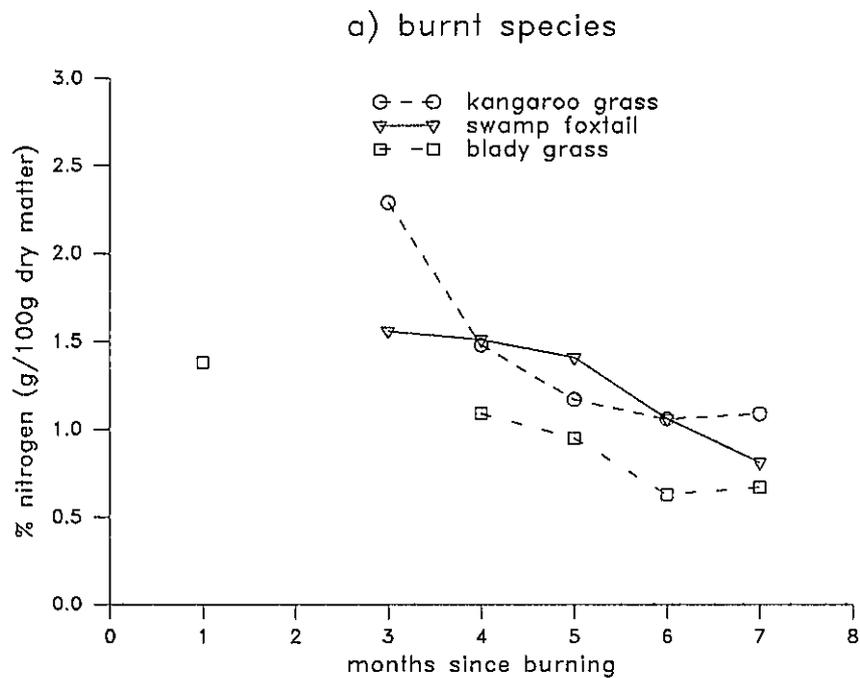


Figure 4.2 Nitrogen levels (g/100 g of dry matter) in leaves of burned grasses (swamp foxtail, kangaroo grass and blady grass) and unburnt grasses (carpet grass, paspalum and kikuyu) in the months following the burning of pasture in July 1987. The samples from September 1987 were lost.

quality of most of the species between December and January and the nitrogen content of blady grass and swamp foxtail fell considerably below that of the most abundant species, carpet grass (see later). The nitrogen content of kangaroo grass was particularly high three months after the burn, reaching similar levels as kikuyu and paspalum, but it declined rapidly after October.

4.3.2 Distribution of kangaroos and wallabies in relation to cover vegetation

Vegetation species were classified as providing cover if they were greater than 30cm tall and if they were physically able to give some protection from the elements or might hide kangaroos or wallabies from potential predators or vice versa. Other vegetation species, which were shorter, did not provide cover, but formed the sward below and between cover vegetation, are referred to as ground species. Examples of cover species are blady grass, tussock grass, kangaroo grass, balloon cotton *Asclepias physocarpa*, Paddy's lucerne *Sida rhombifolia*, thistles, etc. Dense seed-heads could also provide cover if they achieved the right height. Some vegetation species were classified as both ground and cover species depending on their height and maturity, factors which also related to their palatability to herbivores.

The frequencies of sightings of animals in areas that did and did not provide cover were classified by species and sex for each of the four time periods in each season (Table 4.4). In the morning and evening in winter, and the evening in summer, kangaroos were more likely than wallabies to be found in areas providing cover.

Male and female kangaroos were as likely as each other to be found in areas providing cover in each season and in each time period except the morning in winter. The best fitting three-way model fitted to the kangaroo frequencies grouped by cover(C) and sex(S) and time(T) in both winter and summer was S, CT (winter: $df=7$, $G=5.98$, $p=0.54$ summer: $df=7$, $G=6.02$, $p=0.53$), implying that the likelihood of kangaroos being found in cover varied with time of day. Kangaroos were less likely to be amongst cover in the morning and night in winter and in the morning and afternoon period in summer. The difference in response between summer and winter may mean that kangaroos were not responding to the availability of cover itself, but to some other factor varying with the availability of cover. For example, heavily burnt areas did not provide cover in winter and some ground species were particularly associated with a lack of cover (see section 4.3.4).

Table 4.4. A comparison of the percentages, of all sightings, of kangaroos and wallabies in areas providing cover in summer and winter, in each of four time periods. Sample sizes are given in parentheses. For each time period G tests compare the sexes of each species in each season, and the species within each season. The time periods (T1-T4) are described in section 4.2.2.

Species	Sex		T1	T2	T3	T4
Winter						
Kangaroo	male		51.9(52)	96.9(33)	73.9(69)	61.9(42)
	female		28.6(112)	100.0(56)	70.3(118)	51.4(70)
G test between sexes		G	8.25	2.00	0.28	1.17
		p	0.004	0.16	0.60	0.28
Wallaby	male		71.4(35)	55.6(9)	57.7(52)	57.1(28)
	female		73.4(64)	85.0(20)	68.3(82)	47.4(38)
G test between sexes		G	0.05	2.78	1.55	0.62
		p	0.83	0.10	0.21	0.43
G test between species		G	45.39	17.30	1.16	0.02
		p	0.001	0.001	0.28	0.89
Summer						
Kangaroo	male		69.1(81)	80.0(35)	71.2(66)	92.9(28)
	female		70.5(139)	88.2(76)	70.2(114)	90.0(50)
G test between species		G	0.05	1.24	0.02	0.19
		p	0.83	0.27	0.88	0.67
Wallaby	male		88.0(50)	76.5(17)	81.1(37)	63.6(22)
	female		70.9(86)	77.3(22)	75.7(74)	58.3(36)
G test between species		G	5.63	0.003	0.42	0.16
		p	0.02	0.95	0.52	0.69
G test between species		G	1.54	1.60	0.63	17.7
		p	0.21	0.21	0.43	0.001

In winter, female wallabies tended to be found in areas providing cover more often than males although the difference was not significant in any one time period. In summer female wallabies were less likely than males to be found in areas with cover in the morning time period, but not at other times. In both summer and winter the best-fitting three way log-linear model for the data grouped by cover(C), sex(S) and time(T) was a model of total independence C, S, T (winter: df=10, G=14.61, p=0.76 summer: df=10, G=14.02, p=0.17), such that there was no evidence for a difference in the use of cover between males and females over all times, and no difference between time periods.

The percentage of the searched area that was occupied by cover vegetation was calculated from the percentage of quadrats that contained cover vegetation (see section 4.2.3). This percentage was 35.8% in winter and 61.1% in summer. Using the

preference ratio described in section 4.3.1 preference indices were calculated for both species in winter and summer (Table 4.5).

Table 4.5 Indices of the preference of kangaroos and wallabies for areas providing cover, in winter and summer, in four time periods (T1-T4). The index is the ratio of the percentage of animals seen in areas providing cover divided by the proportion of the searched area that provided cover. The time periods (T1-T4) are described in section 4.2.2.

	T1	T2	T3	T4	All
Winter					
Kangaroos	1.0	2.8	2.0	1.5	1.67
Wallabies	2.0	2.2	2.0	1.5	1.83
Summer					
Kangaroos	1.1	1.4	1.2	1.5	1.25
Wallabies	1.2	1.3	1.3	1.0	1.21

Neither species showed a great preference for cover in summer; the proportion of cover in the searched area was much greater in this season because of the regrowth of cover species after the burn in the previous winter. In winter, both kangaroos and wallabies showed their greatest preference for cover in the middle of the day (T2). I was not able to assess the availability of cover in each individual's home range and have used the same figure for the availability of cover for both species. However, there were more wallabies than kangaroos seen on the flats, and the home ranges of those wallabies probably contained a smaller area with cover vegetation than those of other wallabies or kangaroos. Thus, the preference indices for wallabies may be underestimated.

The use of different types of cover was then investigated by dividing the cover species into three categories: blady grass; tussock-forming grasses, which included swamp foxtail, snow grass and kangaroo grass; and 'other' species, which included balloon cotton, thistles, shrubs and ferns. The sightings of kangaroos and wallabies in areas which did provide cover were divided by the type of cover. There were insufficient data from T2 and T4 for comparison of the species and T1 and T3 were combined because the activities of kangaroos and wallabies were similar in these time periods. Burning was included as a factor in the analyses since it drastically altered the height and density of cover provided. Figure 4.3 (a-d) illustrates the percentages of kangaroos and wallabies in each of three types of cover, in summer and winter, in burnt and unburnt areas. No model could be fitted to the data grouped by cover type, species and burnt so separate G tests were used to compare the species on burnt and unburnt areas, in summer and winter (Table 4.6).

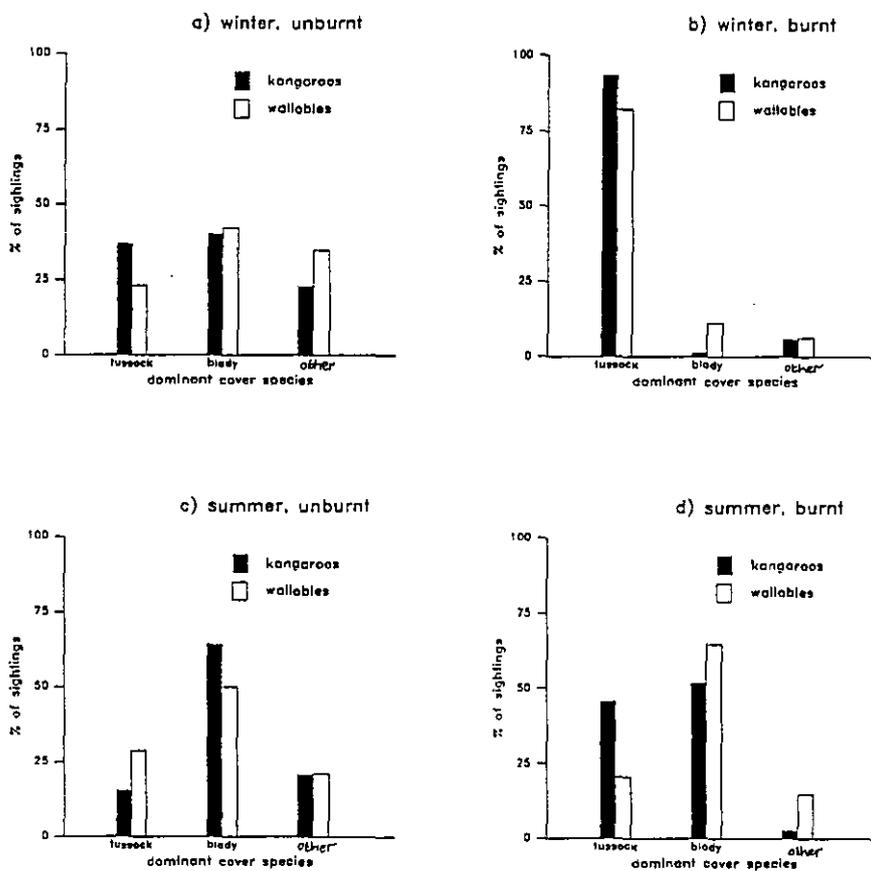


Figure 4.3 The percentages, of all sightings of kangaroos (shaded) and wallabies (blank), of animals that were in areas providing each of three cover types, on unburnt areas in winter (a) and summer (d), and burnt areas in winter (b) and summer (d). The cover types were: tussock grass, including snow grass, swamp foxtail and kangaroo grass; blady grass; and other species (other) which included milkweed, ferns and bracken.

Table 4.6. Results of G tests comparing the frequencies of kangaroos and wallabies sighted on each of three cover types: blady grass; tussock grass; and 'other' cover species. Tests compare kangaroos and wallabies in summer and winter, on burnt and unburnt patches.

Season	Time	d.f	G	p
Winter	unburnt	2	11.86	0.003
	burnt	2	14.29	0.0008
Summer	unburnt	2	10.73	0.005
	burnt	2	11.68	0.003

In winter, the majority of kangaroos and wallabies on burnt patches were in areas dominated by tussock grasses. On unburnt patches kangaroos were most likely to be found in tussock grass areas or blady grass areas whereas wallabies were most likely to be found in areas dominated by blady grass or 'other' species.

In summer, on unburnt areas, wallabies were found more often than kangaroos in tussock grass areas, and less in blady grass areas. On unburnt areas kangaroos were more likely to be found in tussock grass areas and less often in areas providing 'other' cover types. On burnt and unburnt areas, kangaroos and wallabies were found more often in blady grass areas, and less often in tussock grass areas in summer than in winter. This shift in cover type use may have been due to changes in the availability of different cover types.

I was unable to separate out the relative proportions (by area) of different cover types on burnt and unburnt areas, but over all areas (burnt and unburnt combined), in winter, blady grass made up 49% of the cover, tussock grasses 45% and 'other' species 7%. In summer the values were 58%, 36% and 6% respectively. Thus, the increase in summer in the proportion of animals using blady grass areas could just be due to the greater area occupied by that cover type in summer. There appears to be little difference in preference between blady grass and tussock grasses on unburnt areas if the above figures reflect the relative contributions of each cover type to the total cover on unburnt areas alone. However, unburnt areas containing 'other' cover species do appear to be preferred by both species given that the proportion of animals seen in such areas far exceeds the number that would be predicted on the basis of the area occupied by that cover type.

4.3.3 Use of different sward components

The vegetation that comprised the ground sward and cover was divided into five components on, or in, which kangaroos and wallabies could feed. The **inter-tussock sward** was comprised mainly of introduced, mat-forming grasses such as carpet grass, paspalum and kikuyu. Tussocks were unburnt, mature tussocks of swamp foxtail, snow grass or kangaroo grass and usually contained more than 50% dead leaf. Kangaroos and wallabies were never seen to eat the leaves of mature tussocks of swamp foxtail or snow grass, but they did select other grasses which grew within tussocks. Leaves of carpet grass, kikuyu and paspalum growing inside tussocks were much larger than those outside because they escaped grazing by cattle. Animals which selected leaves growing inside tussocks were described as feeding **within tussocks**. In a similar way animals fed **within blady grass** patches; blady grass growing in dense thickets also concealed grasses and forbs and kangaroos and wallabies sometimes foraged within these blady grass patches. In burnt areas, kangaroos and wallabies fed on the new shoots of tussock grasses and blady grass, so **burnt tussock** and **burnt blady grass** were the other two components of the sward that animals could feed on. Occasionally kangaroos, and more often wallabies, would browse on shrubs like Paddy's lucerne but the instances were too low to be analysed.

The search data did not accurately reflect which component of the sward animals were feeding on because animals were often disturbed by my presence before I was able to identify where they had been biting. For this reason the data collected in the 15-minute continuous watches were used. These data were collected on subsets of the populations and observations were made regardless of where the animal was located (see Chapter 2 for methods and schedule). The subsets of the kangaroo and wallaby populations that were used for the 15-minute observations were chosen to represent evenly different population classes and different parts of the study area. When I was searching for the animals in the subsets to observe, I covered the same ground in the study area, in each month, to ensure that the locations of the observations were representative of the distribution of the population. For each of the sward components, I calculated the proportion of animals which spent some time feeding on that component and compared the proportions between species, months and sexes. Table 4.7 presents the proportion of kangaroos and wallabies which spent some time feeding on the sward component in question, in each of five seasons: summer (January-February) 1986; pre-burn (March-July) 1986; post-burn (August-October) 1986; summer (November 86-February) 1987; pre-burn (March-July) 1987.

The inter-tussock sward was used the most frequently of all sward components, with up to 95% of animals watched feeding on it at some time in 15 minutes. Kangaroos and wallabies rarely foraged within blady grass patches and fed on the shoots of tussocks and blady grass only in the six months following burning. Given that the percentage of the

area that provided mature blady grass stands was 17% in winter and 21% in summer kangaroos and wallabies appear to reject this sward component. The proportion of kangaroos and wallabies that were seen feeding on the inter-tussock sward exceeded the proportion expected on the basis of the area covered by this sward component suggesting that they preferred this component to some extent.

Most of the significant differences between the species were seen in the post-burn season of 1986. These months included the height of the 1986 drought when green leaf was very hard to find in the inter-tussock sward, and sward biomasses were at their lowest (see Chapter 2). Kangaroos were less likely to forage within the inter-tussock sward than were wallabies, and instead they fed more often on the new shoots of tussock grass and blady grass, and within mature tussocks. In summer 1986 wallabies were less likely to feed on the inter-tussock sward than kangaroos were and both species fed within tussocks more frequently than in other seasons. In other seasons the use of the different sward components was surprisingly similar for the two species.

Comparisons between the large males, females with pouch-young and females with young-at-foot, for each species and in each month, did not reveal any significant differences between the population classes in their probabilities of using different sward components. There was a tendency for females with young-at-foot to use the inter-tussock sward more often and to forage within tussocks and blady stands less than males, but the differences were not significant. Nor were there any differences between the classes in their use of new shoots of tussock grass and blady grass after burning.

Table 4.7. The percentages of observations, on a subset of the populations, during which the focal animal was seen feeding on the intertussock sward, within mature tussocks, within mature blady grass, on burnt tussock shoots and on burnt blady grass shoots during 15-minute observations, in each of five seasons between January 1986 and July 1987. Most animals were observed twice in the afternoon and twice in the morning in each season. G-tests compare the species in each season. G-tests are omitted where expected values were too low for the analysis. Note that in summer 1986 records for burnt tussock shoots were included in the within tussock category and records for burnt blady shoots are included in the within blady patch category.

species	Summer 1986	Pre-burn 1986	Post-burn 1986	Summer 1987	Pre-burn 1987
sample size					
kangaroo	47	81	94	44	114
wallaby	28	58	52	33	40
inter-tussock					
kangaroo	91.5	89.3	72.2	87.0	83.0
wallaby	66.7	93.3	87.1	95.7	73.7
G	9.32	0.82	5.46	2.38	2.31
p	0.002	0.36	0.02	0.12	0.12
within tussock					
kangaroo	46.8	29.8	28.9	26.1	37.7
wallaby	43.8	24.2	10.0	14.9	35.5
G	0.90	0.41	9.14	1.80	0.09
p	0.76	0.41	0.002	0.18	0.76
within blady patch					
kangaroo	4.3	7.1	10.0	4.3	14.2
wallaby	10.4	6.7	5.7	4.3	3.9
burnt tussock shoots					
kangaroo	-	0.0	25.6	23.9	0.0
wallaby	-	0.0	11.4	10.6	0.0
G			5.26	2.93	
p			0.02	0.09	
burnt blady shoots					
kangaroo	-	0.0	14.4	2.2	0.0
wallaby	-	0.0	4.3	0.0	0.0
G			4.92		
p			0.03		

4.3.4 Use of different ground species

Given that kangaroos and wallabies used the inter-tussock sward most often of all the sward components I was then interested in which of the ground species making up the inter-tussock sward were most important to them. The dominant ground species was recorded for the patch where each kangaroo and wallaby was seen. Tussock grasses and blady grass were recorded as ground species until they were greater than 30cm in height. Some ground species had to be combined because their individual frequencies were too low. Clover, forbs and stemmy grasses are included in the 'other' category and leafy grasses are included with paspalum.

Figure 4.4 (a-h) illustrates the percentages of animals found on each ground species in summer and winter, in each time period. The ground species (except "other") are ranked roughly from left to right in order of their nitrogen content; lowest on the left to highest on the right. There was a tendency for a larger proportion of wallabies to be on the better quality sward types whilst more kangaroos were found on the poorer quality types. This species difference was more noticeable at night when there were more kangaroos on poorer quality types compared to other times of the day and there were more wallabies on the high-quality paspalum-dominated vegetation type compared to other times.

The frequencies of animals seen in areas dominated by different ground species were tabled by season and species for each time period (Table 4.8). Log-linear models could not be fitted to data from the morning or afternoon so the use of areas with different ground cover was also compared between summer and winter for kangaroo and wallaby data separately (G tests). There was a significant difference between the species' use of different vegetation types in each time period, except the afternoon in winter.

Both species showed a significant difference between summer and winter in their use of areas with different dominant ground species. The major seasonal difference was in the use of blady grass and tussock grasses in winter compared to summer. It should be noted that burnt species would not have been classified as ground species in late summer because of their height and maturity. Kikuyu-dominated areas were used more often in summer than winter, except in the afternoon in winter when the use of these areas was especially high. It was in this afternoon time period that the use of the burnt species (blady and tussock grasses) was low (see also section 4.3.1).

Figure 4.4 The percentages, of all sightings of kangaroos (shaded) and wallabies (blank), of animals that were in areas dominated by different ground vegetation species, in four time periods, in winter (a,c,e,g) and summer (b,d,f,h). The ground species were: new shoots of blady grass (bl) and tussock grasses (tu); paspalum (pa); carpet grass (ca); kiyuyu (ki); and other species (ot).

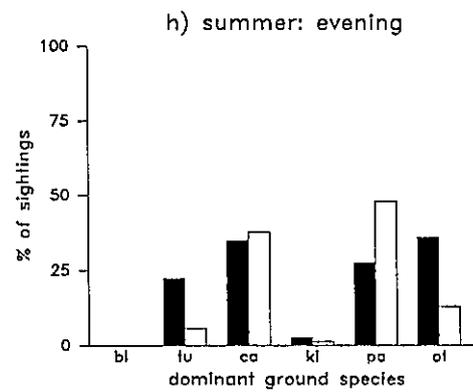
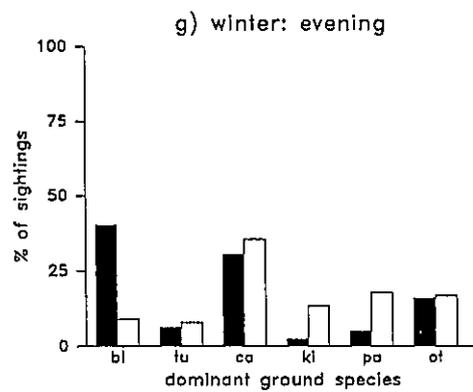
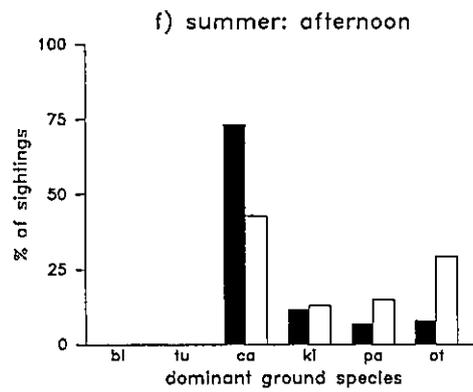
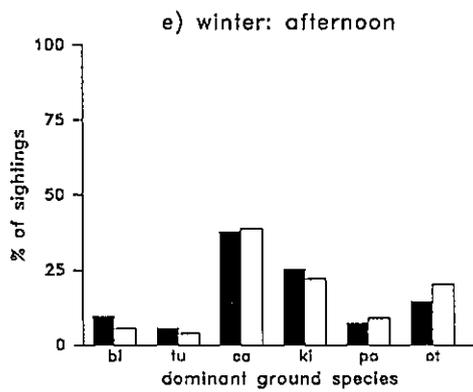
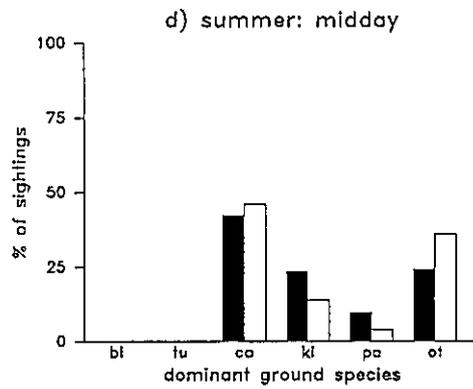
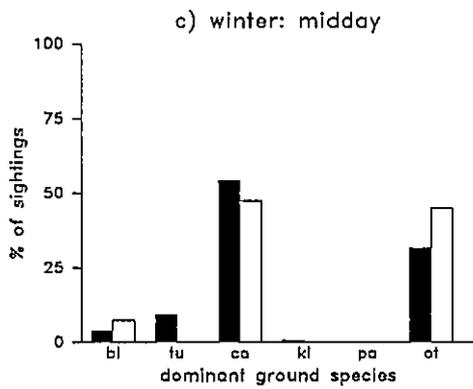
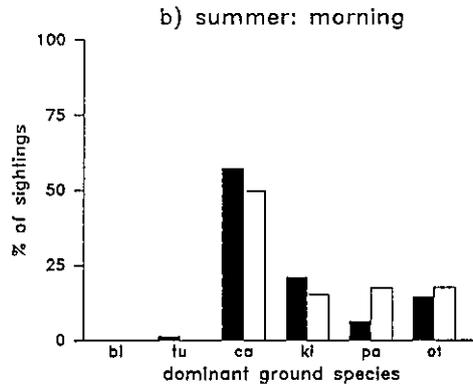
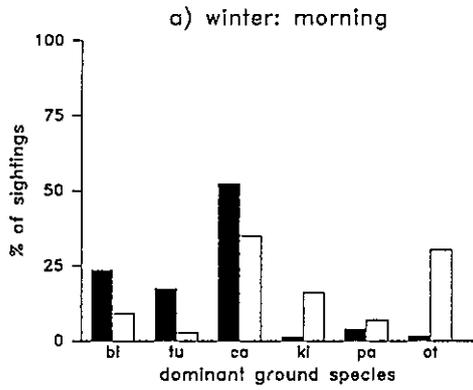


Table 4.8. A comparison of the frequencies of kangaroos and wallabies sighted on each ground-sward type, in each season, and in each time period. A 3-way log-linear model could not be fitted to the data from the morning and afternoon time periods so the results of least likelihood ratio tests, comparing the species in each season, and the seasons for each species, are presented, with the G statistic and significance given. Log-linear models have been fitted to the data, grouped by season(M), species(S) and ground species(G), from the midday and evening time periods. In this case a non-significant G statistic indicates that the model presented fits the data.

Time	model/test	d.f.	G	p
Morning				
Kangaroo	M x G	5	268.2	<0.0001
Wallaby	M x G	5	49.8	<0.0001
Winter	S x G	5	151.8	<0.0001
Summer	S x G	4	20.9	<0.0003
Best fitting log-linear model for data grouped by ground(G), season(M) and species(S)				
Midday				
All	GS, GM	3	0.68	0.879
Afternoon				
Kangaroo	M x G	5	124.3	<0.0001
Wallaby	M x G	5	33.5	<0.0001
Winter	S x G	5	9.8	0.08
Summer	S x G	3	53.8	<0.0001
Best fitting log-linear model for data grouped by ground(G), season(M) and species(S)				
Evening				
All	GS, GM	3	4.88	0.300

In the midday (T2) and evening (T4) periods there were significant interactions between species and ground^{sward type}. In T2 wallabies were found in areas dominated by 'other' species more often than kangaroos and less in areas dominated by burnt tussocks. In the evening, more kangaroos were found on areas dominated by blady grass (winter) or other species (summer), whereas more wallabies were found on the better quality, paspalum dominated areas.

The best fitting models for the frequency data of each species grouped by ground, sex and month did not include the interaction between population class and ground type. This implies that there was no difference between the sexes in their choice of ground type.

The percentages of the searched area that were dominated by each of the ground species or ground-species types (i.e. 'other') were calculated from the frequencies of 0.25-ha grid cells that were dominated by each of the species. The distributions of animals with respect to ground sward type did not differ greatly between the morning and afternoon so I have combined these time periods to represent day-time feeding locations

(animals were nearly always feeding in these time periods). Table 4.9 compares the percentages of animals seen in each of the ground-sward types, the availability of those sward types and a preference index for each species and season.

Table 4.9. A comparison of the percentages of kangaroos and wallabies, that were sighted on each of the ground-sward types, with the percentage of the search area covered by those types, in the 3 hours after first light and the 3 hours before dusk. The preference index used is the percentage of animals on each type divided by the percentage availability of each type (from Petrides, 1975). The nitrogen content (%) of carpet grass, paspalum, kikuyu are given for each season.

	burnt shoots	carpet grass	paspalum	kikuyu	others
Winter					
% area covered by ground-sward type	17.5	60.4	1.7	2.4	18.1
Kangaroos					
% of sightings	28.3	45.0	5.6	13.2	8.2
preference index	1.6	0.7	3.3	5.5	0.5
Wallabies					
% of sightings	10.7	37.0	8.1	19.3	25.0
preference index	0.6	0.6	4.8	8.0	1.4
% nitrogen in the dominant grass species	-	1.3	2.7	2.1	-
Summer					
% of area covered by ground-sward type	-	82.0	5.5	3.5	9.0
Kangaroos					
% of sightings	-	65.0	6.6	16.6	11.2
preference index	-	0.8	1.2	4.7	1.2
Wallabies					
% of sightings	-	46.4	16.2	14.2	23.1
preference index	-	0.6	2.9	4.1	2.6
% nitrogen in the dominant grass species	-	1.4	1.9	1.6	-

Both species showed an slight aversion to the most abundant grass, carpet grass, and a preference for the better quality paspalum and kikuyu grasses. Wallabies showed a greater preference than kangaroos for paspalum and kikuyu in winter, and for paspalum in summer. Both species showed a greater preference for these high quality species in winter, when the difference in nitrogen quality compared to carpet grass was greatest. In winter, the 'other' category included clover dominated patches which are generally avoided by kangaroos and greatly preferred by wallabies. In winter, kangaroos showed a preference for areas dominated by shoots of tussock grasses and blady grass but wallabies showed an aversion to them.

The difference between the species in the choice of cover and the choice of different ground species may be related since some ground vegetation types were typically associated with cover and others were not. Table 4.10 gives the percentages of kangaroos and wallabies, seen on each ground type that were also in cover and compares the frequencies of sightings on different ground-types, with and without cover. The sightings for areas dominated by burnt species (blady and tussock grasses) are included in the 'other' category. Burnt areas were unusual in that in winter they did not provide cover but in the summer many of the burnt grasses had grown sufficiently to provide cover. The data were first analysed for each time period separately but there was no interaction with time period so all time periods have been combined.

Table 4.10. The percentages, of all sightings of kangaroos and wallabies, of animals that were in cover, on each of the different ground-sward types, in summer and winter (all time periods). The ground-sward types are characterised by the dominant species in them. G tests compare the provision of cover on different ground types, for each species, and in each season.

	n	paspalum	carpet grass	kikuyu	other	G	p
winter							
kangaroo	663	97.7	95.4	36.7	81.5	242.2	0.0001
wallaby	451	56.8	86.0	37.6	60.5	69.2	0.0001
summer							
kangaroo	868	90.0	84.6	32.6	95.0	224.3	0.0001
wallaby	570	41.3	89.2	37.9	85.2	116.1	0.0001

The majority of sightings of animals on areas dominated by carpet grass, paspalum or 'other' species were also in areas which provided cover vegetation. Kikuyu-dominated swards were much less likely to provide cover than others.

A model could not be fitted to the three-way data which compared the species as well. However, the major difference between the species was on paspalum-dominated patches. Many of the wallaby sightings on paspalum-dominated patches were associated with a paddock by the creek which did not provide any cover, but which was adjacent to the forest. Kangaroos very rarely used this paddock for feeding, only doing so on wet and windy days.

4.3.5 The distribution of kangaroos and wallabies in relation to the amount of dead vegetation in the sward

When the dominant cover and ground species were recorded for each animal, an estimate was made, to the nearest 10%, of the proportion of dead material in the sward. Figure 4.5 (a-d) illustrates the amount of dead vegetation in the sward where kangaroos

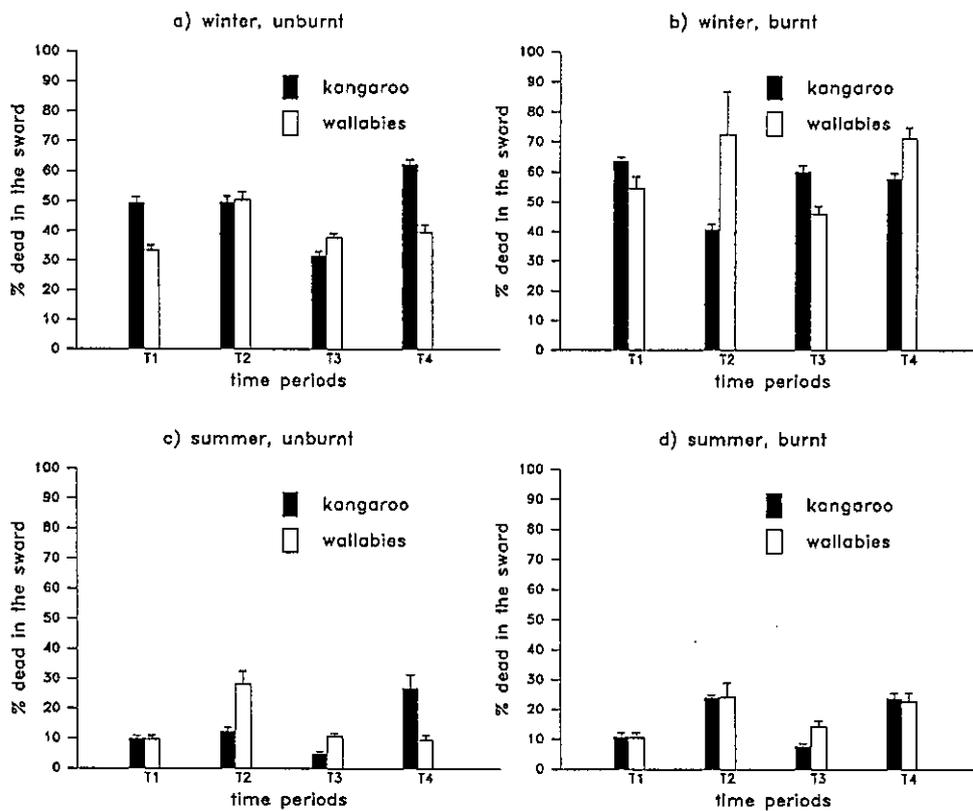


Figure 4.5 The percentages of dead vegetation in the swards where kangaroos and wallabies were sighted, in unburnt areas in winter (a) and summer (c), and burnt areas in winter (b) and summer (d), in each of four time periods. The time periods are: morning (T1); midday (T2); afternoon (T3); and evening (T4).

and wallabies were seen, at different times of the day and in different seasons. The data are further divided by whether the sward was burnt or not; burning had a considerable effect on the amount of dead vegetation in the sward and there were species and seasonal differences in the choice of burnt swards.

Inspection of Figure 4.5 shows that season has the biggest effect on the proportion of dead in the sward. In winter there was a difference between the burnt and unburnt swards chosen, with newly burnt swards having much less green vegetation in them. Even though green biomass may be low in burnt swards it may not necessarily be less available since the green shoots are very visible and appear to be easily accessible to grazing herbivores. In the summer there was little difference in the amount of dead vegetation in burnt and unburnt swards chosen by kangaroos and wallabies.

An analysis of variance was carried out on the data for burnt and unburnt areas, using a log transformation that was suggested by diagnostic plots of means and standard deviations. Season, species and time period were used as grouping factors and cell means were weighted by frequencies (BMDP statistical software). Table 4.11 presents the results of the three-way ANOVA on the percentage of dead in the sward.

Table 4.11 Analysis of variance of the proportion of dead vegetation, in burnt and unburnt patches, where kangaroos and wallabies were sighted, grouped by species(S), season(M) and time period(T).

Analysis of variance						
Source	d.f.	Burnt F	p	d.f.	Unburnt F	p
S	1,1135	0.4	0.51	1,1634	2.7	0.10
T	3,1135	22.1	0.0001	3,1634	47.7	0.0001
M	1,1135	1847.6	0.0001	1,1634	1060.1	0.0001
ST	3,1135	4.3	0.005	3,1634	29.8	0.0001
SM	1,1135	5.1	0.02	1,1634	21.5	0.0001
TM	3,1135	30.2	0.0001	3,1634	3.5	0.01
STM	3,1135	11.2	0.0001	3,1634	4.5	0.004

On unburnt swards, kangaroos were in the areas with the highest percentage of dead material at night and the lowest in the afternoon. Wallabies were found in areas with the highest percentage of dead vegetation in the middle of the day but at other times there were similar amounts of dead material in the swards they were found on. This result again suggests that at night kangaroos were feeding on poorer vegetation types than wallabies.

The proportion of dead vegetation in burnt areas is less an indicator of the quality of the vegetation type and more an indicator of the severity of the burn. After burning, areas which were dominated by tussock grasses or blady grass may have less than 5%

green leaf whereas areas which had an intertussock sward of carpet grass may still have a high proportion of green leaf after the burn. In the three months after burning kangaroos were found in areas with a greater proportion of dead vegetation in the morning and afternoon, but not at night. In summer there was very little difference in the amount of dead vegetation in the patches chosen by the two species; both were in greener areas in the morning and afternoon time periods.

4.3.6 Dietary analysis

Faecal pellet samples were collected from kangaroos and wallabies by P.Jarman and assistants between June 1984 and December 1986, when I began to make the collections. Samples (only one pellet per individual, per month) were identified by species, location, date, sex and, where possible, population class and identity of the individual. All samples have been grouped by species (EGK or RNW) and season for statistical analyses, with July to October as post-burn, November to February as summer, and March to June as pre-burn. There were insufficient samples from wallabies to compare the two animal species in the pre-burn season.

The samples were prepared and analyzed microscopically by K.Phillips, with some of the early samples being analyzed by C.Hollis. The proportions of monocotyledonous (monocot) and dicotyledonous (dicot) plants were estimated from 100 fragments of each sample. The relative proportions of the monocot species were estimated from the relative amounts of epidermal area which they contributed to the total area of epidermis recognized in an inspected sample of faecal material. The methods used for the preparation of samples and analysis are described in full by Jarman and Phillips (in press).

Figures 4.6a and b illustrate the percentages of the six most important species. Species with means of greater than 5% were included and I checked that this subset did not exclude any species which were highly represented in a few samples. The unknown proportion and remaining species were combined as the remaining category. The estimate of the percentage of kikuyu in the diet is based on only the last 58 samples, collected from October 1987 onwards, because kikuyu could only be identified in the last 58 samples. None of the samples where kikuyu was identified came from the pre-burn season so there is no estimate of the proportion of this species in the diet for this season.

The data were analysed by multivariate analysis of variance with weighted cell means and log transformation (BMDP statistical software). The species and season that the sample came from were used as grouping factors. Table 4.12 gives the significant individual and overall species effects; there were no significant species x season interactions. Kikuyu has been omitted from the analysis and the pre-burning season (May to July) was also omitted because of a lack of samples from this season.

Table 4.12 Significant results for multivariate analysis of variance with species (EGK or RNW) and season (July-Oct and Nov-Feb) as grouping factors. Log transformations were used for each variable.

Source of variation	d.f	F	p
Species			
All	6,171	12.15	< 0.0001
paspalum	1,176	54.75	< 0.0001
kangaroo grass	1,176	7.71	< 0.01
swamp foxtail	1,176	5.83	< 0.02
blady grass	1,176	17.22	< 0.0001
Season			
All	6,171	10.71	< 0.0001
carpet grass	1,176	7.00	< 0.01
paspalum	1,176	14.61	< 0.01
kangaroo grass	1,176	6.72	< 0.05
blady grass	1,176	12.90	< 0.001

Wallabies had a higher proportion of paspalum in their diet than kangaroos and less swamp foxtail, kangaroo grass and blady grass. After burning of the pasture, kangaroos and wallabies ate more carpet grass and blady grass, and less paspalum and kangaroo grass than they did in summer.

The preferences of kangaroos and wallabies for different monocot species were compared by calculating a preference index for each grass species from the percentage of the grass species in the diet divided by the percentage of the study area that was covered by the grass species (after Petrides, 1975) (Table 4.13). The index is centered about 1.0, with values greater than 1.0 showing a preference and values less than 1.0 showing an aversion. The percentage of the study area covered by each grass species was calculated from the proportion of each species in 0.25-m² quadrat that was laid in each vegetation survey (see section 4.2.3).

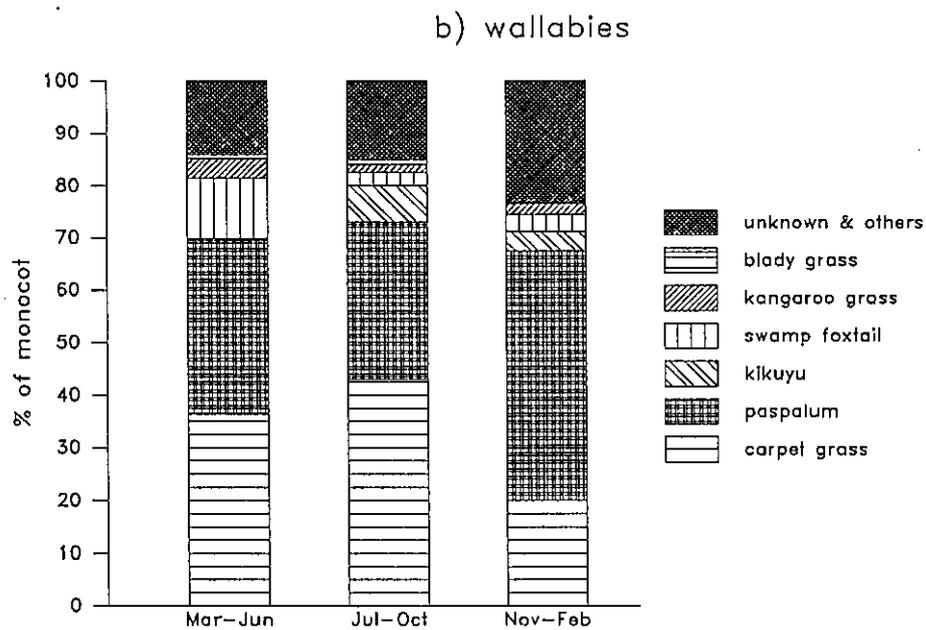
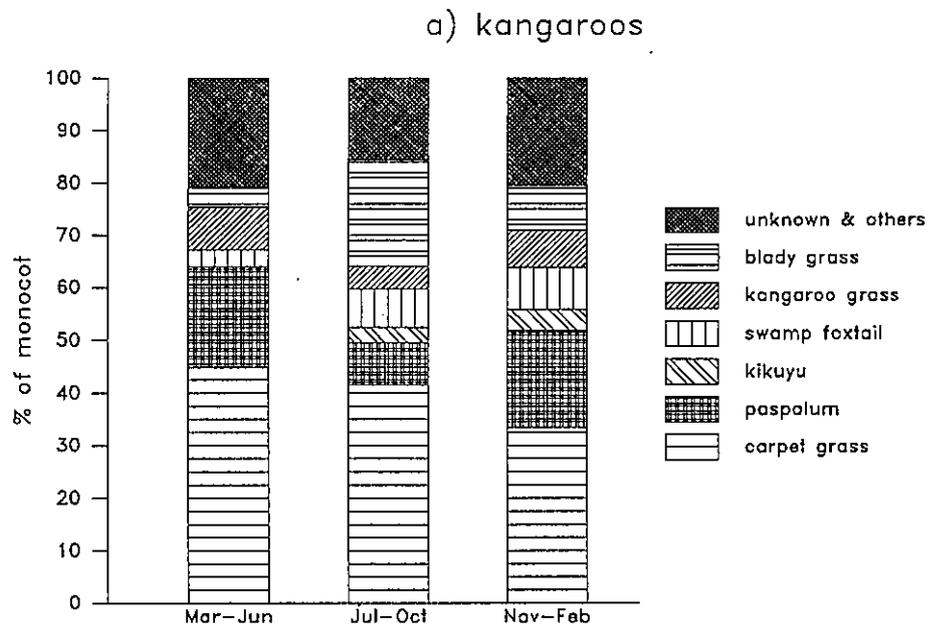


Figure 4.6 The percentages of different grass species in the monocot fraction of the diets of a) kangaroos and b) wallabies, in each season: pre-burn (Mar-Jun); post-burn (Jul-Oct); and summer (Nov-Feb). The unidentified fraction (unknown) is combined with the remaining species (others). Kikuyu was not identified in the pre-burn season and is included in the unknown and others fraction in this season.

Table 4.13 A comparison of the composition of the diets of kangaroos and wallabies and the availability of the grass species in relation to the proportion of the study area that they cover. The preference index is percentage of the grass species in the diet divided by the percentage of the study area covered by the species.

	% of area covered	kangaroos		wallabies	
		% in diet	pref index	% in diet	pref index
Post-burn					
carpet grass	43.9	41.5	1.0	43.0	1.0
paspalum	16.0	8.1	0.5	30.1	1.9
kikuyu	6.2	2.8	0.5	6.9	1.1
swamp foxtail	2.3	7.3	3.2	2.6	1.1
blady grass	16.8	20.3	1.2	1.1	0.1
kangaroo grass	0.7	4.4	6.3	1.4	2.0
Summer					
carpet grass	36.2	33.4	0.9	20.0	0.6
paspalum	9.6	18.4	1.9	47.4	4.9
kikuyu	3.2	4.0	1.3	3.8	1.2
swamp foxtail	5.8	8.0	1.4	3.3	0.6
blady grass	21.7	8.5	0.4	0.3	0.01
kangaroo grass	0.4	7.2	18.0	2.0	5.0

In the post-burn season kangaroos show a strong preference for swamp foxtail and kangaroo grass. The high index for kangaroo grass is partly an artefact of the way in which the availability of kangaroo grass was calculated; the percentage given is for the percentage of the whole study area that species covers; kangaroo grass is only found in the forest at the far north of the study site and kangaroos whose home ranges cover that northern forest will have a much higher percentage of their home range covered by the grass than 0.7%. Even so, the fact that many animals had no access to kangaroo grass meant that the species made up a quite large proportion of the diet of others. By summer, kangaroos selected less swamp foxtail but they maintained their selection for kangaroo grass. Wallabies also selected this species although again, the uneven distribution of the grass in the study area makes interpretation difficult. Wallabies showed a very strong aversion to blady grass, even when there were new young shoots available after the burn. Blady grass was utilized by kangaroos in both seasons, but not as much as its abundance would predict if the kangaroos were not foraging selectively.

Wallabies showed a strong preference for paspalum and managed to select a very high proportion of this species in summer, despite its relatively low abundance. Carpet grass

made up the bulk of the diet of both species in winter, and appeared to be selected neither for nor against.

To compare complete diets, rather than individual components of diets, a cluster analysis was carried out on the faecal sample data using the ten monocot species which had means of greater than 1% and also including the unknown proportion in the diet as a variable in the analysis. Ward's cluster method was used with squared euclidian distance as the measure of dissimilarity. A maximum of five clusters was requested.

Table 4.14 gives the mean percentage of the diet contributed by each species for each of the four clusters, and the number of samples which belonged to each cluster. Kikuyu has been included in the analysis even though it was only identified in the last 58 samples. Observations of kangaroos and wallabies feeding on pure kikuyu swards suggested that this was an important species to them. In the previous samples kikuyu is included in the unknown category.

Table 4.14 Mean percentage of each of the 10 most important monocot species in five diet clusters produced by cluster analysis of the faecal analysis data. The unknown proportion and other species are also included.

Plant species	Cluster				
	1	2	3	4	5
<i>Axonopus affinis</i>	31.8	70.6	29.9	17.8	19.4
<i>Cynodon dactylon</i>	3.5	1.7	1.7	2.2	1.1
<i>Capillipedum spicigerum</i>	1.8	0.5	1.5	3.3	0.6
<i>Eulalia fulva</i>	1.4	0.6	0.5	5.2	0.1
<i>Poa labillardieri</i>	0.9	0.3	4.9	0.9	0.1
<i>Paspalum dilatatum</i>	26.0	11.6	8.3	7.0	29.2
<i>Pennisetum alopecuroides</i>	4.3	1.4	25.4	7.8	5.3
<i>Themeda triandra</i>	7.8	2.5	4.8	5.9	6.4
<i>Imperata cylindrica</i>	5.2	3.5	6.7	36.5	7.2
<i>Pennisetum clandestinum</i>	0.8	0.2	0.7	0.3	16.5
Unknown & others	12.0	4.6	7.5	10.3	8.7
n	87	57	22	38	16

Samples belonging to the largest cluster (C1) had a mean percentage of 31.8% carpet grass *A. affinis* and 26% paspalum *P. dilatatum*, with smaller proportions of the burnt species, blady grass *I. cylindrica*, kangaroo grass *T. triandra* and swamp foxtail *P. alopecuroides*. Samples in the next largest cluster (C2) were dominated by carpet grass (70.5%), with 11% paspalum and only small proportions of the other species. Those in the third largest cluster (C4) had a high proportion of blady grass (36.5%) and a lower percentage of carpet grass (17.8%). The next cluster (C3) was dominated by swamp

foxtail, the tussock forming grass that was burnt, with moderate amounts of carpet grass. Clusters 3 and 4 are considered 'burnt diet clusters' since they contain high proportions of species that are burnt. Samples belonging to the final cluster (C5) had the highest proportion of paspalum (29.2%) and also had a relatively high proportion of kikuyu *P. clandestinum* (16.5%).

Using a cluster number for each sample provided by the cluster analysis the frequencies of samples from each cluster were compared between species and seasons (Table 4.15). There were only 28 wallaby samples in total so expected values were rather low.

Table 4.15 Frequencies of faecal samples belonging to each of four 'diet clusters' and grouped by species and season. The best fitting log-linear model describes the important interactions in the three-way analysis of frequencies and the G statistic tests the fit of the model; a non-significant G value indicates that the model fits the data.

Species	Season	Cluster				
		1	2	3	4	5
EGK	Jul-Oct	12	23	7	25	4
	Nov-Feb	43	13	13	10	2
RNW	Jul-Oct	3	8	0	1	8
	Nov-Feb	6	0	1	0	1

Log-linear model, season(B) x species(S) x cluster(C)

Best fitting model is: CB, CS df=5 G=9.4 p=0.09

The best fitting model for the three-way analysis included the interactions between cluster and season, and cluster and species. Wallaby and kangaroo samples differed most in their contributions to C4 and C5. Of 28 wallaby samples 9 were grouped in C5 which had the highest levels of paspalum and kikuyu compared to 6 out of 152 kangaroo samples. Cluster 4, which had high levels of blady grass, contained only 1 wallaby sample compared to 35 kangaroo samples.

In the post-burn season (July-Oct) most of the kangaroo samples belonged to the 'burnt' cluster C3, and C2 which had a very high proportion of carpet grass. A high proportion of wallaby samples belonged to C2 but as many were in C5, and 2 samples belonged to 'burnt' clusters. In summer the majority of samples of both species were in C1 and the proportion of kangaroo samples belonging to 'burnt' clusters was much lower than in the previous months.

The kangaroo samples were then analysed separately to compare the three seasons and the sexes (Table 4.16). The season x cluster interaction was included in the best fitting model but sex x cluster was not. Thus there was no difference between the proportions of samples from males and females in each cluster.

Table 4.16. Percentage of kangaroo faecal samples belonging to each 'diet cluster' in each of three seasons. A log-linear model is fitted to the three-way data described by season(B), sex(S) and cluster(C).

Season	Sex	n	Cluster				
			1	2	3	4	5
Jul-Oct	male	46	15.2	32.6	8.7	39.4	4.3
	female	19	26.3	21.1	15.8	26.3	10.5
	all	65	16.9	32.4	9.9	35.2	5.6
Nov-Feb	male	42	57.1	19.0	9.5	11.9	2.4
	female	34	50.0	13.9	22.2	11.1	2.8
	all	76	53.1	16.0	16.0	12.3	2.5
May-Jun	male	22	50.0	42.3	3.8	3.8	0.0
	female	46	80.0	10.0	0.0	0.0	10.0
	all	68	56.8	32.4	2.7	5.4	2.7

Log-linear model, season (B) x sex (S) x cluster (C)

Best fitting model is: S, CB df=5 G=9.45 p=0.09

In pre-burn season there were only 3 samples in the burnt diet clusters (C3 and C4). The proportion of samples belonging to C5 was highest in the pre-burn season, and, although kikuyu was only recognized in the last 58 samples, kangaroos did appear to use kikuyu areas heavily in this season; before the first frosts came and killed much of the kikuyu.

4.3.7 Diet selection in 'cafeteria trials'

The faecal analysis described above looked at the diets of kangaroos and wallabies in the wild at Wallaby Creek. The preceding sections described some differences between kangaroos and wallabies in their choice of feeding and resting sites and the types of vegetation available to them to feed on. There were differences in the amount of cover

available at different sites and therefore the amount of protection afforded animals whilst feeding. However, I have not been able to partition the relative importance of cover and food supply in the animals' choices of feeding sites. In an experiment with captive kangaroos I attempted to look just at the feeding preferences of kangaroos by allowing them to select from four sown, single-species swards of the same size. The plots were adjacent to one another, all were bare of cover vegetation and were the same distance to cover as each other.

The experiment was carried out at the University of New England's field station at Newholme near Armidale. The trials were conducted in a large kangaroo-proof pen (100m x 200m) sloping from an open flat area at the bottom, up a rocky slope to the upper 2/3 of the pen which was covered in shrubs and small trees. In October 1987, four strips 10m wide and 40m long were ploughed in the open area at the bottom of the pen and prepared for seeding. The strips were marked off into 10m x 10m plots with 2m high posts. The posts had alternate red and yellow reflective markers at the top which allowed me to identify the boundaries of the plots at night with a spotlight. A 10m wide strip of native vegetation was left in between each experimental strip (see Figure 4.7). The four rows of plots were planted according to different treatments but only the first two rows were used in the trials because of the time it took to keep the plots weed free. Plots were fertilized once with super-phosphate and were watered artificially when rainfall was low. Before the kangaroos were introduced, a fence was built across the pen to keep the kangaroos upslope until the trial plots were ready. An electric fence was placed at the top of the first row of trial plots which left small 10m x 5m plots on the kangaroo side of the fence. These plots were planted with mixed lawn seed to entice the animals to feed in the plots before the electric fence was removed at the start of the trial.

The four plant species used in the trial were carpet grass, *Paspalum*, kikuyu and clover. The first three are the most common grasses found at Wallaby Creek and clover was chosen for its high nutrient content and the fact that it could not be measured in the faecal analysis. One species was planted in one plot of each row; the locations were chosen randomly and changed in the second row to counter possible position effects.

The kangaroos were put in the upper half of the pen 4 months before the start of the trial to accustom them to their surroundings and to the presence of an observer. Four kangaroos, two male and two female, were caught in the University Deer Park, were weighed and measured, and transported to the prepared pen at Newholme. Most days in January and February J.Reid or myself went to the pen to water and weed the grass plots and to try to habituate the animals to our presence. The kangaroos were still very nervous of us just before the start of the trial so a hand-reared young male kangaroo was put with them to try to accustom them to people more quickly.

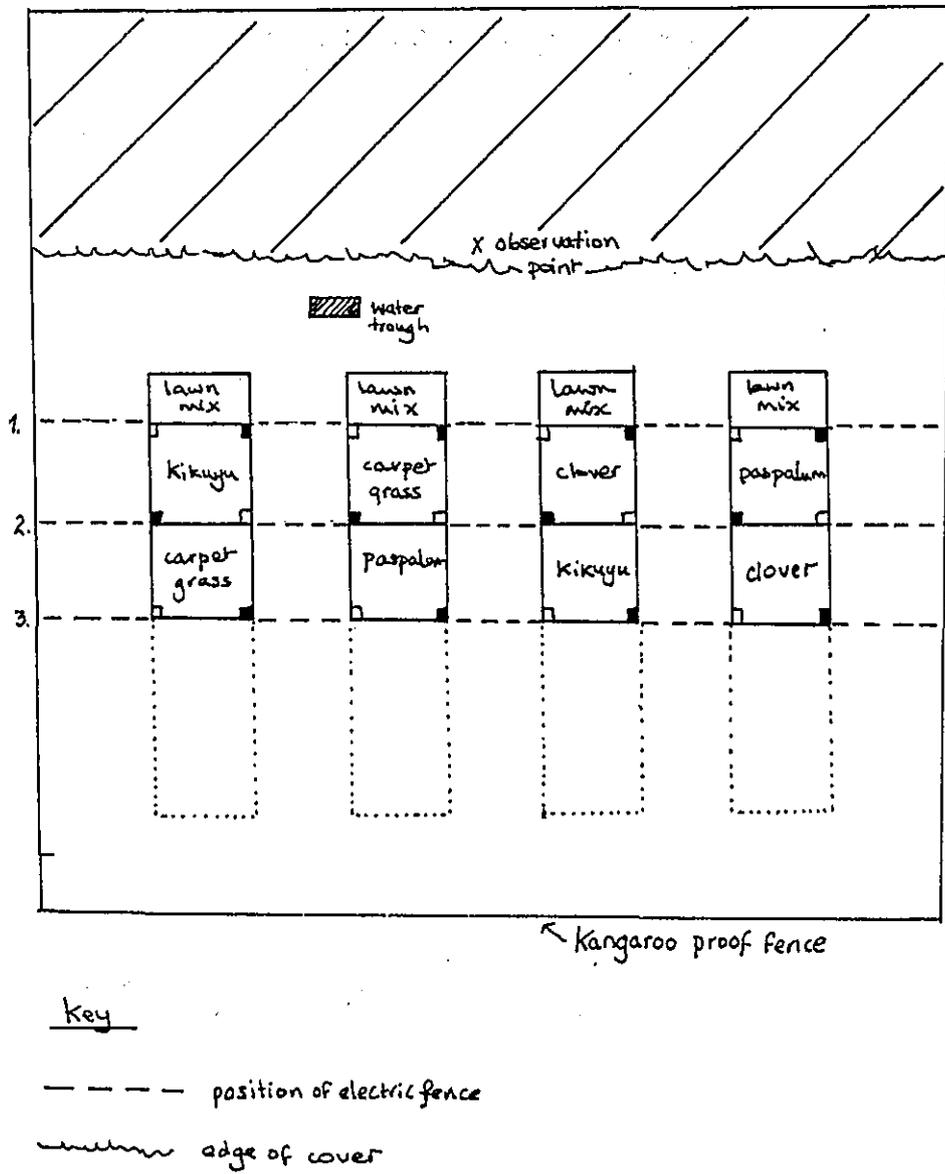


Figure 4.7 Diagram of the experimental plots used for the 'cafeteria' trails at Newholme Research Station. Kangaroos rested in the area providing cover at the top of the paddock and moved down to the plots a few hours before dusk. The electric fence was in position 1 prior to the trial, at position 2 at the start of the trial, and at position 3 one month after the start of the trial.

A month before the trial was due to begin the kangaroos were allowed to use the lower half of the pen to accustom them to feeding in the open. Unfortunately the kangaroos soon learned to get through the electric fence and began to eat the grass in the trial plots before it was ready to be used. The animals were so attracted to the plots that they would pass through the electric fence several times a day to feed in them. When we approached the pen each day the kangaroos were scared off the plots and jumped through the electric fence. In this way they began to associate seeing us with getting an electric shock and their approachability did not improve.

At the start of the trial the electric fence was moved from the front to the back of the first row of plots and the kangaroos were free to feed on the trial plots. Each day, three hours before dark, J.Reid or myself went to the pen and sat in a tent (which acted as a hide) 30 m from the plots. We had to arrive well before the kangaroos came downslope in the evening to feed so that we did not disturb them. Feeding rate observations were made on the animals when possible, although our presence often disturbed them and observations had then to be abandoned. Observations were made using binoculars with spotlights or the night vision binoculars at night. Because the kangaroos often moved off the plots because they were disturbed by our presence, I decided to count the number of faecal pellets and faecal-pellet groups deposited in each plot as a measure of the animals' preferences for the different species. Every morning for 15 days the pellets in each plot were counted and removed after the last kangaroo had left the plots to go back upslope to rest. After a month of being allowed to feed on the first row of plots the electric fence was moved to the back of the second row, giving the kangaroos a choice of 8 plots, 4 in each row.

Height and point-quadrat measurements were made on each plot at the start of the trial to look at the density of the swards at different heights, the proportion of invading weeds in the plot and the proportions of dead vegetation and seed heads in the sward.

Results

Regression analysis was carried out on the cumulative pellet and pellet group counts in each plot. Figures 4.8a and b show the cumulative plots for the pellets and pellet groups found in each grass plot, in the first row, over a fifteen day period. The most obvious difference in the use of the different plots was the almost total avoidance of clover by the kangaroos. The carpet grass plot was also used little and with little rate of change over the fifteen days. The kikuyu and paspalum plots were both attractive; kikuyu was preferred at the start of the trial but by day 7 or 8 preference for kikuyu dropped and that for paspalum increased.

Regressions were fitted to each curve and linear regressions were found to give the best fit for each. Table 4.17 gives the regression equations for each plot.

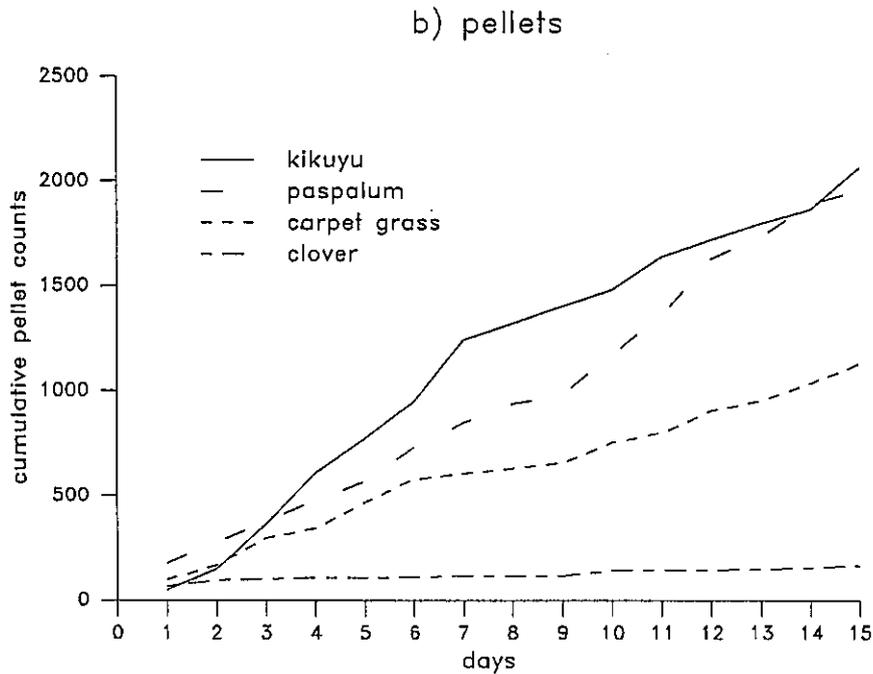
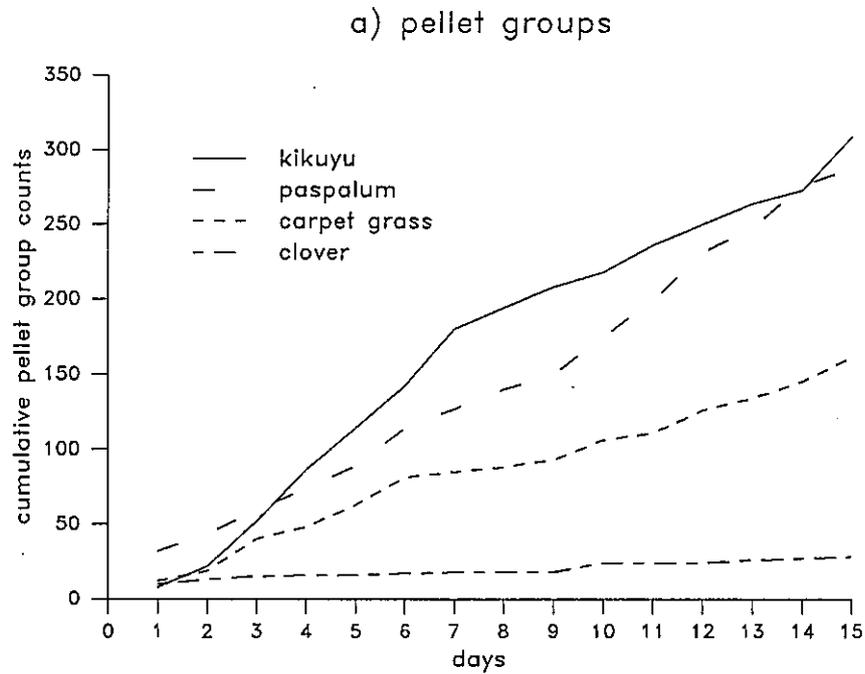


Figure 4.8 Cumulative counts of the number of pellet groups (a) and pellet totals (b) accumulated over 24-hour periods, on each of the experimental plots, on 15 consecutive days following the introduction of the kangaroos to the plots. Pellets were from five eastern grey kangaroos that were allowed to feed on the plots as well as the surrounding pasture. The plots are described by the dominant species growing in them.

Table 4.17 Regression equations for cumulative pellet counts on each plot and comparison of regression lines for homogeneity of slopes using analysis of covariance (Sokal and Rohlf, 1981).

Species	Regression	d.f.	R (adj.)
Kikuyu	$y = 24.3 + 142x$	13	96.7
Carpet grass	$y = 76.0 + 68.8x$	13	98.4
Clover	$y = 76.5 + 5.7x$	13	93.3
Paspalum	$y = -47.1 + 132x$	13	98.2

Analysis of covariance				
Source of variation	d.f.	MS	F	p
Among regressions	3	365.7	147.9	< 0.0001
Within regressions	52	2.5		

The first step of an analysis of covariance compared the homogeneity of slopes of the regression lines and gave a highly significant result for a difference. I was unable to complete the analysis of covariance to test for differences in the adjusted means for each group because the test for equal slope was highly significant. The same analysis for the faecal pellet groups also showed a significant difference in the slopes of the four regressions ($F_{3,52}=479.8$, $p<0.0001$).

The number of pellets deposited in each of the plot types (defined by the species sown in them), in each row are recorded in Table 4.18, with counts 1,5 and 9 days after the kangaroos were first allowed on the second row of plots. Pellets were removed from the plots the day preceding the count.

Table 4.18 Number of pellets found on each plot (having accumulated in 24 hours) on Days 1, 5 and 9 after kangaroos were first allowed to feed on row 2 plots. G tests compare plot species x row for each day measured and row x day for each plot species. * indicates significance at 0.0001 level.

Time	Row	Kikuyu	Carpet	Clover	Paspalum	G
Day 1						
	1	0	0	0	3	
	2	18	217	11	441	
Day 5						
	1	117	160	7	478	63.1*
	2	372	201	58	821	
Day 9						
	1	67	8	0	106	34.7*
	2	97	47	0	81	
G		28.3*	191.1*	2.3 ns	370.3*	

Only three pellets were found on the first row of plots after the first night of the plots becoming available. Expected values were too low for a frequency comparison of rows 1 and 2 on the first day but counts in the four plot types did differ significantly between rows, on the fifth and ninth days after the start of the second trial. On the fifth day pellet number was highest in the paspalum plots (row 2 the most) and lower in row 1 than row 2. The second highest count was in the carpet grass plot in row 1 and the kikuyu plot in row 2. Four days later the paspalum plot in row 1 had the highest count followed by kikuyu row 2, paspalum row 2 and kikuyu row 1. Carpet grass and clover were the least favoured.

Paspalum plots were the most favoured by the kangaroos but preference for these and other plots must have also been determined by other characteristics of the sward besides species. The swards in the first row of plots are illustrated in plates 13 - 16. The sward in the kikuyu plot was the tallest and most dense, with very little bare ground showing. The carpet grass and paspalum plots had the most bare ground suggesting that the amount of bare ground was probably not an important factor in the kangaroos' choice of plots. By the start of the second trial the paspalum plot in row 1 had been heavily grazed and had a large amount of grass seed heads above the sward surface. The kikuyu plot had dried out whereas the carpet grass plot continued to establish itself. All the new plots in row 2 had a higher biomass than their counterparts in row 1 at the same time. However, the clover and paspalum plots in row 2 were noticeably poorer in terms of



Plate 13 Surface view of the carpet grass plot in the first row of the experimental plots.



Plate 14 Surface view of the paspalum plot in the first row of the experimental plots.



Plate 15 Surface view of the clover plot in the first row of the experimental plots.



Plate 16 Surface view of the kikuyu plot in the first row of the experimental plots.

greenness and biomass than their counterparts had been at the start of trial 1 whereas the carpet grass and kikuyu plots were the same or better. Analysis of leaves of each species in the first row of plots established that the ranking of species on the basis of their nitrogen content differed slightly from the same species growing at Wallaby Creek. Clover still had the highest levels, but carpet grass showed the next highest nitrogen levels at Newholme, followed by paspalum and kikuyu.

4.4 Discussion

4.4.1 Use of burnt vegetation

Fire has been an important feature of the Australian continent for millions of years, influencing the evolution of Australia's flora and fauna (Recher and Christensen, 1981). The frequency and intensity of fire has changed through evolutionary and recent time such that adaptations of animals and plants are not to fire *per se*, but to a particular regime of fire frequency, intensity and seasonal occurrence (Gill 1975). Before the arrival of Aboriginal humans, fires would have started from lightning strikes and were probably sporadic and intense. Aborigines used fire to drive animals for hunting and to produce new growth of grasses to attract game. They set regular fires, but burning was more controlled because there was less fuel to burn, and a mosaic pattern of burnt and unburnt areas was created. Since the arrival of European settlement, fires have been a seasonal event in most areas. Although there are still wildfires, the introduction of mat-forming grasses into pastures to replace the native tussock-forming grasses, and a high intensity of grazing sufficient to minimize fuel accumulations, has reduced the intensity of fires on improved pastures.

During the course of my study at Wallaby Creek fires were set in winter in the areas dominated by blady grass and tussock grasses, and the areas dominated by heavily grazed, introduced grasses were not burnt. The native grasses produced new shoots very quickly after a fire and the nutrient quality of those shoots was similar to, if not higher than, carpet grass which occupied most of the ground layer at Wallaby Creek. In winter, the proportion of dead leaf in the ground layer of unburnt areas was very high, and sward biomasses were low, making it difficult for animals toprehend the green leaves amongst a dense mat of dead vegetation. The upright shoots of blady grass and tussock grass after burning appeared to be easier for animals to grasp. Kangaroos and wallabies were very adept at pulling these shoots out of their sheaths so that they got the full benefit of the succulent leaf bases. After about five months it became much more difficult for the leaves to be pulled from their sheaths and kangaroos and wallabies had to bite the leaves off, making prehension more difficult. The quality of the shoots (as defined by nitrogen and fibre levels) also declined rapidly six months after burning, and by the summer when the biomass of green leaf of introduced grasses was high and of high quality it seems unlikely that foraging could have been as efficient on the burnt native grasses. The relative feeding rates on burnt and unburnt pastures will be considered in Chapter 5.

In an earlier study of the effect of fire on pasture utilization by kangaroos, wallabies and cattle at Wallaby Creek by Southwell and Jarman (1987), the density of kangaroos on burnt areas peaked in the second month after burning, as it did in this study. In their study densities of kangaroos were 3 times as high on burnt grid cells as on unburnt control cells between 3 and 16 months after burning. The differences between densities

on burnt and unburnt areas were not as great in this study, perhaps because Southwell and Jarman's study spanned a particularly dry year when the lack of summer rain would have reduced the growth of introduced grasses such that the benefits of feeding on burnt native pastures would have persisted for longer. The differences in densities in my study did persist over the seven months, and the densities did not change significantly over that time.

The red-necked wallabies in Southwell and Jarman's study began utilizing burnt areas more than control ones four months after the burn and continued to do so through to month 16. In my study wallaby densities were always higher on control grids than burnt ones although my densities of red-necked wallabies were higher than in their study. From the proportion of the study area that was burnt, wallabies in this study showed a preference for unburnt areas in the post-burn season and in the following summer. Southwell and Jarman recorded animal sightings on transects of the study area whereas I recorded sightings on systematic searches. It is possible that the transect counts underestimated the density of wallabies in unburnt areas because wallabies were often found in amongst dense vegetation and may be less likely to be flushed from cover by someone walking in a direct route than someone making a thorough search of an area.

Southwell and Jarman suggested that red-necked wallabies may have been responding to fine-grained changes in the vegetation, causing them to respond much later to pasture burning than kangaroos. The dietary data presented here suggest that burnt shoots of blady grass and tussock grasses are relatively unimportant in the diets of wallabies at Wallaby Creek and that wallabies actually avoided blady grass, even in the post-burn season. Being a small animal, wallabies have high metabolic requirements (Kleiber, 1961; Dawson and Hulbert, 1970), and to meet them they should require a better quality diet than the larger kangaroos (Jarman 1974, Jarman, 1984; Dawson, in press). The digestibility of the blady and tussock grass shoots may have been too low for wallabies to utilize to any great extent. The availability of clover, a highly preferred food item for wallabies, in unburnt areas in winter meant that wallabies did not need to use the burnt shoots at this time as much as kangaroos did. Kangaroos on the other hand, require larger absolute amounts of food because of their body size. In winter, when the biomass of other grasses was comparatively low, the intake of large enough quantities of food may have been more important than its quality (providing quality remained above a threshold value), resulting in kangaroos utilizing burnt areas heavily.

The areas that were burnt had provided shelter for wallabies prior to burning, especially during their resting periods, and the lower densities of wallabies on burnt pastures may well be related to this lack of cover. Christensen (1977) radio-tracked a number of woylies *Bettongia penicillata* after an experimental fire and found that a number died as a result of predation, presumably because of the loss of dense undergrowth.

The improved pasture at Wallaby Creek is very different from native pasture and in summer the introduced grasses such as carpet grass, kikuyu and paspalum provided a higher quality diet than the native grasses that were burnt six months before. During the time when kangaroos and wallabies were evolving adaptations to the effects of fire, the benefits of burnt areas would probably have persisted for much longer than they do in improved pastures, where introduced grasses increase in biomass rapidly after summer rain. Kangaroos may persist in using burnt areas long after the quality of the shoots falls below that of other grasses available because in the past they benefitted from foraging on burnt areas for long periods after the fire.

The use of burnt areas by kangaroos and wallabies appeared to vary with time of day, with an interaction between season and time of day. Immediately after the burn both species used burnt areas less in the middle of the day, when they were resting, presumably because these areas provided less shelter. By the summer, when the burnt vegetation was taller, burnt areas were used almost as frequently for resting. Woylies in Western Australia reversed resting and feeding areas after burning because unburnt areas provided more shelter and burnt areas provided new shoots (and hypogean fungi) for feeding (Christensen 1977). Both kangaroos and wallabies used burnt areas much less in the afternoon in winter, choosing instead to use kikuyu dominated areas more often at this time. It is possible that after feeding on burnt areas throughout the night and morning, the animals needed to feed on more digestible grasses in the afternoon. Alternatively, the water content of grasses may be too low in the afternoon for the more fibrous burnt shoots (as opposed to improved pasture species) to be digested (Jarman, pers comm.). However, the level of feeding on burnt areas was as high as on unburnt ones in the afternoon in summer making these possibilities less likely.

In this study kangaroos used recently burnt pastures much more heavily than unburnt pastures but wallabies did not. The new shoots of the burnt grasses were important in the diet of kangaroos which had burnt areas in their home range; some kangaroos appeared to shift the centre of their home range to include burnt areas for the first few months after burning. Prior to burning, areas dominated by tussock grasses and blady grass were used by wallabies more for resting than for feeding, and when burning removed that shelter wallabies began to use those burnt areas less. Johnson (1985) found no evidence of a seasonal difference in the size of wallabies' home-ranges at Wallaby Creek or the heterogeneity of their use by wallabies. My searches of the area did not indicate any flux of wallabies into, or out of, burnt areas. Wallabies may instead have shifted their activity from one part of their home range to another.

4.4.2 Use of cover

At some times of the day at least, kangaroos were more likely than wallabies to be found in areas providing cover. Although wallabies were feeding in more open areas than kangaroos, they were usually feeding closer to the forest edge or a gully and when disturbed they fled into these shelters. Southwell (1987) related the densities of kangaroos and wallabies at Wallaby Creek to a number of environmental variables and found that wallaby density was negatively associated with distance to forest edge whilst kangaroo density was positively associated with it. He could find no strong correlation between the density of either species and tussock-grass biomass or blady-grass biomass, although at night there was a weak negative association with wallaby density and tussock-grass biomass. This suggests that factors other than the provision of cover by blady grass or tussock grasses affect kangaroos' and wallabies' choices of feeding site.

Caughley (1964b) found a positive correlation between densities of eastern grey kangaroos and cover (not canopy cover), but no such relationship for red kangaroo densities. He suggested that eastern grey kangaroos were more likely to have been exposed to predators in their evolutionary past and that the association with cover was an adaptation to avoid predators. There can be no such explanation for the difference between kangaroos and wallabies since they live sympatrically over much of their range. Instead I suggest that other sward factors, such as biomass or quality of grasses play a more important role in deciding where an animal feeds. Southwell (1987) found that the most important factors affecting kangaroo distribution of those he measured were canopy cover (-), altitude (-), tussock-greenness (+) and cattle density (+). The signs in parentheses indicate whether the relationship between the environmental factor and animal density was positive (+) or negative (-). For red-necked wallabies the important factors during the morning and afternoon were distance from the forest edge (-), ground vegetation diversity (+), canopy cover (-) and evenness of other-grass biomass (-). Thus, although wallabies appear not to be constrained by the availability of cover whilst feeding, they may still be constrained to feeding in areas close to the forest edge.

Kangaroos were not found amongst cover more often when resting in the middle of the day than at other times, although kangaroos did usually rest beneath the shade of trees, especially in summer. Wallabies were not seen amongst cover more often in the middle of the day either, although because I did not search the forest where many of the wallabies rested, the proportion of wallabies in cover in the middle of the day would have been under-estimated.

The type of cover used by the species did differ, with wallabies using 'other' cover species more often than kangaroos. Balloon cotton was the most common 'other' cover type and dense patches of the weed provided very good cover for wallabies. The ground vegetation in these patches was often dominated by *Paspalum* so the patches provided both concealment and high quality food items. Kangaroos appeared to avoid this type of

cover in the day-time, perhaps because it would have made group cohesion impossible. Kangaroos did feed amongst such cover at night; some of the kangaroos which were lost at night on the 24-hour followings were concealed in balloon cotton stands up to 2m in height and were almost impossible to find, even with spotlights.

Male and female kangaroos did not differ in their use of cover, despite the fact that females, especially with large pouch-young or newly emerged young-at-foot, are likely to be more vulnerable. However, eastern grey kangaroos are a gregarious species, living in open membership groups of both sexes. If kangaroos use grouping as a method of predator detection then there is no reason why females, more than males, should be found in areas providing cover. Female wallabies did tend to use cover more often than males in winter, but in the morning in summer they were found amongst cover less often than males. Again some interaction between the sexes' choice of cover and some other factor in the vegetation seems likely. The use of cover in relation to anti-predator strategies will be considered further in Chapter 7.

4.4.3 Ground species of feeding site and diet quality

Diet selection occurs at a number of levels; firstly an animal may choose where to feed, then on which plants to feed and finally which parts of the plant to bite (Jarman and Sinclair, 1979; Bunnell and Gillingham, 1985). One of the factors affecting the choice of feeding site is the availability and quality of food items there. Although I categorized sites based only on the dominant grass species within them, the divisions separated the most common vegetation types. Only the category of 'other' dominant types, which included clover, weeping grass *Microlaena stipoides*, annual stemmy grasses and other more succulent grasses, combined a number of vegetation types of varying quality. Casual observation indicated that wallabies seen on 'other' types were more likely to be on good quality patches than kangaroos on 'other' types. Weeping grass has soft succulent leaves and was common on gully floors and creek banks that were favoured sites for wallabies. Patches on the flats dominated by clover were also favoured by wallabies but not by kangaroos.

Kangaroos were found in locations with poorer ground vegetation types more often than wallabies, with the greatest differences between the species being in the use of burnt types and paspalum-dominated areas. Both species used areas dominated by carpet grass the most, as expected from the dominance of this grass over the study area. However, the high use of paspalum dominated areas by wallabies far exceeded the availability of this grass species over the study area and wallabies showed a high degree of selection for the species, especially in summer. Clover was rarely dominant in a patch but in winter wallabies often fed in areas containing clover and it appeared to be an important part of their diet at a time of year when the grasses were in short supply. Unfortunately the

technique used for faecal analysis is unable to detect clover because the soft epidermis is easily broken down. Kangaroos were never seen eating clover.

Both species used kikuyu-dominated areas little in winter but the preference indices for this species were very high because of the poor availability of the grass in that season. Kikuyu, though high in nutrient content in the leaves, is badly affected by frost and after the first frost in winter kikuyu swards had a very high proportion of dead vegetation in them. Although kikuyu-dominated areas were selected, kikuyu itself was not highly selected in the diet in winter.

The pattern of use of sites with different ground species was also reflected in the dietary analysis. Wallabies had a much higher proportion of paspalum in their diet than kangaroos and lower proportions of the burnt tussock grasses and blady grass. Wallabies did have a lower monocot proportion in their diet than kangaroos although Jarman and Phillips (in press) found that the red-necked wallabies at Wallaby Creek had a lower dietary diversity than eastern grey kangaroos, and that they relied heavily on a few species. Southwell (1987) found that the density of red-necked wallabies on transect counts was positively related to ground-vegetation diversity whereas kangaroo density was not. While wallabies may feed in more diverse patches than kangaroos the dietary data suggest that they do not select a broader range of monocot species than kangaroos.

In a comparative study of all the macropod species found at Wallaby Creek, using the same data for red-necked wallabies and eastern grey kangaroos as here, these two species were noticeably similar to each other, and different from other species, in their diet selection (Jarman and Phillips, in press). Whiptail wallabies ate higher proportions of kangaroo grass and blady grass, reflecting their greater use of the northern forest; and black-striped wallabies took a larger proportion of snow grass. The smallest species, the long-nosed potoroo, rufous-rat kangaroo and pademelons fed on a more varied diet which included much less grass and more fruits and fungi. The dietary separation between the *Macropus* species appeared to be as much related to habitat choice as selection of food plants, since red-necked wallabies and eastern grey kangaroos overlapped most in their habitat use (Southwell and Jarman, 1987) and most in their diet (Jarman and Phillips, in press).

Comparison with other dietary studies of macropods is limited because of the huge difference in availability of different grass species. The high proportions of introduced grasses in the diets of macropods at Wallaby Creek do illustrate the animal's preference for these species over the native grasses which comprise the majority of the diet in other studies (Taylor, 1983a; Hollis *et al.*, 1986).

The higher quality diet of wallabies compared to kangaroos is predicted by theory relating diet quality to body size (Bell, 1970; Jarman, 1974, 1984). High quality food items are rarer in the environment than low quality ones so small animals are forced to be more selective (Jarman 1974, Janis 1976). At the same time larger animals require a

larger absolute quantity of food, which may restrict them to feeding in areas with a high biomass (Clutton-Brock *et al.*, 1987; Illius and Gordon, 1987). Through evolution this led to small animals having morphological adaptations to selective feeding, such as narrow muzzle width (Bell, 1970; Jarman, 1974; Bunnell and Gillingham, 1985; Gordon and Illius, 1988) and large animals to having gut morphologies that cope with large quantities of food of low digestibility (Hofmann and Stewart, 1972; Demment and Van Soest 1985).

Optimal foraging theory may provide a compatible explanation for the differing diets of kangaroos and wallabies. Ungar and Noy-Meir (1988) have suggested that in some circumstances (e.g. when forage quality is homogenous), sheep may select bites to optimize bite size rather than bite quality. Black and Kenney (1984) have also provided experimental evidence that sheep select swards which allow them a fast intake rate; for example sheep prefer tall sparse swards to short dense swards because the bite size on the former is greater. The cafeteria trials demonstrated that leaf quality was not the most important factor affecting the sward preferences of kangaroos, although foraging choices may well balance the relative contributions of leaf quality and the potential rate of intake. There is some suggestion here that kangaroos, that are able to tolerate poorer quality grass than wallabies, select on the basis of sward structure and its effect on the rate of food intake.

Both kangaroos and wallabies were able to successfully select preferred species from amongst others. Jarman and Phillips (in press) suggest that the ability of kangaroos and wallabies to select a very high proportion of grass leaf (as opposed to sheath and stem) compared to grazing ungulates is due in part to their narrower incisor arcade and mode of grasping and plucking individual leaves. Macropods are also able to use their forepaws to manipulate food items and to part tussocks, enabling them to more easily grasp the higher quality leaves within. The foraging methods of kangaroos and wallabies, in relation to their body size and dietary-selectivity will be further considered in Chapter 6.

The degree of sexual dimorphism in both species changes considerably with age; the ratio by weight of female to male eastern grey kangaroos is about 0.7:1 at the time of females sexual maturity but can reach nearly 0.5:1 by the age of 8 years (Jarman 1983). The difference in body size of male and female red-necked wallabies at full maturity is of the same order (Johnson, 1985). The species fall at the divergent end of the sexual dimorphism spectrum shown by the Bovidae and Cervidae, where the maximum difference is given when females are 45% of adult male weight, compared to 55% for eastern greys and red-necked wallabies (Jarman, 1983). Given the large difference in body weight between males and females of both kangaroos and wallabies it is perhaps surprising that the sexes do not appear to differ in feeding site location or diet. Differences in feeding behaviour and habitat use have been shown for many sexually

dimorphic mammals, including some species of macropods (Taylor, 1984; Johnson and Bayliss, 1981), primates (Boinski, 1988), and ungulates (Clutton-Brock *et al.*, 1987).

Unlike the macropods, many of the species showing differences in habitat use have separation of the sexes for some or all of the year (Jarman, 1983). This separation is sometimes maintained by males keeping other males away from females (*ibid*, Jarman and Jarman, 1973), although in the case of red deer the separation appears to be due primarily to the inability of males to cope with low biomass of plants on the better quality swards that are preferred by females (Clutton-Brock *et al.*, 1987). Grey kangaroos form open-membership groups of mixed composition, with only large males and females with young-at-foot tending to be more solitary than other classes (Southwell, 1984b). This may provide the opportunity for these classes to utilize better pastures as suggested by Johnson and Bayliss (1981). For other classes there may be little opportunity for much segregation between the sexes if kangaroos are to maintain contact with one another in the group. In addition the energetic requirements of the other population classes differ less, reducing the need for differences in their selectivity.

Johnson (1985) did find some differences between male and female red-necked wallabies at Wallaby Creek in their choice of habitat; females concentrated on pastures adjacent to cover on the creek flats and gully floors, and whilst males also used these areas, they spent more time than did females between gullies and above creek flats. Taylor (1981) found that male kangaroos and wallaroos ate more tussock grass than females, although his sample sizes were very small and in the case of the wallaroo, males were shot in areas particularly abundant in tussock grass. Johnson and Bayliss (1981) reported that large male red kangaroos and heavily lactating female red kangaroos predominated on better pastures than other classes of animal. The pastures at Wallaby Creek have been greatly improved by the introduction of highly digestible grasses and it is possible that foraging differences between the sexes are not necessary under such good pasture conditions.

The cafeteria trials provided some insight into the sward characteristics on which animals may base their feeding site selections. In order to feed in the sown grass plots the kangaroos had to leave the cover of the shrubs and boulders upslope, feed in my presence and, in the early stages, negotiate an electric fence. The high cost that the kangaroos were prepared to pay to feed in the artificial grass plots instead of the native pasture suggest that the ease of selection in the single-species swards, and the high digestibility of the grasses were important in their selection.

In the absence of any other factors relating to anti-predator strategy kangaroos consistently selected the paspalum and kikuyu plots over the others. Their total avoidance of the clover plots was surprising since the nitrogen levels of the leaves were the highest of all the species. Clover has a very high water content and low fibre content so the kangaroos may have avoided it because they could not achieve a high enough

intake rate. Although the biting rates of kangaroos feeding on different plots did not differ significantly, bite size is also an important component of intake. The large differences in the height and density of the swards would appear to explain the avoidance of the sparse vegetation of the carpet grass plot, despite its high nitrogen content, and the preference for the continuous sward in the kikuyu plot.

One male in the study group consistently moved onto the grass plots first, being closely followed by the others which appeared to be trying to maintain group cohesion. Observations at Wallaby Creek suggest that similar situations arise in the wild, especially when females select a location to feed and accompanying males follow to feed in the same place. One of the costs to maintaining a group may be in having to move to feed where the rest of the group or the 'group leader' wishes to feed.

4.5 Conclusions

1. Kangaroos utilized burnt areas preferentially in the first six months after a fire whilst wallabies tended to avoid burnt areas. The difference between the species is due, in part, to the removal of the cover vegetation by burning which makes burnt areas a less preferred location for resting. The species difference is also due to the selection of burnt shoots by kangaroos. Burnt species comprised an important part of the diet of kangaroos in the post-burn seasons, but were of little importance to wallabies.
2. Wallabies showed a strong preference for areas dominated by the better quality grasses that are low in fibre and high in nitrogen. They also showed a strong preference for the high quality species in their diet. The differing patterns of dispersal of the preferred food types of kangaroos and wallabies may cause the species to adopt different foraging strategies e.g. moving more often or spending more time selecting each bite. The feeding and movement rates of the two species are compared in Chapter 6, and the consequences of foraging on different sward types are investigated in Chapter 5.
3. Wallabies tend to use areas which provide cover less than kangaroos, although the distance to the nearest cover may be an important factor in feeding-site choice. Wallabies do not appear to use cover vegetation to conceal themselves whilst feeding although they may do so whilst resting. Their use of open areas may enable them to spot predators quickly; being a small species that is unable to outrun its predators, the wallaby must detect a predator before being detected itself. Alternatively, the use of areas lacking in cover vegetation may relate to an interaction between sward quality and availability of cover.
4. The choice of which plant species to feed upon does not appear to be solely dependent on plant quality because:
 - a) kangaroos continued to feed on burnt shoots even after the levels of nitrogen in them dropped below those in species in the intertussock sward;
 - b) kangaroos and wallabies select different diets from the same areas;
 - c) the levels of nitrogen in grasses in the cafeteria trial did not relate directly to the kangaroos' preferences. Sward structure and its effect on rate of intake appear to be equally important in determining bite preferences, particularly for the larger kangaroos that are able to tolerate lower quality herbage.

CHAPTER 5

Foraging Behaviour and its relationship with sward characteristics

5.1 Introduction

Whilst herbivores may determine the energy, nutrient and fibre content of food items they consume by a process of diet selection, their rates of energy and nutrient intake are also dependent on bite size and biting rate (Allden and Whittaker, 1970). Their total intake over 24 hours is further dependent on total grazing time (*ibid*). Thus, grazing animals have control of the quality of their diet, and also how much and how fast they eat. The degree of this control has been illustrated in many studies of grazing ruminants; the digestibility and metabolizability of the diet of domestic ruminants varies by a factor of two, whilst herbage intake has been shown to vary by a factor of at least four, even under relatively unrestricted conditions (Hodgson and Grant, 1981 ; Hodgson, 1982; Minson, 1982).

Most studies of the foraging behaviour of wild herbivores have concentrated on total foraging times and diet quality, yet studies with domestic animals have shown that sward characteristics play an important role in determining intake rates (Arnold and Dudzinski, 1966; Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Hodgson, 1981). In turn, intake rates have been shown to influence diet preferences. For example, sheep offered dried forages of different particle size chose the forages they could eat the fastest and intake rate had a greater influence on their diet preferences than forage digestibility (Kenney and Black, 1984). Thus, it is important to understand the factors influencing herbage intake in order to predict intake levels and perhaps to explain dietary preferences. The factors influencing herbage intake include the variations in sward conditions which exert direct effects upon intake, and the compensating animal responses (Hodgson, 1982).

Studies of the control of food intake of domestic and wild herbivores have followed very different approaches. Studies with domestic herbivores have concentrated on the role of the vegetation in determining animal responses (see Hodgson, 1982 for review), although the role of animal factors (e.g. physiology and reproduction) in affecting feed intake have also been acknowledged (see Weston, 1982 for review). Studies with wild herbivores have instead looked for feeding strategies which, for a given animal, describe

a complex of behaviour and morphology best suited to gather food energy in a particular environment (Schoener, 1971). That environment not only contains the food available, but also shelter, predators and other conspecifics which all affect the forager to some degree.

In this introduction I review some of the relationships between sward characteristics and foraging behaviour that have been found in studies to date. Most of the studies have been of domestic ruminants, grazing relatively uniform pastures and some of the relationships discussed may not apply to the native pastures of Australia. I will also discuss some of the findings of studies of wild herbivores and comment on differences with domestic herbivores. Finally I will discuss some of the differences between macropods and ruminants and the pastures they graze, in order to predict which of the relationships may be expected for grazing macropods at Wallaby Creek and elsewhere in Australia.

Herbage intake over 24 hours can be considered as the product of time spent grazing and the rate of herbage consumption per unit of foraging time; the rate of herbage consumption is itself the product of the amount of food ingested per bite and the rate of biting during grazing (Allden and Whittaker, 1970). In studies of domestic sheep and cattle bite size is generally the most variable component of intake (Stobbs, 1973; Hodgson, 1981; Milne *et al.*, 1981) but foragers can regulate their biting rates and grazing times to some extent to compensate for variations in bite size (*ibid*; Arnold and Dudzinski, 1966; Hodgson, 1981, 1982). Allden and Whittaker (1970) have described the relationships found between the grazing time and intake rate of sheep, with herbage availability. As herbage declines in quantity, an animal's intake is at first unaffected, until a stage is reached when herbage availability apparently imposes limitations on the rate at which an animal can ingest feed. At first these limitations are compensated for by an increase in grazing time, but compensation becomes progressively more incomplete and, over a wide range of low herbage masses, an upper limit to grazing time is set by gut fill or the time constraints of other essential activities.

Allden and Whittaker (1970) also describe the relationships found between bite size, bite rate, intake rate and tiller length. Bite size increased almost linearly with increasing tiller length but the rate of biting, after an initial increase from the lowest rate, showed a steady decline. As a result, rate of intake first increased rapidly with increasing tiller length, then remained constant over a wide range of tiller lengths (*ibid*).

Increasing biting rates with declines in forage biomass or sward height have been demonstrated in a number of other studies of grazing herbivores, including some wild species: calves and lambs (Jamieson and Hodgson, 1979; Hodgson, 1981); red-deer (Loudon *et al.*, 1984); Bennett's wallabies (Clarke and Loudon, 1985). There is a large degree of variation in the response in individual studies that may be attributable to differences in sward type (especially differences between temperate and tropical swards),

the measure used for herbage availability, and the species of animal under study. Although variations in sward height and mass are often closely correlated, Hodgson (1982) suggests that on intensively managed temperate swards, height of the grazed surface is more important than herbage biomass in determining intake rate (the product of bite rate and bite size). On tropical swards variations in bulk density and leaf:stem ratios appear to be more important (Stobbs, 1973; Chacon and Stobbs; 1976; Hendrickson and Minson, 1980). Hodgson (1982) also suggests that on tropical swards, which usually reach greater heights than temperate swards, the relationship between intake rate and herbage availability may be quadratic because of the increasing difficulty of prehending and ingesting excessively long leaves.

It is not clear whether the differences in response on tropical and temperate swards reflect fundamental differences between temperate and tropical forage plants, or animal responses at different ends of a continuum of responses to variations in sward structure (Hodgson, 1982). I mention this point because at Wallaby Creek the introduced grass species form a dense mat which is kept relatively short by grazing pressure from cattle and macropods. The native grasses have a more discontinuous distribution, with grasses forming tussocks, which contain a high biomass of dead and senescent material. The results of grazing process models of Ungar and Noy-Meir (1988) suggest that the considerable variation in functional responses to herbage availability reported in the literature is due to the interaction of sward structural attributes to producing heterogeneity in potential bite weights.

The relationship between intake rate and herbage mass or height is further complicated by the general decline in forage quality with decreasing sward height. This relationship was illustrated for grasses at Wallaby Creek by the changes in nutrient level of blady grass and swamp foxtail shoots after burning and the lower nitrogen levels in grasses growing inside tussocks compared to the same species growing outside tussocks.

The preceding discussion concerns the behaviour of domestic animals feeding on intensively managed swards where there is little opportunity, or requirement, for diet selection. Animals grazing natural pastures or semi-improved rangelands experience a much greater variation in plant quality than domestic animals. Studies on these communities suggest that diet selection plays a more important role than sward biomass or height in determining intake rates, at least for the more selective feeders (Loudon *et al.* 1984; Armstrong and Hodgson, 1986). For example, in a study of cattle and sheep grazing indigenous hill plant communities sheep tended to maintain diet digestibility at the expense of intake, whilst the less selective cattle tended to maintain rate of intake at the expense of digestibility (Armstrong and Hodgson, 1986). Studies with wild herbivores have also yielded different results; reindeer increased their grazing times but decreased their rate of biting with declining biomass (Trudell and White, 1981).

It is interesting to consider whether domestic animals still have the capability for selection that their ancestors had or whether, as Schwartz and Ellis (1981) suggest, they have been bred by humans to be generalist herbivores which respond to declines in herbage availability by eating faster rather than by becoming more selective. Arnold (1987) suggests that sheep are capable of both strategies since they have been shown to be highly selective on mixed pastures with very low biomass (Broom and Arnold, 1986). Some animals are able facultatively to change their foraging strategy depending on prevailing conditions (white-tailed deer: Schwartz and Ellis, 1981).

The following conclusions can be drawn from studies of domestic ruminants:

1. Generalist herbivores select pastures or species which give them the highest intake rates. For them, intake rate appears to be more important than bite quality in determining selection.
2. Intake rate is the product of bite size and bite rate. Bite size declines with declining forage availability, and, although ruminants tend to increase their rates of biting and grazing time to compensate, compensation may not be complete at low biomasses.
3. Tropical swards grow to greater heights than temperate swards and have a higher leaf:stem ratio. In these instances difficulty in prehending tall grasses, especially those with high leaf to stem ratios, may reduce feeding rates at high pasture biomasses (Hodgson, 1982).
4. Studies of wild ruminants and domestic ruminants on natural pastures suggest that the relationships between biomass and foraging described in point 2 above may not apply in more natural systems. Sward diversity may be more important than sward biomass in these situations (Loudon *et al.*, 1984; Armstrong and Hodgson, 1986).

Attempts to model foraging behaviour of wild herbivores must take into account other factors, besides food availability, which affect the survival and reproductive success of the herbivore. For example, some animals may need to minimize the time that they spend feeding, either to reduce the amount of time they are vulnerable to predation and extremes of temperature, or to maximize the time they have available for other activities (Owen-Smith and Novellie, 1982). Others may require particularly high nutrient intakes which entail long search times and foraging times (*ibid*). In one of the first attempts to find an optimal foraging model for wild grazing herbivores Owen-Smith and Novellie (1982) suggested that large herbivores have two alternative foraging tactics:

- (1) If all nutrient requirements for maximum performance can be met, then these should be secured in the shortest possible time. This tactic (time-minimizer) appears to be the one adopted by most domestic ruminants grazing good pasture.
- (2) If nutrient requirements cannot be met, then animals should minimize the shortfall by maximizing the assimilation rate of the most limiting nutrient. This tactic (nutrient-maximizer) could entail narrowing the acceptance range of diet items under

submaintenance conditions, and perhaps explains the greater tendency of some animals to become more selective when food availability is low.

Prior to European settlement the grasslands on the east coast of Australia and in Tasmania were characterised by tussock-forming grasses, particularly *Themeda triandra* kangaroo grass and *Poa labillardieri* snow grass, interspersed with other tall perennials and forbs (Norton, 1972; Kirkpatrick *et al.* 1988). Tussock-forming grasses form a discontinuous layer of widely varying quality and snow grass and kangaroo grass have a low nutrient content. Such conditions probably favour herbivores that can be highly selective for young grass shoots in tussocks, or for grasses and forbs dispersed between tussocks (see plates 17 and 18). In addition, the mouthparts of macropods are narrow compared to those of ruminants of a similar body weight and kangaroos and wallabies may need to be selective to maintain a high enough nutrient intake level. Of course, the narrow muzzle may be the result of selection for mouthparts which enable selective grazing.

In one of the few studies of the foraging rates and intake levels of macropods, red kangaroos and western grey kangaroos grazing a progressively depleted arid zone pasture did increase the number of harvesting bites they made per unit time, with declining biomass (Short, 1986). However, in that study biting rates were considerably lower than those reported for ruminants and Short suggests that the slow biting rates may enable kangaroos to be more selective of food items.

In this chapter I compare the foraging behaviour of kangaroos and wallabies on different sward types and in different seasons, to try to establish which are the important sward factors affecting foraging behaviour. I also look at changes in sward characteristics and foraging behaviour on each sward type, over a period of time, to eliminate some of the variation in sward characters and to try to discover which are the best predictors of foraging behaviour. Although I look at the behaviour of both species, I reserve a comparison of their foraging methods for Chapter 6.



Plates 17 and 18 Small female eastern grey kangaroo foraging within tussocks and with her head raised, chewing and surveying. Note that whilst the sward contains a large proportion of dead vegetation, the kangaroo has only green leaf in her mouth, in this case that of carpet grass.

5.2 Methods

5.2.1 3-minute observations

The fine details of foraging behaviour were recorded in the 3-minute continuous observations of biting/feeding behaviour described in Chapter 2. These observations were abandoned if the animal ceased to feed for longer than 1 minute, if the animal hopped on to another vegetation type, or if group sizes changed during the three minutes. The variables calculated for use in this chapter are described in Table 5.1.

Table 5.1 Description of the variables calculated from the 3-minute observations which are used in this chapter and following chapters.

<i>Bites/select</i>	Proportion of 3 minutes the animal had its head down, biting or selecting bites.
<i>Survey/chew</i>	Proportion of 3 minutes the animal had its head raised, surveying and chewing.
<i>Interrupted biting rate (BR1)</i>	Bites/min calculated from the number of bites taken in 3 minutes.
<i>Uninterrupted biting rate (BR2)</i>	Bites/min calculated from the time taken for 10 bites without interruption.
<i>Biting Ratio</i>	Ratio of BR1/BR2.
<i>Bites/mouthful</i>	Mean number of bites taken from putting the muzzle to the sward to raising the head to chew.
<i>Chew/bite</i>	Mean ratio of chews/bites for each mouthful.
<i>Head-up rate</i>	Number of times per minute the focal animal lifted its head from the sward to survey.
<i>Step total</i>	The total number of steps taken in 3 minutes.
<i>Step sequence</i>	The mean number of steps taken from the cessation of biting at one feeding station until the animal next stopped to take a bite from the sward i.e. between patches.
<i>Bites/patch</i>	Mean number of bites taken in a patch before the animal took a step to a new patch.
<i>% patches accepted</i>	The percentage of steps which were immediately followed by the animal biting from the patch.
<i>% steps away from neighbour</i>	The percentage of steps taken that were in the opposite direction to the focal animal's nearest neighbour. Group size 1 excluded.

5.2.2 Location of foraging observations

In order to relate the foraging behaviour of kangaroos and wallabies to sward conditions, it was necessary to make detailed measurements of sward canopy composition and height. These measurements were very time consuming to make and their use in predicting foraging variables was reduced with the amount of variation in each sward variable. In Chapter 4 I used the dominant ground species in a vegetation area to delimit vegetation types. Although areas around the study site which belonged to the same vegetation type contained similar ratios of the dominant ground species, there was a large amount of variation in the biomass available, sometimes due to stocking levels in different parts of the study area. Chemical analyses of grass species collected in different parts of the study area indicated that there were locational differences in grass quality, probably because of differences in soil type and grazing pressure. For these reasons I decided to delimit a number of ^{areas} in which I made regular measurements of the sward characteristics and where I observed kangaroos and wallabies feeding (see Chapter 2 for methods).

The areas used for comparison in this chapter (areas 1 to 4) are illustrated in Figure 2.5. The species composition of the swards and the cover vegetation were relatively uniform within each area, though they differed between areas. Two of the areas were paddocks surrounded by fences which the kangaroos and wallabies could pass through easily. Kangaroos and wallabies varied their use of the areas throughout the year depending on sward conditions inside and outside the areas. Changes in the condition of areas 1 - 4 are illustrated by plates 19 - 32.

Measured characteristics of the swards in each area are given in Tables 5.7 and 5.8. The following is a general description of each area:

Area 1 was a paddock on the alluvial flats approximately 2 ha in area, dominated by paspalum and carpet grass with a high proportion of *Bromus* sp, at some times of the year. The sward was generally low in biomass and completely lacking in cover vegetation. It was used frequently for feeding by wallabies whose homes ranges were in the south of the study site. Kangaroos rarely used the paddock and days when kangaroos were found there were generally wet and windy.

Area 2 was also a paddock on the alluvial flats with an area of approximately 1.5 ha. It had a greater diversity of plant species, and contained a greater proportion of forbs than area 1. The area did not have cover vegetation most of the year, although in summer thistles and stemmy forbs grew tall enough to provide some cover. Area 2 was an important area for clover growth in winter, having been sown with clover in the past. Again wallabies used this paddock regularly for feeding but kangaroos were rarely seen there.

Area 3 was an area of 1.5 ha surrounding the main dam on the southern property. The ground sward was dominated by carpet grass, interspersed with paspalum and had patches of kikuyu. Tussocks of snow grass up to 75 cm in height occupied about 30% of the total area. The area was used heavily by kangaroos all the year around, with quite large groups congregating there to feed. The area was used less often by wallabies.

Area 4 was a small area of about 0.5 ha adjacent to the road and bordering a small creek. The sward was almost entirely composed of kikuyu grass which varied greatly in height according to the time of year and grazing pressure. The ground was often damp because of the small creek and after heavy rain some parts became quite boggy. The area did not provide any cover vegetation. Area 4 was used heavily by kangaroos for some parts of the year and was used less frequently by wallabies for most of the year.

5.2.3 Seasonal delimitations

None of the four areas (areas 1-4) used in comparisons in this chapter were burnt during the course of the study. Data for the sward height and percentage of dead vegetation in the sward for each area (section 2.5.1) suggested that the year could be divided into two periods between which vegetation characters differed greatly; winter comprised April to October and summer comprised November to March. I have used these 'seasonal' divisions in this chapter and data for the vegetation areas are compared for winter and summer.

The observations for the comparisons of kangaroos and wallabies foraging on burned and unburned sward components were made in areas 5 and 6 (see section 2.4.3). Burning of some pastures occurred in July 1986 and July 1987. The height and quality of burnt swards changed four to six months after burning (section 4.3.1) so comparisons of kangaroos feeding on burnt tussocks or blady grass shoots with those feeding on other sward components include only data from the first four months after burning.



Plate 19 View of Area 1 in August 1987



Plate 20 Sward of Area 1 in August 1987



Plate 21 View of Area 1 in February 1988



Plate 22 Sward of Area 1 in February 1988



Plate 23 View of Area 2 in August 1987



Plate 24 Sward of Area 2 in August 1987



Plate 25 View of Area 2 in February 1988



Plate 26 Sward of Area 2 February 1988



Plate 27 View of Area 3 in August 1987



Plate 28 Sward of Area 3 in August 1987



Plate 29 View of Area 3 in February 1988



Plate 30 Sward of Area 3 February 1988



Plate 31 View of Area 4 in August 1987

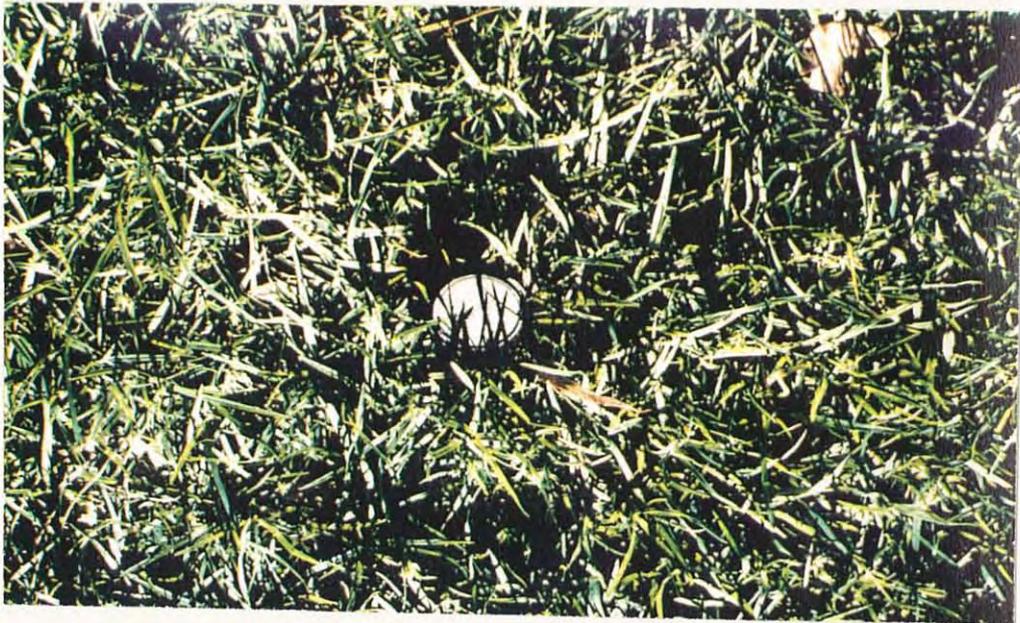


Plate 32 Sward of Area 4 in August 1987

5.3 Results

5.3.1 Comparison of kangaroos foraging on different vegetation components.

The different components of vegetation were described in detail in section 4.3.3, but are summarized here. The intertussock sward between tussocks is comprised of short mat-forming grasses; animals foraging on this component were described as foraging in the **intertussock** sward. Palatable grasses of the intertussock sward also grow, sparsely but tall, within mature tussocks of unpalatable grasses. Kangaroos, and occasionally wallabies, foraged within these tussocks for the palatable species and in doing so were described as foraging **within tussocks** (Plates 17 and 18). Animals foraging within patches of mature blady grass were described as feeding **within blady grass**. Those foraging on green shoots exposed after burning or on new shoots that appeared after burning were described as feeding on **burnt tussocks** or **blady grass shoots**.

Foraging in tussocks, in stands of blady grass or in the sward between such tall vegetation poses different problems for animals. Tussocks could be considered as patches containing a high biomass of unwanted, indigestible plant material through which the forager must search for preferred food items. Each of these food items is larger than would be found outside the tussock because it has escaped being grazed by other less selective herbivores. Although higher in biomass the plants growing within tussocks have a higher fibre content and lower nitrogen content than plants of the same species growing outside tussocks, the latter being regularly cropped by herbivores. The nitrogen and fibre levels of the three major intertussock species are presented for samples taken from inside and outside tussocks of Area 3 in one month (May 1986) (Table 5.2). In other months, and in all seasons, there were similar differences between the quality of grass growing inside and outside tussocks.

Table 5.2 The composition of non-tussock forming grasses growing inside and outside tussocks in May 1986. Composition is expressed as percentages of dry-weight of N, NDF, ADF and ash.

	% N	% NDF	% ADF	% ash
Carpet grass				
outside tussock	2.0	67.8	34.7	8.9
inside tussock	1.6	74.5	35.9	7.9
Kikuyu				
outside tussock	3.6	63.8	28.8	9.2
inside tussock	3.1	61.0	29.6	12.0
Paspalum				
outside tussock	3.2	63.8	30.8	9.0
inside tussock	2.4	68.7	38.2	8.8

Area 3 contained a 30% covering of tussocks of snow grass, swamp foxtail and *Juncus* sp. rushes. In descending order of frequency, the intertussock grasses found growing in tussocks were paspalum, kikuyu and carpet grass. Most of the sightings of animals feeding within tussocks appeared to involve animals selecting paspalum, which I could distinguish from the other two species by its appearance. Kangaroos were never seen to eat the leaves from mature tussocks of snow grass, *Juncus* sp. or swamp foxtail, and wallabies were very rarely seen to eat plants in tussocks at all. Kangaroos and wallabies did feed on the mature tussocks of kangaroo grass in the northern forest, especially at night.

Three-minute observations were made of kangaroos foraging within tussocks and in the intertussock sward in Area 3. Sample sizes of kangaroos feeding within tussocks are small because kangaroos were not often seen foraging within tussocks for a 3-minute period; if they switched to feeding outside the tussock then the observation was abandoned. Table 5.3 presents foraging parameters for kangaroos foraging within tussocks and in the intertussock sward in winter only. There were insufficient observations of kangaroos foraging within tussocks in summer for a comparison with winter.

Table 5.3 Medians of foraging parameters for kangaroos feeding outside and inside tussocks in Area 3. Kruskal-Wallis tests for the difference between group medians with H adjusted for ties. See Table 5.1 for definition of foraging variables.

Variable	outside tussock	inside tussock	H	p
sample size	53	9		
bite/select	0.79	0.58	11.3	<0.001
survey/chew	0.18	0.42	13.6	<0.001
head-up rate	4.0	6.0	11.6	<0.001
interrupted bite rate	29.8	17.4	11.8	<0.001
uninterrupted bite rate	42.4	39.1	0.6	n.s.
chew/bite	0.3	1.3	17.4	<0.001
bite/mouthful	31.9	12.4	8.2	<0.005
bite/patch	33.5	15.7	3.9	<0.05
step sequence	1.0	1.0	0.08	n.s.
% patches accepted	100	100	0.23	n.s.
% steps away from neighbour	100	100	0.17	n.s.
step total	2.0	2.0	0.01	n.s.

The behaviour of kangaroos foraging within tussocks differed in many respects from those foraging outside tussocks, in the intertussock sward. Kangaroos selecting bites inside tussocks spent less of their feeding time with their heads down, biting and selecting bites so their interrupted biting rates were lower, although their uninterrupted biting rates were the same. Kangaroos foraging within tussocks took 30% fewer bites per mouthful than those foraging outside tussocks, causing them to raise their heads more frequently. However, kangaroos foraging within tussocks took four times as many chews per mouthful as those foraging outside tussocks, and spent more time chewing and surveying. There were no differences in the movement of kangaroos feeding inside and outside tussocks over the three minute time period although those feeding inside tussocks took fewer bites in a patch before moving on to a new feeding station.

Kangaroos foraging on burned and unburned vegetation components

The foraging behaviour of kangaroos foraging in intertussock swards, on burnt and unburnt tussocks and on burnt and unburnt blady shoots are compared in Table 5.4 for the four months following the 1987 burn (August-November).

The proportion of time kangaroos spent biting or selecting bites during feeding was higher for those feeding on burnt tussocks, blady grass shoots or within unburnt blady stands, and their surveying time was lower. There was almost no difference in these parameters between those feeding inside and outside tussocks, unlike those animals observed only in area 3 (Table 5.3). Kangaroos lifted their heads more frequently when feeding on intertussock swards and least when feeding in unburnt blady stands. This is surprising given the high rate of kangaroos lifting their heads when feeding within tussocks (Table 5.3).

Interrupted bite-rates were quite uniform for kangaroos feeding on intertussock and burnt swards, but uninterrupted bite-rates were higher on the inter-tussock sward. Feeding rates were much lower for those selecting plant material from within tussocks or within blady grass stands. Kangaroos took fewer bites per patch and more steps when feeding on burnt vegetation components.

Table 5.4 A comparison of the foraging of kangaroos on different vegetation components: intertussock sward (it); within unburned tussocks (tu); within unburned blady grass (bl); on burned tussocks (btu); and burned blady grass shoots (bbl). Data are from 3-minute observations in the four months August to November, 1987 and are presented as medians of feeding parameters, with Kruskal-Wallis tests for each variable comparing the medians for each component. Significance levels: $p > 0.05$ (n.s.); $p < 0.05$ (*); $p < 0.01$ (**); and $p < 0.001$ (***)

Foraging variable	it	unburned tu	bl	btu	burned bbl	H	sig
<u>Biting</u>							
Bite/select	0.72	0.70	0.84	0.85	0.85	23.0	***
Survey/chew	0.25	0.28	0.13	0.14	0.14	20.1	***
head-up rate	5.0	4.0	3.0	4.0	4.0	17.3	**
interrupted bite rate	36.3	20.2	18.9	36.1	30.3	48.0	***
uninterrupted bite rate	52.1	29.7	26.8	42.8	37.4	82.0	***
Biting ratio	0.72	0.62	0.88	0.83	0.81	23.5	***
chew/bite	0.6	1.2	0.8	0.3	0.5	15.8	**
bites/mouthful	18.2	11.9	-	22.7	22.8	10.3	*
bites/patch	30.5	25.0	14.5	26.5	21.6	14.5	**
<u>Movement</u>							
step sequence length	1.0	1.0	1.0	1.0	1.0	2.9	n.s
% patches accepted	1.0	1.0	1.0	1.0	1.0	2.8	n.s
% steps away	1.0	1.0	1.0	0.6	0.9	2.6	n.s
step total	2.0	2.0	2.0	4.0	3.0	18.7	**
n	134	19	6	32	44		

5.3.2 Comparison of wallabies foraging on different vegetation components.

Wallabies were rarely seen foraging within tussocks or stands of mature blady grass, but they did feed on the new shoots of burnt tussocks in the first four months after burning. Table 5.5 compares the medians of foraging parameters of wallabies feeding on intertussock swards and burnt tussock shoots and the results of Kruskal-Wallis tests comparing the medians for each variable (H is adjusted for ties).

Table 5.5 A comparison of the foraging of wallabies on the intertussock sward (it) and on burnt tussocks (btu). Data are from 3-minute observations in the four months August to November, 1987 and are presented as medians of feeding parameters, with Kruskal-Wallis tests comparing the medians for each variable between components.

Foraging parameters	inter tussock	burnt tussock	H	p
bite/select	77.0	56.0	4.25	<0.05
survey/chew	21.0	36.0	3.78	<0.1
head-up rate	6.0	8.0	7.02	<0.01
interrupted bite-rate	30.2	28.30	0.45	n.s.
uninterrupted bite-rate	42.4	47.4	4.27	<0.05
biting ratio	0.75	0.56	3.89	<0.05
chew/bite	0.8	1.3	2.43	n.s.
bites/mouthful	14.8	8.7	3.82	<0.05
bites/patch	25.0	36.0	0.86	n.s.
step sequence	1.0	1.0	0.21	n.s.
proportion steps accept	1.0	1.0	0.00	n.s.
proportion steps away	1.0	1.0	0.68	n.s.
step total	3.0	2.0	0.41	n.s.
hop total	0.0	0.0	0.05	n.s.
n	36	18		

Wallabies feeding on burnt tussocks had higher uninterrupted biting rates than those feeding on intertussock swards. The burnt shoots were often the only green leaf available in burnt areas so wallabies did not need to spend as much time selecting bites as in a mixed sward. Wallabies foraging on burnt tussocks also surveyed for longer and raised their head from the sward more frequently such that the number of bites they took in 3 minutes was the same.

Wallabies foraging on burnt tussocks spent a greater proportion of their feeding time surveying. This may be a response to their feeling more vulnerable because of the lack of cover in burnt areas or because of larger bite sizes on the tussocks. Wallabies feeding on burnt tussocks took fewer bites per mouthful although the difference in the number of chews per bite was not significant.

5.3.3 Comparison of wallabies feeding in different vegetation areas.

Of the four areas monitored, the two where wallabies were seen most regularly were Area 1 and Area 2. Both were alluvial paddocks by the creek that had been sown to introduced grasses and clover in the past. The foraging behaviours of wallabies feeding in these two areas are compared in two seasons in Table 5.6. There were no differences between the head-up rate, bites/patch or movement variables of wallabies feeding in the two areas and these variables are not included in the table.

Table 5.6 A comparison of wallabies feeding in Areas 1 and 2 in winter 1986 (April-October) and summer 1986/87 (November-March). Data from 3-minute observations presented as means (\pm s.e.m) of foraging parameters. Subscripts indicate significant differences ($p < 0.001$) between pairs of values using Student's *t* tests. Significant results of two-way analyses of variance given, with season and area as grouping factors.

	winter 1986		summer 1986/87	
	Area 1	Area 2	Area 1	Area 2
bite/select	85.2+2.5	81.4+2.9	83.7+3.4	76.7+4.5
survey/chew	12.6+2.0	16.9+2.5	15.2+3.6	19.4+2.3
interrupted bite-rate	24.0+1.0	24.8+1.0	36.2+2.7 ₁	26.1+2.4 ₁
uninterrupted bite-rate	30.3+1.5	33.7+1.5	42.9+2.4 ₁	35.2+1.4 ₁
biting ratio	0.78+0.13	0.77+0.04	0.84+0.03	0.74+0.05
sample size	28	30	11	7

Source of variance	d.f.	F	p
Bite rate 1			
season	1,72	12.6	0.002
area	1,72	7.7	0.007
season x area	1,72	10.8	0.002
Bite rate 2			
season	1,70	11.5	0.001
season x area	1,70	7.2	0.01

There were no significant differences in the biting or surveying time of wallabies feeding in the two vegetation areas but feeding rates did differ. The interrupted biting rate differed between the areas, although there was an interaction with season. The results of Student's *t* tests comparing wallabies feeding in the areas in each season showed a difference only in summer. Similarly, uninterrupted biting rates on the two vegetation areas differed significantly only in summer.

There were a number of differences between the swards which may have influenced foraging behaviour. Table 5.7 gives some sward measurements and descriptions of the two areas during the period January 1986 to February 1988.

Table 5.7 Comparison of the swards in Areas 1 and 2 in winter 1986 and summer 1986/87. Surface characteristics from 100 hits of the sward surface and point quadrat data from 100 points with an inclined point quadrat (see Chapter 2 for methods). The most dominant two species in each sward are given in parentheses below the percentage of the live leaf that they comprised: carpet grass (ca); *paspalum* (pa); couch (co); and leafy forbs (fl).

	Area 1	winter Area 2	Area 1	summer Area 2
surface characteristics				
% live leaf	51	35	74	62
% dead leaf	49	65	0	0
% flower head	0	0	21	34
live leaf height (cm)	3.0	1.8	8.0	8.2
point quadrat data				
number of species	6	7	4	9
number of hits in 100 points	125	123	189	156
% of live leaf 1st ranked	23.9 (ca)	36.8 (ca)	50.3 (pa)	39.6 (ca)
2nd ranked	26.1 (pa)	33.3 (fl)	36.6 (ca)	18.8 (co)
total	50.0	70.1	86.9	58.4

In summer, there were more species and species groups in Area 2 and the two most common species there (carpet and couch grass) made up 58% of the live leaf whereas *P. dilatatum* and carpet grass made up 87% of the live leaf in Area 1. Thus Area 2 had a more diverse sward than Area 1 and there was a greater opportunity for selection there, especially in winter when the amount of green leaf available in Area 2 was lower than Area 1. Sward density was also higher in Area 1 than in Area 2 in summer, but not in winter.

5.3.4 Comparison of kangaroos feeding in two vegetation areas.

The two areas chosen for a comparison of kangaroo feeding behaviour also differed in the biomass of grass available and the diversity of the sward. Area 3 was an area surrounding the dam which was heavily used by kangaroos for feeding. There were tussocks of snow grass interspersed by carpet grass, paspalum and kikuyu. The sward in Area 4 was almost entirely made up of kikuyu and there were no tussock grasses present. Table 5.8 compares some characteristics of the swards of the two areas in four seasons.

The most obvious difference between the two areas is that the live leaf of Area 4 is almost entirely kikuyu. In Area 3 carpet grass is the most common grass, comprising a bit over 50% of the live leaf, with kikuyu the second most abundant species and paspalum the third. Secondly, Area 3 has a 10% covering of snow grass tussocks whereas Area 4 has no tussocks at all. The proportions of dead leaf in the sward surface are similar for both areas in each season, as are the proportions of live leaf, except in summer 1987 when flower heads of carpet grass covered 35% of the sward surface in Area 3. Thus, Area 4 contains an almost single-species sward, with a higher biomass and less obstruction on the sward surface than the sward in Area 3. Table 5.9 compares the foraging behaviour of kangaroos feeding in the two areas in each of four seasons.

Table 5.8 Sward characteristics of Areas 3 and 4 in summer and winter 1986-1987. Point-quadrat information is for 1986 only, although variables were similar within seasons between years. The most dominant two species in each sward are given in parentheses below the percentage of the live-leaf that they comprised: carpet grass (ca); kikuyu (ki); and clover (cl).

	summer 1986	winter 1986	summer 1987	winter 1987
surface characteristics				
% live leaf				
Area 3	83	34	59	45
Area 4	95	34	99	63
% dead				
Area 3	5	66	6	54
Area 4	5	66	1	37
% flower head				
Area 3	11	0	35	0
Area 4	0	0	0	0
live leaf height (cm)				
Area 3	5.9	3.5	8.0	7.1
Area 4	10.5	5.3	14.2	6.1
% live leaf grazed				
Area 3	16.0	18.8	10.9	38.5
Area 4	27.4	11.8	29.6	41.3
point quadrat data				
	summer Area 3	Area 4	winter Area 3	Area 4
number of species	5	2	5	3
% of live leaf:				
dominant	52.6 (ca)	99.3 (ki)	56.8 (ca)	91.4 (ki)
sub-dominant	34.3 (ki)	0.7 (cl)	16.2 (ki)	5.7 (cl)
total	86.9	100.0	73.0	97.1

Table 5.9 A comparison of kangaroos feeding in Areas 3 and 4 in four seasons between summer 1986 and winter 1987. Data from 3-minute observations presented as means (\pm s.e.m). of foraging parameters. Sample sizes given in parentheses for only the first foraging variable. Significant results of two-way analyses of variance given for each foraging variable, with season and area as grouping factors.

		summer 1986	winter 1986	summer 1987	winter 1987
bite/select	Area 3	68.0 \pm 2.5	82.7 \pm 2.6	71.2 \pm 2.9	69.8 \pm 3.8
n		(41)	(33)	(50)	(22)
	Area 4	68.3 \pm 2.6	83.0 \pm 5.5	73.7 \pm 3.1	72.1 \pm 3.9
n		(32)	(5)	(27)	(10)
<i>season: F_{3,212}=3.65 p=0.01</i>					
survey/chew	Area 3	30.9 \pm 2.5	16.3 \pm 2.5	24.9 \pm 2.4	27.5 \pm 3.2
	Area 4	29.3 \pm 2.2	17.0 \pm 5.5	22.5 \pm 2.8	27.2 \pm 4.1
<i>season: F_{3,212}=4.67 p=0.003</i>					
bite rate 1	Area 3	30.2 \pm 1.6	31.6 \pm 1.8	29.1 \pm 1.6	27.9 \pm 1.9
	Area 4	27.9 \pm 1.4	26.9 \pm 1.8	34.5 \pm 1.7	36.2 \pm 2.6
<i>season x area: F_{3,222}=3.56 p=0.01</i>					
bite rate 2	Area 3	48.1 \pm 1.8	38.2 \pm 2.2	42.9 \pm 1.5	41.0 \pm 1.9
	Area 4	48.4 \pm 2.1	33.9 \pm 1.9	52.6 \pm 2.8	54.8 \pm 5.5
<i>season: F_{3,198}=5.63 p=0.001 area: F_{1,198}=5.68 p=0.02</i>					
<i>season x area: F_{3,198}=4.08 p=0.008</i>					
biting	Area 3	0.70 \pm 0.03	0.80 \pm 0.03	0.70 \pm 0.03	0.69 \pm 0.04
ratio	Area 4	0.64 \pm 0.03	0.78 \pm 0.04	0.68 \pm 0.04	0.72 \pm 0.05
bites/patch	Area 3	35.9 \pm 3.9	28.8 \pm 4.3	43.3 \pm 4.1	25.3 \pm 3.2
	Area 4	41.8 \pm 5.9	26.7 \pm 5.9	40.8 \pm 4.8	45.7 \pm 10.2
head-up	Area 3	6.2 \pm 0.4	2.9 \pm 0.3	4.4 \pm 0.4	4.5 \pm 0.5
rate	Area 4	6.3 \pm 0.4	3.8 \pm 0.7	5.7 \pm 0.7	7.1 \pm 1.2
<i>season: F_{3,222}=6.64 p=0.0003 area: F_{1,222}=7.25 p=0.008</i>					
step total	vp3	3.6 \pm 0.8	5.3 \pm 1.0	2.8 \pm 0.4	2.1 \pm 0.5
	vp4	3.5 \pm 0.7	2.2 \pm 0.7	3.1 \pm 0.6	1.8 \pm 0.7

Like wallabies, the kangaroos did not devote more feeding time to biting/selecting or survey/chewing in one area than in another. However, there were considerable differences between these variables in different seasons and years. In 1986 the pasture conditions in summer and winter differed markedly because of the lack of autumn and winter rain. Kangaroos spent more of their feeding time biting and selecting bites in this

winter than in the preceding summer or following seasons. They also spent correspondingly less time surveying whilst foraging in this winter and raised their heads less often to survey. There were no seasonal differences in the interrupted biting rates of kangaroos but the uninterrupted biting rates were lowest in winter 1986. Thus, when green leaf was scarce kangaroos were spending more of their feeding time selecting each bite although the actual number of bites they took during a feeding bout was the same.

The uninterrupted biting rate gives a better indication of the animal's feeding response to sward characteristics because it is independent of the amount of time an animal spends surveying and/or chewing. This rate differed between the two areas in each season except summer 1986, although the direction of the difference changed with season. In winter 1986 biting rates were higher in Area 3 than Area 4 but in the following year biting rates were higher on the kikuyu-only sward of Area 4.

Kangaroos feeding on the kikuyu sward of Area 4 raised their heads more often to survey than did those on Area 3. Kangaroos raised their heads when they were disturbed, when they had collected a suitable mouthful of grass or at regular intervals to survey the surroundings. Since kangaroos feeding in Area 4 did not spend more time surveying, each surveying bout must have been shorter. The lack of cover vegetation for concealment whilst feeding may have required kangaroos to look around more often, but also allowed a quick assessment of the surroundings because their field of view was not obstructed.

The sample size of kangaroos feeding on kikuyu in winter was low because both kangaroos and wallabies appeared to avoid feeding on kikuyu patches in winter, probably because of the large amount of dead material in the sward at this time of year (see Chapter 4). Kikuyu was more affected by frost than other species and died off soon after the first frosts of winter.

There was no difference in the total number of steps taken by kangaroos feeding in the two areas, or between seasons. Other movement characteristics were not normally distributed and could not be analysed by analysis of variance.

5.3.5 Foraging behaviour of kangaroos in relation to sward characteristics

There were a number of sward characteristics that differed between areas, making it difficult to separate which were the most important variables determining the foraging behaviour of animals feeding in each area. The following section describes the relationship between sward characters and foraging behaviour within areas over time.

The vegetation areas that I defined differed in their sward compositions, the availability of cover, distance to cover and the individual kangaroos and wallabies that used those areas. To look at the effects of sward characters alone on foraging behaviour, the foraging behaviours of kangaroos and wallabies were compared in different months in the same vegetation areas. The surface characteristics of the swards were measured

every month by recording the height and identity of one hundred contacts of a measuring pole with the sward surface (see Chapter 2 for methods).

Many of the sward characters were correlated with each other so a stepwise regression analysis was carried out to find out which of the sward variables explained most of the variation in foraging behaviour. The stepwise regression used a forward stepping procedure with a minimum acceptable F value to enter of 4.00 and a minimum F value to remove of 3.90 (BMDP statistical software).

In Area 3, four sward characters were chosen as independent variables: the percentage of the sward surface that was obstructed by grass seed heads and stalks; the percentage of the sward surface occupied by dead vegetation; the percentage of live leaf that had been grazed; and the surface height of the intertussock sward. Means for each foraging variable were calculated for each month where there were more than five biting observations for kangaroos and the regression analysis was carried out on the means for each group. Levene's test for equal variances between groups was satisfied for each variable included below and an analysis of variance confirmed a difference between group means (each group represented a month's data) for each foraging variable.

The relationships between the sward variables are illustrated in Table 5.10 with a correlation matrix. Sward height was positively correlated with proportion of cover by seed heads and showed a weak correlation with the amount of dead vegetation in the sward surface.

Table 5.10 Correlation matrix for the sward variables in Area 3: sward height (HT); percent of sward surface covered by grass seed heads (SE); percentage of dead vegetation in the sward surface (DE); Percentage of live leaves in the sward surface that have been grazed (GR).

	HT	SE	DE
SE	0.87		
DE	-0.61	-0.53	
GR	0.11	0.09	-0.06

Table 5.11 presents the partial correlation coefficients between the foraging variables and the sward characters at the final step of the stepwise regression. Asterisks indicate variables that were included in the regression equation at that step and partial correlation of a variable in the equation is its correlation with the dependent variable after removing the effect of the remaining variables in the equation.

Table 5.11 Partial correlations between each foraging variable for kangaroos and four sward variables in Area 3 for 11 months at the final stage of stepwise regression. Data are from 11 months between 1985 and 1988. Regression equations are given where at least one independent variable was included in the stepping procedure and the F value for that variable to enter the equation is given. Abbreviations in parentheses are those used in the regression equations.

dependent variable		height (HT)	% cover seed heads (SE)	% dead in sward (DE)	% grazed leaf (GR)
bite/select	(BS)	0.30	-0.72*	0.24	0.30
survey/chew	(SC)	-0.08	0.84*	-0.13	-0.31
interrupted bite-rate	(BR1)	-0.08	-0.20	-0.22	0.23
uninterrupted bite-rate	(BR2)	0.26	0.28	-0.56	0.03
chew/bite	(CB)	0.23	0.90*	-0.36	0.23
bites/patch	(BP)	0.28	0.24	-0.51	0.18
head up rate	(HU)	-0.18	0.78*	-0.27	-0.16
step total	(ST)	0.38	0.08	-0.24	0.14
Regression equations		R ²		F to enter	
BS = 80.50 - 0.39 SE		0.52		8.83	
SC = 16.56 + 0.39 SE		0.71		19.93	
CB = 0.36 + 0.01 SE		0.80		32.56	
HU = 3.10 - 0.06 FL		0.59		11.41	

Significant regressions were found between four dependent foraging variables and the independent sward variables. In each case the proportion of the sward surface covered by carpet grass seed heads gave the highest correlation with the foraging variables, and in the stepwise regression it was the only sward variable included in the final equation. Each of the foraging variables, for which there was a significant regression with the proportion seed head cover, were related to the amount of time that kangaroos spent surveying their surroundings whilst feeding. In months when a large proportion of the sward surface was covered with grass seed heads kangaroos spent more foraging time with their heads up surveying, they raised their heads more often and they took more chews per bite than when the sward surface was clear.

The presence of seed heads indicated tall grass, with much long leaf yet despite this feeding rates did not appear to be related to this sward obstruction. The uninterrupted biting rate was more dependent on the amount of dead vegetation in the sward; biting rates were slower when there was more dead leaf and less green leaf in the sward surface.

Area 4 contained an almost single-species sward with no obstruction on the sward surface. It therefore provided a good opportunity to look at the effect of other structural differences between the swards on foraging behaviour. There were five or more observations for eight months in Area 4 and stepwise regression was completed using three sward variables. Carpet grass was very sparse in the kikuyu dominated sward of Area 4 and the proportion of seed head covering the sward surface never exceeded 1% so this variable was excluded. Like the sward in Area 3, in Area 4 there was a negative correlation between sward height and the proportion of dead vegetation in the sward surface.

Table 5.12 presents the partial correlations from the final step of the regression analysis.

Table 5.12 Partial correlations between each foraging variable of kangaroos and four sward variables in Area 4, at the final stage of stepwise regression. Data are from 11 months between 1985 and 1988. Regression equations are given where at least one independent variable was included in the stepping procedure and the F value for that variable to enter the equation is given. Abbreviations in parentheses are those used in the regression equations.

dependent variable		height (HT)	% dead in sward (DE)	% grazed leaf (GR)
bite/select	(BS)	-0.73*	0.60	-0.07
survey/chew	(SC)	0.66*	-0.12	0.00
bite rate 1	(BR1)	0.27	-0.49	-0.56
bite rate 2	(BR2)	0.87*	-0.54	-0.65
chew/bite	(CB)	0.31	0.15	0.34
bites/patch	(BP)	0.42	-0.55	-0.58
head-up rate	(HU)	0.72*	-0.22	-0.17
step total	(ST)	0.22	-0.30	0.23
Regression equations			R ²	F to enter
BS = 89.10 - 1.67 HT			0.54	6.98
SC = 11.44 + 1.42 HT			0.44	4.75
BR2 = 23.79 + 2.31 HT			0.75	18.30
HU = 2.63 + 0.35 HT			0.52	6.60

The height of the intertussock sward explained most of the variation in the foraging variables on its own and the addition of other sward characters did not add significantly to the regression equations. Kangaroos spent less time selecting bites and more time surveying with increasing height of the sward surface they were feeding from. They also fed faster, taking less time to select each bite (faster uninterrupted bite rate), when the sward was tall. Kangaroos raised their heads more frequently when feeding on tall swards, perhaps because they took less time to collect a mouthful of grass; they were biting faster and their bites would have been larger because of the taller grass.

There were sufficient data on kangaroos foraging on burnt blady grass shoots after the 1987 burn to compare only four months (August to November 1987). With a sample size of four, only the biting rates showed a significant correlation with sward characters. In both cases the amount of dead vegetation and bare ground in the sward showed the highest correlation with bite rates, and height and grazed leaf were not included in further steps. Below are the regression equations for the interrupted (BR1) and uninterrupted (BR2) biting rates and the proportion of dead vegetation and bare ground (DB):

$$BR1 = 40.56 - 0.18 DB \quad R^2=0.80$$

$$BR2 = 52.98 - 0.24 DB \quad R^2=0.87$$

In this case the amount of dead material and bare ground in the sward did decline each month over the four months following burning. Thus the biting rates of kangaroos feeding on new shoots increased with time since the burn.

5.3.6 Foraging behaviour of wallabies in relation to sward characteristics

There were sufficient data on wallabies foraging in Area 2 in six months between February and October 1986 for a stepwise regression analysis using the same four independent variables used for kangaroos on Area 3. The relationships between the sward variables are illustrated with a correlation matrix in Table 5.13. The correlations between the sward variables are all in the same direction as those for Area 3 and the values are similar except that the correlation between sward height and the proportion of the surface covered by seed heads is weaker.

Table 5.13 Correlation matrix for the sward variables in Area 3: sward height (HT); percent of sward surface covered by grass seed heads (SE); percentage of dead vegetation in the sward surface (DE); percentage of live leaves in the sward surface that have been grazed (GR).

	HT	SE	DE
SE	0.65		
DE	-0.64	-0.57	
GR	0.36	0.07	0.18

The partial correlation coefficients for each foraging variable with each sward variable are given in Table 5.14. Again, asterisks indicate variables that were included in the regression equation at the final step.

Table 5.14 Partial correlations between each foraging variable of wallabies and four sward variables in Area 2, at the final stage of stepwise regression. Data are from 11 months between 1985 and 1988. Regression equations are given where at least one independent variable was included in the stepping procedure and the F value for that variable to enter the equation is given. Abbreviations in parentheses are those used in the regression equations.

dependent variable		height (HT)	% cover seed heads (SE)	% dead in sward (DE)	% grazed leaf (GR)
bite/select	(BS)	-0.86*	-0.29	0.67	0.10
survey/chew	(SC)	0.82*	0.44	-0.44	-0.01
bite rate 1	(BR1)	-0.57	-0.54	0.32	-0.61
bite rate 2	(BR2)	0.64	-0.01	-0.58	-0.09
chew/bite	(CB)	0.54	0.41	-0.30	0.23
bites/patch	(BP)	0.72*	0.15	0.01	0.67
head up rate	(HU)	0.42	-0.07	-0.73*	0.29
step total	(ST)	-0.96*	0.83	-0.98*	0.99*

Regression equations	R ²	F to enter
BS = 106.8 - 8.88 HT	0.74	11.52
SC = 7.87 HT - 5.62	0.67	8.29
BP = 11.91 + 2.13 HT	0.52	4.3
HU = 8.41 - 0.07 DB	0.53	17.6
ST = 13.01 - 1.25 HT - 0.03 DB - 0.15 G	0.99	55.63

The proportion of time spent biting/selecting bites and the number of steps taken decreased as intertussock-sward height increased, whilst the proportion of time spent head-up, chewing and the number of bites taken per feeding patch decreased. Although the correlation was not significant, wallabies tended to have higher uninterrupted feeding rates when sward height was high, suggesting that wallabies were being less selective when biomass of the sward was high. This is supported by wallabies taking more bites in a patch before moving on when sward surface height was high, and taking fewer steps whilst feeding on tall swards.

The proportion of seed heads covering the sward surface did not contribute to the variation in any of the foraging parameters, which contrasts with the heavy influence this sward character had on kangaroos feeding in Area 3. Wallabies raised their heads from the sward less often when there was more dead material in the sward surface, possibly because they were being more selective when there was little green leaf to choose from.

5.4 Discussion

5.4.1 Foraging on different components of the vegetation

Kangaroos and wallabies both foraged for palatable grass species within mature, unburnt tussocks (Chapter 4), but very few wallabies foraged within them for long enough for me to make a three-minute observation of their behaviour. The lower nitrogen levels and higher fibre levels of grasses growing within tussocks compared to those growing outside may explain this species difference, but so too might the effect of tussock structure on foraging behaviour.

Kangaroos spent more time surveying, and raised their heads to survey more often, when foraging in tussocks than when they foraged in the intertussock sward. Kangaroos were probably not able to see their surroundings as well when they were selecting food items inside tussocks and thus were more vulnerable to surprise by predators than those animals feeding on short grass, which could see around them whilst biting. Wallabies are probably less able to outrun their predators than kangaroos, and are more vulnerable to attack from eagles because of their small size; they appear to rely on being able to see a predator first to escape attack. The potential risks of foraging within tussocks may, therefore, deter wallabies more than kangaroos.

Kangaroos foraging within tussocks took fewer bites per mouthful and per feeding patch than those foraging outside tussocks. They also took almost four times as many chews per bite as those feeding on the shorter intertussock sward and spent more time surveying and chewing, suggesting that they got larger sized bites. One of the reasons for the greater proportion of time spent surveying whilst feeding could have been the extra time needed to manipulate and chew the large mouthfuls of grass gathered when feeding within tussocks. Casual observations of kangaroos selecting grasses hidden inside tussocks supported these conclusions; animals took a few bites and then raised their heads, showing large blades of grass hanging out of their mouth. It could take minutes before the kangaroo had manipulated all the grass into its mouth and during that time it surveyed its surroundings.

Sheep and cattle grazing indigenous hill communities in Scotland showed lower biting rates when feeding on *Nardus* communities, which contained tussocks, than on *Agrostis/Festuca* communities which did not (Armstrong and Hodgson, 1986). In that study intake per bite and total intake were higher for animals feeding on the tussock community than for those feeding on the community without tussocks. It is interesting to note that intake per bite (per unit of live weight) of the sheep was almost twice that of the cattle, and that sheep were able to maintain higher levels of digestibility than cattle (*ibid*). The width of the incisor arcade appears to affect the degree to which animals can be selective in choosing food items (Jarman 1974; Gordon and Illius, 1988; Janis, in press),

and the proportionately narrower muzzles of sheep probably enhanced their ability to select grasses within tussocks.

Prior to European settlement the grasslands on the east coast of Australia and in Tasmania were characterised by tussock-forming grasses, particularly kangaroo grass *Themeda triandra* and snow grass *Poa labillardieri*, interspersed with other tall perennials and forbs (Norton, 1971). The relatively narrow palate of macropods compared to ungulates of a similar size (Janis, in press) may result from the benefit of having a small incisor arcade when foraging within tussocks for young green leaf. Tussock-forming grasses are much less common in the grasslands of Africa, where mat-forming grasses may encourage selection for broader muzzles amongst grazers (Jarman, 1974, pers.comm.).

Kangaroos feeding on burned vegetation components had uninterrupted biting rates 30-40% higher on burnt tussocks and blady shoots than on unburned ones but the same as on unburned, intertussock swards. The removal of dead, moribund leaves by burning, exposed green leaves which were then easier for macropods to pick out. Within days of burning new shoots began to appear within tussocks and on patches of bare ground. Kangaroos and wallabies seemed to find it easier toprehend the tall, upright shoots than the small leaves in the short swards that characterized the intertussock sward in winter. Experiments with sheep feeding on artificial swards of varying height and density suggest that for a given biomass, animals have a higher intake on tall sparse swards than on short dense ones (Black and Kenney, 1984). In that study, the best predictor of pasture intake rate was mass per area effectively covered by one bite.

Without knowing the comparative bite size of kangaroos feeding on shoots produced after burning and those feeding on the intertussock sward it is not possible to calculate the actual intake of nutrients and energy by kangaroos feeding on the two components. Whilst the quality of grasses after burning is similar to, though usually lower than, grasses in the intertussock sward (Chapter 2), biting rates are similar on both components and bite size may be greater for animals feeding on tall burnt shoots. It is possible, therefore, that rates of nutrient intake on burnt patches are equal to, if not greater than, those on the intertussock sward. This perhaps explains why kangaroos continue to feed in burnt areas, even when quality of the burnt grasses falls below that of unburnt species (Chapter 4).

The greater movement of kangaroos feeding on shoots of tussocks or blady grass after burning are probably explained by the sparse distribution of shoots after burning. Biomass per unit area was also much lower on burnt areas such that feeding patches were probably depleted more quickly than in the intertussock sward. The fewer number of bites taken in each patch in burnt areas also suggests this.

The comparison of wallabies feeding on burnt tussocks and the intertussock sward suggested wallabies could also achieve larger bite size when foraging on burnt tussocks; they took fewer bites per mouthful and needed more chews per bite for each mouthful. Being able to collect a mouthful of food very quickly (they also had higher uninterrupted biting rates on burnt tussocks) may have allowed them to spend more time surveying, although the longer time spent surveying may simply reflect the greater amount of chewing time required per mouthful. Ferguson *et al.*, 1988 have suggested that because caribou are more vulnerable to predation on the mainland than on an island, they select forbs on the mainland, which provide a large bite size and therefore allow them more time to watch for predators.

If foraging on burnt tussocks allows wallabies more time to survey why do wallabies use burnt areas less than unburnt areas? (see Chapter 4). Although intake rates may have been higher for wallabies foraging on burnt tussocks, bite quality was probably not. Being small in body size, diet quality is relatively more important for small animals than large ones (Bell, 1970; Jarman, 1974) and perhaps in winter, when quality of grasses is low (Chapter 2), diet quality is more important to wallabies than the amount of time spent looking for predators. The burnt areas were also devoid of cover whereas before the burn plenty of cover was available. This lack of cover may have made the wallabies more nervous leading to their longer survey time and increased rate of surveying. However, as pointed out in Chapter 4, cover vegetation can also conceal a predator's approach and so does not necessarily equate with safety.

5.4.2 The effect of sward characteristics on the foraging behaviour of wallabies

In summer, the swards in Areas 1 and 2 were the same height and therefore bite sizes of wallabies feeding in the two areas were probably similar. If the bite sizes of macropods are related to sward structure in the same way as sheep bite sizes are, then the greater density of vegetation in Area 1 (as measured by the number of hits in 100 points in a point quadrat analysis) may have led to a larger bite size in this area (Jamieson and Hodgson, 1979; Hodgson, 1981; Black and Kenney, 1984; Armstrong and Hodgson, 1986). If this were the case a slower biting rate would be expected in Area 1 whereas the reverse was found.

The lower uninterrupted biting rate in Area 2 was probably due to the wallabies spending more time selecting each bite. The diversity of plants in Area 1 declined in summer due to good growth of *Paspalum* which came to dominate the sward. *Paspalum* is a species highly favoured by wallabies (see Chapter 2), and its abundance would have made selection easier, leading to faster biting rates. The proportion of the sward surface that was covered with grass seed heads was also higher on vegetation area 2; the seed heads made selection within the sward more difficult as animals had to push through this layer to feed on the grass leaf below.

In winter the density of the swards and the number of species and species groups represented were approximately the same in each area. There was a greater amount of dead material in the sward in Area 2 and the sward was also shorter there, suggesting a lower total green biomass. The drought of 1986 was at its height in winter and the amount of green leaf available in all swards was much lower than normal (see Chapter 2). The wallabies responded to this decline by decreasing their feeding rates and becoming more selective; there was a seasonal difference in both feeding rates in Area 1 but not in Area 2. It may be that the slow feeding rates seen in Area 2 represented the lower limit of feeding rates; as herbivores become more selective their rate of biomass ingestion declines and a point will be reached at which the increase in food quality with selection no longer compensates for the decline in biomass intake.

The partial correlation analysis did not give any strong correlations between feeding rates and sward variables, although height did appear to be more important than other variables. The correlation between height and the uninterrupted bite rate was positive and not negative as has been found in many ruminant studies: calves and lambs, Jamieson and Hodgson, 1979, Hodgson, 1981; red-deer, Loudon *et al.*, 1984. A negative relationship between sward height and biting rate was also found for Bennett's wallabies (Clarke and Loudon, 1985). The study of Bennett's wallabies included a larger range of sward heights (2-7 cm compared to 2-5 cm in this study), and the taller swards included a mixture of tussock grasses and intertussock grasses. The different relationship between biting rates at different sward heights found in that study compared to this may therefore relate to the differing foraging tactics of wallabies feeding in tussocks and out of tussocks.

A greater amount of time spent surveying/chewing, a large number of bites per patch and a smaller rate of movement with increasing sward height all suggest that wallabies on tall swards found more to eat, needed less time to select each bite and took larger mouthfuls of grass. Presumably at much taller sward heights their rate of biting would have declined again as they found it increasingly difficult toprehend leaves of long grasses (as occurs when they are feeding in tussocks, for example). When the proportion of dead leaf in the sward surface was high wallabies raised their head from the sward less often, and spent more time selecting each bite. Thus, whilst ruminants appear to respond to declining pasture biomass by increasing biting rates and grazing times (Arnold, 1964; Allden and Whittaker, 1970), wallabies also increase grazing times but reduce biting rates and become more selective in their foraging.

5.4.3 The effect of sward characteristics on the foraging behaviour of kangaroos

In the comparison of kangaroos foraging in Areas 3 and 4 there were more seasonal differences in their foraging and surveying behaviour than there were inter-area differences. Differences in proportion of time spent surveying suggested that it was not so much changes in danger that caused animals to survey more or less, but that differences in the amount of time required for biting and selecting bites changed with availability of food items and that biting and selecting took precedence over surveying.

The proportion of foraging time that kangaroos spent biting/selecting bites was highest in winter 1986, at the height of the drought, whilst the proportion of time spent surveying was lowest at this time. Biting/selecting time did not remain high in the following summer, despite the kangaroos' continuing poor condition following the drought (Chapter 2). In that summer live leaf height and percentage of greenness of the swards were very high, and kangaroos probably required little search time per bite and had a high intake per bite as a result.

Kangaroos in Area 4 surveyed more often, but for shorter periods, than those in Area 3. The differences could be due to differences in bite size which allowed kangaroos feeding in Area 4 to collect a mouthful of grass more quickly. However, the differences in survey time were not most marked in summer 1986 when the differences in sward height and greenness were greatest. As with the tussock-intertussock comparison, it is difficult to tease apart the possible effects of danger (there was no cover vegetation in Area 4) and bite size on biting and surveying behaviour because I was not able to measure either variable.

The feeding rates of kangaroos in the two areas varied with season and area, and differences were not consistent across seasons. In summer 1986 feeding rates were almost the same in the two areas. In winter 1986 feeding rates were higher in Area 3 but in the following two seasons they were higher in Area 4. The faster biting rates on the single-species kikuyu sward in 1987 could have been due to the ease of selection there; the amount of green leaf was also higher on this sward in 1987 and there were no grass seed heads covering the kikuyu sward surface as were found on the swards dominated by carpet grass.

Sward height and biomass also contribute to bite size of ruminant herbivores and when bite size is large feeding rates are often reduced (Arnold 1964; Allden and Whittaker, 1970; Hodgson, 1982). Sward height was very low in Area 3 in winter 1986, which may be why in that season biting rates were faster on the carpet grass sward of Area 3 compared to the kikuyu sward of Area 4.

The comparisons between the areas suggested that sward height played an important role in determining foraging behaviour of kangaroos foraging in Area 4, through its effects on potential biting rates and bite size. On the more diverse sward in Area 3 the presence of grass seed heads appeared to be important in the summer of 1987 in

increasing the amount of time kangaroos spent selecting each bite. Some of these results were confirmed by the partial correlation and stepwise regression analyses.

In Area 3 kangaroos increased their survey time, number of chews per bite and head-up rate with increasing proportion of the grass surface covered by seed heads. As before, at least two possible explanations for the relationship exist. Kangaroos may feel more vulnerable to surprise attack from predators when foraging with their muzzles buried in a layer of grass seed heads, and therefore survey more frequently and for longer. Alternatively, the positive correlation between sward height and seed-head cover could mean that kangaroos foraging in swards with a large covering of seed heads are also getting larger bites and therefore need to raise their heads more frequently to manipulate and chew each mouthful. The strong positive correlation between seed-head cover and chews/bite suggest that the latter explanation is more likely.

Surprisingly, kangaroo feeding rates were poorly correlated with the proportion of seed head cover in Area 3 which I would have expected if the seed heads made selection of grass in the sward underneath difficult. The uninterrupted biting rate was more highly correlated with the proportion of dead leaf in the sward surface; as the proportion of dead leaf in the sward surface increased, biting rate declined, presumably because of the greater search time required to find each bite of green leaf.

In Area 4 as sward height increased kangaroos spent less time biting/selecting, more time surveying/chewing, took bites faster during uninterrupted biting and raised their heads from the sward more frequently. Like wallabies foraging in Area 2, kangaroos in Area 4 (and possibly area 3) responded to declining sward biomass by taking more time to select each bite, presumably in an attempt to maintain diet quality. I expect that over a wider range of sward heights biting rates would have eventually declined with increasing sward height, as animals required more time to manipulate each bite and mouthful.

When kangaroos were foraging in areas that had been burnt, their rates of biting increased with decreasing proportions of bare ground. Thus, for at least the first few months after burning, kangaroos had faster biting rates as more new shoots emerged in the sward. Again, the implication is that as more green leaf was available for selection, kangaroos spent less time looking for each bite.

5.4.4 Sward characteristics and herbage intake: a comparison with ruminant species

There are many differences, between the nature of this study and those of domestic ruminant species, which are relevant to any comparison between the two. Firstly, the studies relating feeding behaviour to changes in sward height or biomass have generally involved sheep or cattle grazing relatively uniform swards, of low diversity, with sward height being reduced over a relatively short period of time e.g. Le Du *et al.*, 1970; Alden and Whittaker, 1970; Jamieson and Hodgson, 1979; Hodgson, 1981. In this study, and in many involving free-ranging wild herbivores, changes in pasture height and biomass

occurred over the course of different seasons and were associated with quite large changes in pasture quality (see Chapter 2). The inclusions of large amounts of dead leaf in the sward and the presence of obstructions such as grass seed heads also contributed to the diversity and distribution of food items in the sward.

Even with little variation in the quality of food available in a sward (in grazing trials for example), intake rate at a given herbage mass can still vary greatly depending on the spatial organization of the herbage (Ungar and Noy-Meir, 1988). For example, herbage mass could decline as a result of a decline in bulk density where as increase in bite size may be an alternative means of maintaining intake. Where changes in sward height are associated with other sward changes relating to the quality and dispersion of food items, animals could increase feeding rates in response to declining sward biomass, but in doing so would risk a decline in diet quality. Alternatively, they may try to maintain or improve diet quality by spending more time selecting each bite. Presumably the importance of diet quality to an animal, and the relative values for grass quality and abundance, will determine which strategy an animal adopts.

The two strategies approximate to the strategies of selective and generalist herbivores (Arnold 1987) although there appears to be a continuum of strategies in between, including facultative changes from generalist to selectivist with season e.g. white-tailed deer (Schwartz and Ellis, 1981). It appears that during the course of radiation of antelopes (and perhaps macropods; Jarman, 1984), from medium sized ancestors, changes in body size, gut morphology, mouth parts and social organization have enabled exploitation of abundant, but uniformly poor-quality grasses by unselective, bulk feeders, and highly dispersed fruits and browse of high quality by selective feeders (Jarman, 1974). Natural selection has continued to modify herbivores, such that at opposite ends of the spectrum large generalist herbivores may be unable to be selective in a heterogenous environment because of their broad mouthparts whilst small selective feeders may not be able to maintain sufficient rates of intake of nutrients on poor quality, continuous pastures. Sheep should fall into the same selective browser category as deer on the basis of their size, but Schwartz and Ellis (1981) suggest that human selection has made them generalists despite their relatively small size. However, sheep have been shown to be highly selective on mixed pastures with a very low biomass (Broome and Arnold, 1986) but relatively unselective when there is little difference between the acceptability of pasture components (Milne *et al.*, 1981).

The narrower muzzle of macropods, compared to ruminants of a similar body weight (Janis, in press), may have arisen because of their more selective mode of foraging. The requirement for selective mouthparts of macropods probably does not stem from a greater nutrient requirement; marsupials have a lower metabolic rate than eutherians and therefore have lower energy requirements per unit of body weight. In addition macropods are better able to utilize low quality forage than sheep (Hume, 1982). Instead, I suggest

that the unusual distribution of Australian native grasses into separate tussocks, and the necessity of a narrow muzzle to forage within tussocks for green leaves and shoots, has encouraged the selection of a narrow muzzle in macropod grazers. Macropods also use their forepaws to make foraging within tussocks easier (Jarman, 1984; Janis, in press, pers. obs.).

To find out whether macropods are just following the best strategy under the conditions prevailing at Wallaby Creek, or whether they are restrained by some evolutionary difference to being selective feeders, it would be necessary to conduct grazing trials for macropods, under similar conditions to the domestic ruminant studies. In a grazing trial using red and western grey kangaroos grazing on arid-zone pasture neither species showed a difference in biting rates or stepping rates with declining pasture biomass (Short, 1986), although the number of harvesting bites did increase with declining biomass. It seems likely that macropods, like many ruminant species, can have differing responses to declines in forage availability, depending on the uniformity and abundance of pasture on offer.

Kangaroos and wallabies at Wallaby Creek use different components of the vegetation, have different diets and select different feeding site locations. The influence of diet selection and sward characteristics on foraging behaviour described in this chapter suggest that differences in foraging behaviour, and particularly movement during feeding, should be expected between the species. The comparative foraging behaviour of the two species will be considered in the next chapter.