

CHAPTER 6

Comparison of the foraging behaviour of kangaroos and wallabies and their population classes

6.1 Introduction

Eastern grey kangaroos and red-necked wallabies differ markedly in body size and in the extent to which they form groups. Jarman (1974) has argued that amongst African antelopes there is a general relationship between feeding style and body size, and that the range of feeding styles shown by different species relates to their selecting food items of a specific quality and dispersion. He further argues that feeding style is one of the important determinants of group size, either directly through competition for food items, or indirectly through the anti-predator behaviour required by the location of their preferred food items. Jarman (1984) has suggested that similar relationships may exist for macropod marsupials, a group which also shows a range of body sizes, feeding styles, habitat uses and grouping behaviours, but a range that is smaller than that shown by bovids.

In Chapter 4 I discussed the differences in the diets and chosen feeding sites of kangaroos and wallabies, concluding that the diets of kangaroos included more abundant, low quality food items compared to the diet of wallabies and that wallabies were found in feeding sites which were characterized by inter-tussock species that were less common in the study site. Although I have not actually measured the dispersion of food items used by kangaroos and wallabies it seems likely that differences in feeding styles between the species should^{arise} as a result of them exploiting different components of their foraging environment.

In Chapter 5 I discussed ways in which herbivores are able to alter their rate of intake on a sward by behavioural means. These means include changing the ratio of time spent biting/selecting items in the sward to the time spent chewing and surveying, changing bite size and biting rates, and changing total foraging times. Varying rates of intake may be another way, besides diet selection, whereby animals of different body size can meet their differing energy requirements.

The ratio of time that animals spend with their heads down biting and selecting bites, to the time that they spend with their heads up surveying and chewing mouthfuls of vegetation, depends on a number of factors including: the energy requirements of the animal; food availability and its effect on foraging efficiency; the risk of the animal from predators and its efficiency of detecting predators by surveying; and the need for the animal to survey in order to maintain contact with other group members. Body size has an effect on a number of these factors and there are adaptive reasons why large animals should spend less time surveying, and more time foraging than small animals:

1. Kangaroos are larger than wallabies so that the adults at least should have less to fear from dingoes, eagles and other predators. If kangaroos are less vulnerable to predators than wallabies, they would not need to be as vigilant as wallabies. The reduced vigilance may take the form of less time spent surveying, shorter surveying bouts or a reduced frequency of surveying.
2. Kangaroos have higher absolute energy requirements than wallabies because of their larger body size (Bell, 1970; Jarman 1974; Janis 1976), and because their diet is of a lower quality (see Chapter 4), they must forage for longer or faster than wallabies; the mouthparts of large macropods are relatively narrow (Janis, in press) and it is unlikely that differences in bite size alone could meet the higher absolute energy requirements of kangaroos.
3. Kangaroos are found in larger groups than wallabies, and, since group size and individual surveying time tend to be negatively correlated (Jarman, 1987; Southwell, 1981; but see also Chapter 7), kangaroos should spend less time surveying than wallabies. However, animals in large social groups may also need to survey more frequently to enable group cohesion to be maintained or they may be more likely to raise their head in response to a neighbour's behaviour (Underwood, 1982a). Thus the effects of group size on surveying behaviour may be complex, and separation of the time spent surveying the environment from the time spent looking at other group members may be necessary in order to sort out which plays the more important role.

The above reasons for predicting greater surveying times for larger animals are not exclusive and are likely to operate in conjunction with one another. If there is a difference in surveying behaviour of kangaroos and wallabies in the expected direction then by comparing the response at different resource levels and different risk levels it may be possible to discover which factor plays the most important role.

The ratio of biting/selecting time to surveying time during feeding bouts should be based on the relative costs and benefits of those behaviours to individuals. Individuals, whose survival or reproductive success depend primarily on nutrient intake, may place priority on foraging time whilst those whose greatest risks are from predation may place more importance on the time they have available to survey for predators. Thus, the motive determining surveying time may differ between animals i.e. whether the time devoted to surveying is decided by the animal's need to survey the environment or whether the time required to forage takes priority, and surveying is done in the time that remains. With changing seasonal abundance of foods and corresponding changes in animal body conditions, we might expect that the balance of costs and benefits of surveying behaviour will change over time and in different habitats. The suggestion that animals can balance the relative costs and benefits of foraging have been examined experimentally with fish, with both positive (Sih, 1980, Holbrook and Schmitt, 1988) and negative (Cerri and Fraser, 1983) results.

Surveying or vigilance behaviour may serve other purposes beside the detection of predators. Underwood (1982b) showed that indices of foraging efficiency of small antelopes correlated with their rate of surveying, suggesting that scanning may form a part of foraging behaviour by acting as a less energetically costly form of searching than movement (*ibid*). While the above might hold for selective browsers, the preferred food items of selective grazers like kangaroos and wallabies are likely to be better hidden and perhaps distributed less patchily than browse making surveying a less useful method of searching. Alternatively animals may survey to locate other animals that have found suitable feeding sites, before going to join them. Kangaroos in the cafeteria trial did appear to follow the lead of one kangaroo in choosing where to feed although they may have followed to maintain group cohesion rather than to find better feeding sites (see section 4.4).

Differences in foraging behaviour between the sexes of sexually dimorphic species may also be predicted on the basis of body size. When reproductive success of males is determined by fighting ability, the traits which favour fighting ability, such as large body size and muscle bulk, may have heavy energetic costs (Clutton-Brock *et al.*, 1982a). Male kangaroos and wallabies eventually achieve body weights almost double those achieved by adult females and, unlike females, continue growing throughout their adult life (Jarman, 1983). In addition to their high basal metabolic costs due to a large body size, large males have additional energy costs associated with movements to locate females and interactions with other males to maintain their position in the dominance hierarchy. The high energy requirements of large males in particular may require them to select a different diet, feed for longer, or have a higher rate of food intake than females.

Some female mammals may also have additional energetic costs, above basal metabolic requirements, associated with pregnancy and lactation (Hanwell and Peaker, 1977). Such costs can account for increases in their daily feeding times and feeding rates (Milne *et al.*, 1981; Loudon and Kay, 1984; Clutton-Brock *et al.*, 1982b; Clarke and Loudon, 1985). The timing and duration of the energetic costs of lactation differ for marsupials compared to eutherians because the energy costs of pregnancy are very small for marsupials, and the energetic costs of marsupial milk production change with the age of the pouch-young (Green, 1984). Thus, there may be differences between females in their energetic requirements, and the differences between the energetic requirements, and hence foraging behaviours, of males and females are expected to be at their greatest between large males and females that are not lactating.

In Chapter 4 I found little evidence for a difference between the sexes in diet or feeding site location. I suggested that male and female macropods may be constrained to utilize very similar diets because of their tendency to associate with one another in open-membership, mixed-sex groups (Jarman and Coulson, in press). However, there is some scope for males and females to alter their foraging behaviour and thereby their rate of food intake, even when feeding in the same location (see Chapter 5). In this chapter I will investigate to what extent males and females differ in their foraging behaviour, and when sample sizes allow, compare different size classes of males, and females belonging to different reproductive classes.

Body size may also affect the risk of each sex from predators. The heavy shoulders, and large forepaws and claws, that large male kangaroos and wallabies develop in order to succeed in intra-sexual competition (Jarman, 1983) may also protect them from attack by predators. There are many accounts of large male kangaroos drowning dogs after they have been chased into dams or creeks; during the course of my study, one of the property owners at Wallaby Creek watched the alpha male eastern grey kangaroo try to drown his cattle dog (G. Kennedy, pers. comm.). Dingo predation can have a considerable effect on the reproductive success of female eastern grey kangaroos and red-necked wallabies in this study area, in particular through their impact on the survival of young-at-foot (Stuart-Dick, 1987; Stuart-Dick and Higginbottom, in press). Females that guard their young-at-foot may increase the chances of their young surviving but males will gain little benefit from guarding young-at-foot because they cannot be certain of paternity, especially after a period of delayed implantation and a long pouch-life. For these reasons, I predict females with newly emerged young-at-foot would profit more from vigilance behaviour than males and females with pouch-young. Females with large pouch-young may be vulnerable themselves because of the extra weight they have to carry in their pouch when fleeing from a predator.

Because males are capable of engendering many more progeny than are females, their reproductive success is usually limited by the number of breeding females to which they can gain access (Clutton-Brock *et al.*, 1982a). This leads males into direct competition with other males for access to females and also requires them to spend time looking for, and following, females coming into oestrus. These disruptions to the male's routine may bring about changes in their foraging behaviour, and eventually in their condition. Thus, there is a conflict of interests for large males; to spend time looking for and courting females, and to spend time foraging to maintain their body condition and hierarchical status. Instead of trying to maximise both behaviours simultaneously, males may not forage efficiently every day. They may have periods (hours or days) where they concentrate on feeding, perhaps separating themselves from other animals to do so, and other periods when feeding takes second place to interacting with other males or females.

In this chapter I will first compare the foraging activities and movements of a subset of the eastern grey kangaroo and red-necked wallaby populations, which I observed regularly over an 18-month period. The emphasis in the first section will not be on how kangaroos and wallabies, males and females, respond to the same vegetation and sward types, but how their foraging behaviours are affected by the differences in their habitat use and diet. In the second section I will compare details of foraging behaviour and feeding rates of the two species feeding on the same sward types, to see if there are consistent differences in the way in which the species use the same sward.

6.2 Methods

The results of two types of observation are presented in this chapter; 3-minute observations (section 6.2.11) and 15-minute continuous watches (sections 6.2.1 to 6.2.10). The methods used in recording the 3-minute observations are described in section 2.4.2. The description of the variables calculated from the 3-minute observations, and which are used in this chapter, are given in Table 5.1. This chapter includes 3-minute observations recorded following 15-minute observations, those recorded for animals feeding in Areas 1 to 4, and those made on searches between August 1987 and February 1988.

The 15-minute observations were made between January 1986 and July 1987, on consistent subsets of the kangaroo and wallaby populations. The subsets were chosen to represent each population class (except young-at-foot) equally in number. The subsets included only animals that were approachable and not disturbed by close observation. When an animal in the subset died or dispersed I replaced it with another of the same population class. Each of the animals in the chosen sub-sets was watched continuously for a 15-minute period in the morning and afternoon at some time during two months. The schedule for the observations is described in more detail in section 2.4.1. After experimenting with watches of different lengths 15 minutes was chosen because it was long enough to give a representative picture of how animals moved whilst feeding, but it was not so long that there were many major changes between resting and feeding activities or between feeding sites. Each session I went out with a list of animals that I wanted to observe, and animals, when found, were watched regardless of whether they were feeding or not.

During the fifteen minutes each change in activity and posture was recorded to the nearest second, as were each movement, change in nearest neighbour or group size, displacement by other group members and the total distance moved over the 15-minute period. The categories and states of behaviour that I used to record behaviour and posture are given in Table 2.3. The variables that were calculated for each observation for use in this chapter are described in Table 6.1. Note that if animals were not biting/selecting or surveying they were lying down. The sum of the proportions of time spent in these three activities may exceed 100% if the animal spent some time browsing since animals could bite, select and survey at the same time when engaged in this activity.

Table 6.1 Description of the variables, calculated from 15-minute continuous-observations, which are used in this chapter.

<i>Bit/select time</i>	Proportion of total time spent with head down, biting or selecting bites.
<i>Survey time</i>	Proportion of time with head up, surveying when not lying down; survey chewing included and browsing with head up included.
<i>Interact time</i>	Proportion of time spent interacting with other group members.
<i>Not alert</i>	Proportion of Survey time during which the animal was not alert (alert: ears and eyes focussed on some source of disturbance).
<i>Alert outside</i>	Proportion of Survey time during which <i>the group</i> the animal was alert to a disturbance outside the group, excluding that caused by myself or other co-workers.
<i>Alert inside</i>	Proportion of Survey time during which <i>the group</i> which the animal was alert to another group member. Those in group size 1 were excluded from analyses.
<i>Crouched</i>	Proportion of Survey time during which the animal was in a crouched position.
<i>Bent</i> <i>Upright</i>	Proportion of Survey time during which the animal was in a bent position. Proportion of Survey time during which the animal was in an upright position.
<i>Head-up rate</i>	Number of times per minute that the animal lifted its head from the sward whilst feeding.
<i>Mean surveying-bout</i>	Mean duration for which an animal kept its head up, surveying, after lifting its head from the sward.
<i>Displaced by another</i>	Number of times in 15 minutes that the focal animal was displaced from a feeding patch by another group member. Those animals alone for some or all of the watch were excluded.
<i>Displaced another</i>	Number of times in fifteen minutes that an animal displaced the focal animal from a feeding patch. Those animals alone for some or all of the watch are excluded.

6.3 Results

6.3.1 Activity from 15-minute observations

The proportions of time that kangaroos and wallabies spent biting/selecting bites are compared for the five seasons in Figure 6.1a. There was a distinct seasonal difference ($F_{4,584}=12.14$, $p<0.0001$: B-F), both species showing a high proportion of time biting in the first post-burn season (at the height of the 1986 drought) and also in the following summer. Kangaroos spent a greater proportion of their time biting/selecting than did wallabies ($F_{1,586}=9.59$, $p<0.01$: B-F), this difference being seen in every season except post-burn in 1986.

The proportions of time that animals spent surveying are compared in Figure 6.1b. The proportions followed the reverse seasonal pattern to biting, being higher in the post-burn months and the following summer than in other seasons. The seasonal differences were again significant ($F_{4,516}=6.05$, $p<0.0001$: B-F). Wallabies spent more time surveying than kangaroos ($F_{1,517}=114.42$, $p<0.0001$: B-F), the difference being greater in those months when total surveying time was highest.

There was no difference between the sexes, of either kangaroos or wallabies, in the amount of time spent biting and selecting bites. Table 6.2 illustrates the how close the male and female values for feeding time were and the results of a two-way analysis of variance with sex and season as grouping factors.

Table 6.2 Comparison of the proportion of time male and female kangaroos and wallabies spent biting/selecting bites in morning and afternoon time periods. Seasons are: Summer 1986, Jan-Feb; Pre-burn 1986, Mar-Jun; Post-burn 1986, Jul-Oct; Summer 1987, Nov-Feb; Pre-burn 1987, Mar-Jun. The number of observations in each group are given in parentheses.

	Summer 1986	Pre-burn 1986	Post-burn 1986	Summer 1987	Pre-burn 1987
kangaroo					
male	58.1±6.1	62.2±4.9	66.2±6.1	75.7±8.3	54.3±4.6
(n)	(15)	(35)	(32)	(6)	(49)
female	60.8±5.4	62.9±3.1	70.3±3.4	68.3±2.9	55.3±3.1
(n)	(36)	(51)	(60)	(41)	(72)
sex: $F_{1,387}=0.0$, $p=0.95$					
wallaby					
male	51.8±5.0	48.4±6.0	73.5±6.0	63.5±4.0	54.4±5.0
(n)	(19)	(30)	(21)	(15)	(32)
female	49.7±5.1	50.2±4.3	68.9±4.5	67.3±4.2	49.5±3.9
(n)	(29)	(47)	(41)	(28)	(53)
sex: $F_{1,305}=0.1$, $p=0.74$					

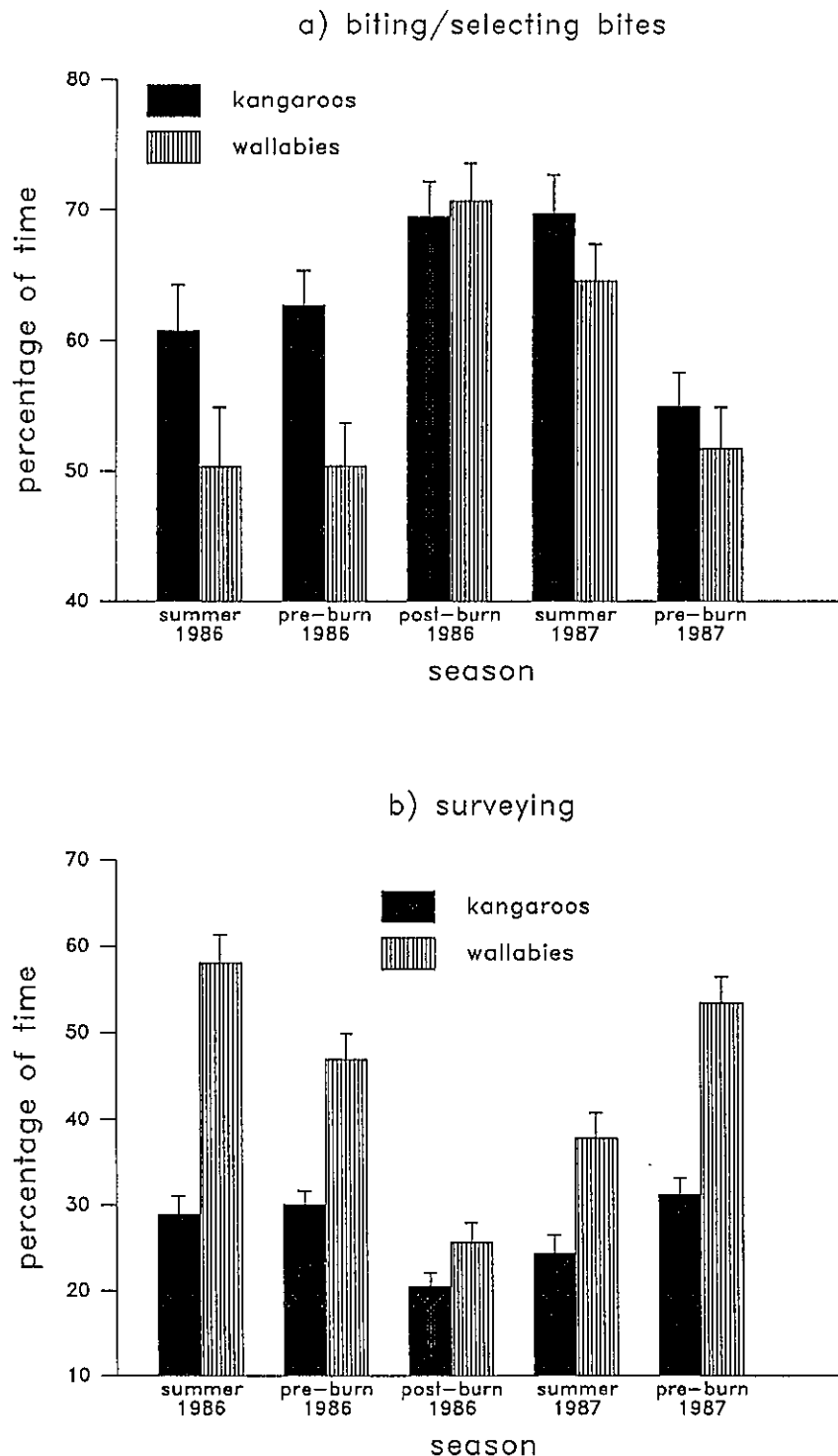


Figure 6.1 Mean (+ s.e.m.) percentages of time that kangaroos and wallabies spent a) biting or selecting bites and b) surveying, in each of five seasons between January 1986 and July 1987 (morning and afternoon time periods are combined). Data are based on 15-minute continuous observations of animals, with approximately four observations per individual per season. The number of observations per season are given in Table 6.1. The sum of the times spent biting or selecting bites and surveying may exceed 100% if animals spent time browsing with their heads up.

The values for the sexes were remarkably similar and did not show values for one sex consistently higher than the other. There were also no differences in the proportions of time spent biting/selecting bites between large males, small males, females with pouch-young and females with young-at-foot. It is perhaps surprising that males, given their relatively large body size, did not spend more time feeding than females. Although males did not appear to choose higher quality food items to feed on than females (see Chapter 4) males could have been feeding faster than female; this is investigated in section 6.11.

6.3.2 Levels of alertness from 15-minute observations

The time spent surveying described in section 6.3.1 was divided into four categories of alertness; whether the animal was not alert, alert to another group member, alert to some distraction outside of the group and alert to myself or one of my co-workers. The proportion of time spent alert to me (i.e. obviously distracted from its current activity by my presence) was zero or very small in most cases, and if an animal continued to be alert to my presence for more than a minute the watch was abandoned. For this reason the proportion of time spent alert to myself was not analysed.

The mean percentages of survey-time that animals spent in the other three alertness states were calculated, and compared between the species and the seasons using a two-way analysis of variance (Table 6.3). The variable Alert in Group was not normally distributed because the majority of animals watched did not spend any time alert inside the group. A mean value would be meaningless and the medians for each group were all zero. Therefore, for this variable the percentages of animals observed that did spend some time alert to other group members are given and the variation in frequencies is explained by the best fitting log-linear model.

Table 6.3. Mean percentage ($\pm$ s.e.m.) of survey time (standing only) during which kangaroos and wallabies were "not alert" and "alert outside the group", in five different seasons. Seasons as for table 6.2. Brown-Forsythe Analysis of Variance used for "not alert" and "alert outside the group". The percentages of animals observed that spent some time "alert inside the group" are presented and a 3-way contingency model is fitted to the frequency data. The number of observations for each group is given in parentheses.

Variable	Summer 1986	Pre-burn 1986	Post-burn 1986	Summer 1987	Pre-burn 1987
Not Alert					
Kangaroos	69.5 $\pm$ 3.6 (51)	62.7 $\pm$ 2.8 (86)	45.7 $\pm$ 3.0 (92)	32.3 $\pm$ 3.7 (47)	27.9 $\pm$ 2.8 (121)
Wallabies	54.5 $\pm$ 3.9 (48)	44.5 $\pm$ 3.1 (77)	25.2 $\pm$ 3.1 (62)	12.4 $\pm$ 3.3 (43)	26.7 $\pm$ 3.5 (85)
Species: $F_{1,554}=51.10$, $p<0.0001$ Season: $F_{4,551}=53.53$, $p<0.0001$					
Alert Outside the Group					
Kangaroos	21.1 $\pm$ 3.1 (47)	30.7 $\pm$ 2.8 (89)	46.3 $\pm$ 3.1 (94)	60.7 $\pm$ 3.7 (48)	60.1 $\pm$ 3.1 (130)
Wallabies	42.2 $\pm$ 3.0 (47)	51.0 $\pm$ 3.1 (78)	69.3 $\pm$ 3.3 (63)	83.7 $\pm$ 3.3 (44)	70.1 $\pm$ 3.4 (97)
Species: $F_{1,575}=87.32$, $p<0.0001$ Season: $F_{4,572}=52.46$, $p<0.0001$					
Alert Inside the group(% of animals that spent some time alert in group)					
Kangaroos	43.1 (47)	41.0 (89)	40.0 (94)	35.2 (48)	49.2 (130)
Wallabies	14.0 (47)	24.3 (78)	34.5 (63)	33.3 (44)	25.0 (97)
Three-way log-linear model: species(S) x season(M) x alert in(A): best model M, AS df=12 G=14.06 p=0.30					

Kangaroos spent less time alert than wallabies with interspecific differences being up to 15-20% for all seasons except pre-burn 1987. The percentage of survey time during animals were Not Alert declined dramatically over the course of five seasons.

The proportion of animals watched which spent some time alert to other group members was greater for kangaroos than wallabies. Animals which were alone for part or all of the observation were excluded from the analysis but no further adjustment was made for group size differences. It seemed possible that the smaller typical group size of wallabies accounted for this difference in degree of disturbance from other group members. There was no significant correlation between the time spent "Alert in Group" (in secs) and group size, when only animals which did spend at least some time "Alert in group" were included (kangaroos: $R^2=0.17$; wallabies: $R^2=0.16$). However, the median

group size of kangaroos which spent some of their time alert to others in the group (median=7.0) was significantly higher than the median group size of those that did not (median=5.0) (Mann-Whitney U test; $W=67715.0$, $p<0.0001$). The median group size of wallabies that did (median=3.0) and did not spend time alert in the group (median=3.0) did not differ significantly (Mann-Whitney U test; $W=7375.5$, $p=0.26$).

Male and female kangaroos spent the same proportions of time in the different modes of alertness as each other, as did male and female wallabies. There was no evidence to suggest that females, because of their smaller size and expected higher vulnerability (especially when accompanied by young), spent more time looking for predators or more time alert to potential danger.

6.3.3 Posture whilst surveying during 15-minute observations

Given that kangaroos spent less time surveying than wallabies and less time alert, I was interested in which postures the two species used for surveying. More upright postures give animals a better view of their surroundings but also make them more visible. Table 6.4. gives the percentages of time spent in different postures by kangaroos and wallabies whilst surveying.

Table 6.4. Percentages of Survey time spent in different postures in each of the five seasons between summer 1986 and pre-burn 1987 (mean $\pm$ s.e.m.). Significant results of 2-way AOV are given for Crouched and Bent variables. Percentages do not add up to 100% because the Upright variable had a highly skewed distribution and mean is not given. Values for Upright are percentages of animals that spent some of the observation period in the upright posture and 3-way contingency model is fitted to the frequency data. Number of observations in each group are given in parentheses.

Posture	Summer 1986	Pre-burn 1986	Post-burn 1986	Summer 1987	Pre-burn 1987
Crouched					
Kangaroos	46.5 $\pm$ 3.0 (47)	46.9 $\pm$ 2.9 (89)	43.4 $\pm$ 3.0 (94)	44.0 $\pm$ 4.6 (48)	50.3 $\pm$ 3.0 (130)
Wallabies	29.3 $\pm$ 2.9 (47)	29.1 $\pm$ 3.0 (78)	33.3 $\pm$ 3.0 (63)	37.6 $\pm$ 3.3 (44)	31.6 $\pm$ 3.4 (97)
Species: $F_{1,509}=44.6$, $p<0.0001$ (B-F)					
Bent					
Kangaroos	43.5 $\pm$ 3.9 (47)	47.2 $\pm$ 2.7 (89)	50.9 $\pm$ 3.0 (94)	50.1 $\pm$ 4.0 (48)	39.9 $\pm$ 2.7 (130)
Wallabies	63.0 $\pm$ 3.0 (47)	60.2 $\pm$ 3.4 (78)	59.8 $\pm$ 3.3 (63)	57.6 $\pm$ 3.4 (44)	54.2 $\pm$ 3.5 (97)
Species: $F_{1,707}=33.3$, $p<0.0001$					
Upright					
Kangaroos	39.2 (47)	26.5 (89)	32.5 (94)	24.1 (48)	40.0 (130)
Wallabies	34.0 (47)	22.9 (78)	20.7 (63)	20.0 (44)	37.1 (97)
Three-way log-linear model: species(S) x season(M) x upright(U): best model U, M df=10 G=13.67 p=0.188					

The posture used by either species did not differ between seasons, contrasting with the marked change in alertness with successive seasons. Kangaroos used the bent posture less and the crouched posture more than wallabies, although kangaroos used the two postures equally often. Use of the upright posture differed seasonally but there was no increase in the use of the upright posture over the seasons, nor was the seasonal difference consistent across years. Both kangaroos and wallabies were more likely to use the upright posture in summer 1986 and pre-burn 1987.

For both species, the sexes differed markedly in the posture adopted for surveying the surroundings. Male kangaroos spent 70% of survey time in the crouched posture compared to 38% for female kangaroos ($F_{1,371}=79.05$, $p<0.0001$), and 26% of survey time

in the bent posture compared to 49% for females ($F_{1,371}=60.71$, $p<0.0001$). The sex difference for the wallabies was in the same direction and of almost the same magnitude. Males spent 42% of their survey time in a crouched posture compared to 26% for females ($F_{1,188}=28.8$, $p<0.0001$, B-F). There was no difference between the proportion of males and females which used the upright posture at some time during the observation, although the percentage of time they spent in this posture did appear to differ; the median percentages were both zero but the means were 4% for male kangaroos and 13% for females. Thus, although males and females spent the same amount of time surveying the surroundings (whether for predators or conspecifics), they did so from different positions. Females adopted the more conspicuous, but also more effective, bent (and perhaps upright) posture more often than males.

6.3.4 Rate of surveying and length of surveying bouts during feeding

Having shown that kangaroos surveyed for less time and in less upright postures than wallabies I was interested to see how the rate of lifting the head from the sward to survey differed between the species and what the average length of each surveying bout was during feeding. A greater proportion of time spent surveying may not necessarily imply a greater surveying efficiency. It is possible that animals which spend a small proportion of their time surveying may do so efficiently by surveying often but for short lengths of time. If the animal is able to take in the relevant details of the environment in that short space of time and it surveys more regularly, it may be as efficient at keeping track of conspecifics or detecting predators as an animal that surveys for long bouts but with long inter-bout intervals. The rate of lifting the head from the sward can also be dependent on the bite size and number of bites per mouthful that an animal makes whilst feeding (see Chapter 5) since surveying may profitably accompany the processing of prehended food while further biting is prevented..

Figures 6.2 and 6.3 illustrate the rate of lifting the head to survey when feeding and the mean length of those surveying bouts. Wallabies raised their head more often to look around than kangaroos did, but their mean surveying-bout length was shorter than the kangaroos'. The results of two-way analyses of variance for the two variables, grouped by season and species are given in Table 6.5.

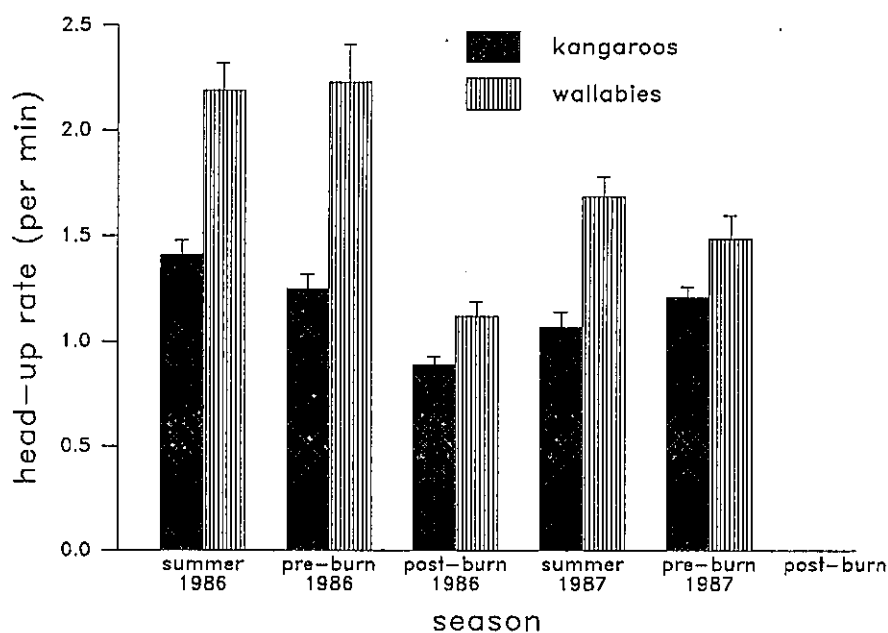


Figure 6.2 The mean rates (+ s.e.m.) of kangaroos and wallabies raising their heads to survey during feeding bouts (head-up per minute), in each of five seasons. Data from morning and afternoon time periods are combined. Data are from 15-minute continuous observations of a sub-set of each population, with approximately 4 observations per individual per season. The number of observations per season are given in Table 6.2.

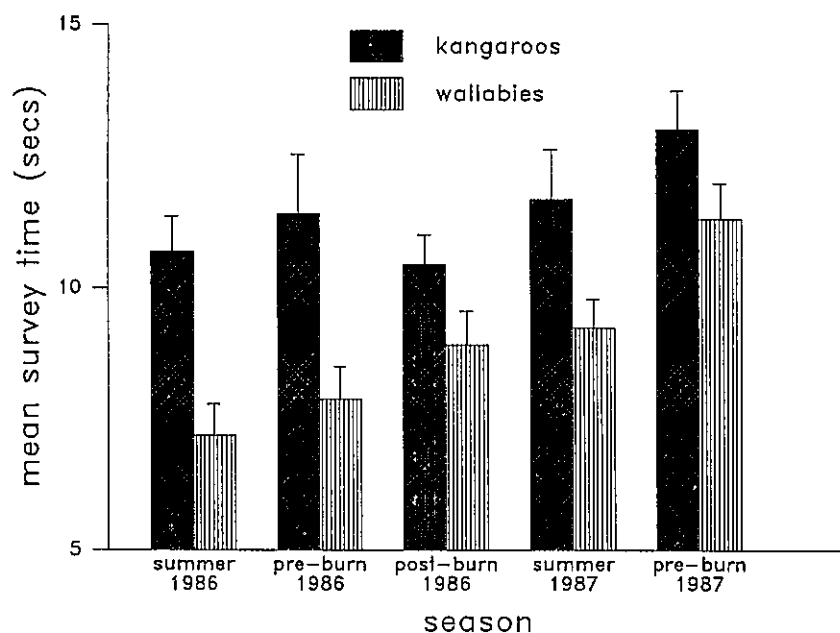


Figure 6.3 The mean lengths of time, in seconds, for which kangaroos and wallabies surveyed during feeding bouts, in each of five seasons. Data from morning and afternoon time periods are combined. Data are from 15-minute continuous observations of a sub-set of each population, with approximately 4 observations per individual per season. The number of observations per season are given in Table 6.2.

Table 6.5. Comparison of the mean rate (number of instances per minute) of lifting the head to survey during feeding (Head-up Rate) and the mean length of the surveying bouts during feeding (Mean Surveying-bout Length). Means in Figures 6.2 and 6.3 are compared here with a Brown-Forsythe, two-way analysis of variance on Head-Up Rate and Mean Surveying-bout Length, with species and season as grouping factors. Brown-Forsythe method used because variances of groups were not equal (BMDP statistical software).

Source of Error	d.f.	F	p
Head-up rate			
species	1,674	87.24	0.0001
season	4,329	21.59	0.0001
species x season	4,329	5.41	0.0003
Mean Surveying-bout Length			
species	1,517	34.50	0.0001
season	4,514	7.53	0.0001
species x season	4,514	0.64	0.64

Wallabies are therefore spending more time surveying the environment than kangaroos because they are looking up from feeding more often (greater Head-up Rate), even though the time they spend with their head up each time is slightly less than for kangaroos (shorter Surveying-bout Length).

The rate of animals lifting their heads from the sward was lower after the burn in 1986, at the height of the drought. The seasonal changes in head up rate corresponded to the changes in total survey time (see Figure 6.1b); for both species head-up rate and total survey time declined, from summer 1986 to post-burn 1986, and then increased in the following two months. These changes suggested that kangaroos and wallabies were sacrificing the frequency of looking up and total time spent surveying when vegetation was very poor (post-burn 1986).

The seasonal pattern in mean length of surveying bouts (Figure 6.3) was not the same as that for total surveying time (Figure 6.1b), but instead showed a general increase over the successive seasons. This pattern was more pronounced for wallabies than kangaroos and followed the pattern shown for the amount of time animals spent alert.

There were no differences between the sexes of either species in the mean surveying-bout length or the rate at which animals lifted their heads to survey. Both sexes showed the same seasonal changes in these variables although the degree of variation was slightly higher for males.

6.3.5 Rate of stepping

The pattern of an animal's movement during feeding bouts is the result of, amongst other things, its movement to select preferred food items and its movement to or away from nearest neighbours. By comparing the distances moved by kangaroos and wallabies, the amount of time they spent feeding in each patch and the distance moved between patches, it may be possible to separate out some of the causes of movement. Both species moved very little in the middle of the day and what movement did take place was usually to or from a resting site. For this reason observations from only the morning and afternoon were included in the following analyses as the majority of these observations were on feeding animals.

The number of steps taken per minute (step-rate) was calculated from the total number of steps taken in 15 minutes. The data were not perfectly normally distributed but the distributions were close enough to normality for analyses of variance to be calculated and interpreted with caution. Figures 6.4 a (kangaroos) and b (wallabies) compare the stepping rates of males and females in the five seasons. The analysis of variance with season and species as grouping factors showed significant effects of season and species (Table 6.6).

Table 6.6. Results of analyses of variance comparing the step-rates of kangaroos and wallabies in five seasons and comparing the sexes for each species. The Brown-Forsythe method used does not require equal variances between groups (BMDP statistical software).

Source of Error	d.f.	F	p
species	1,370	29.04	0.0000
season	4,368	13.75	0.0000
species x season	4,369	1.30	0.27
kangaroos			
sex	1,27	2.39	0.13
season	4,25	4.46	0.007
sex x season	4,25	0.55	0.71
wallabies			
sex	1,73	7.01	0.01
season	4,74	7.86	0.0000
sex x season	4,74	1.76	0.14

The step-rate of kangaroos was higher than for wallabies in each season although in summer 1986 the rates for the two species were almost the same. Mann-Whitney tests comparing the species within each season all showed that kangaroos took more steps than wallabies, supporting the results of the analysis of variance. Both species took considerably fewer steps in the pre-burn season of 1987 but the seasons of maximum

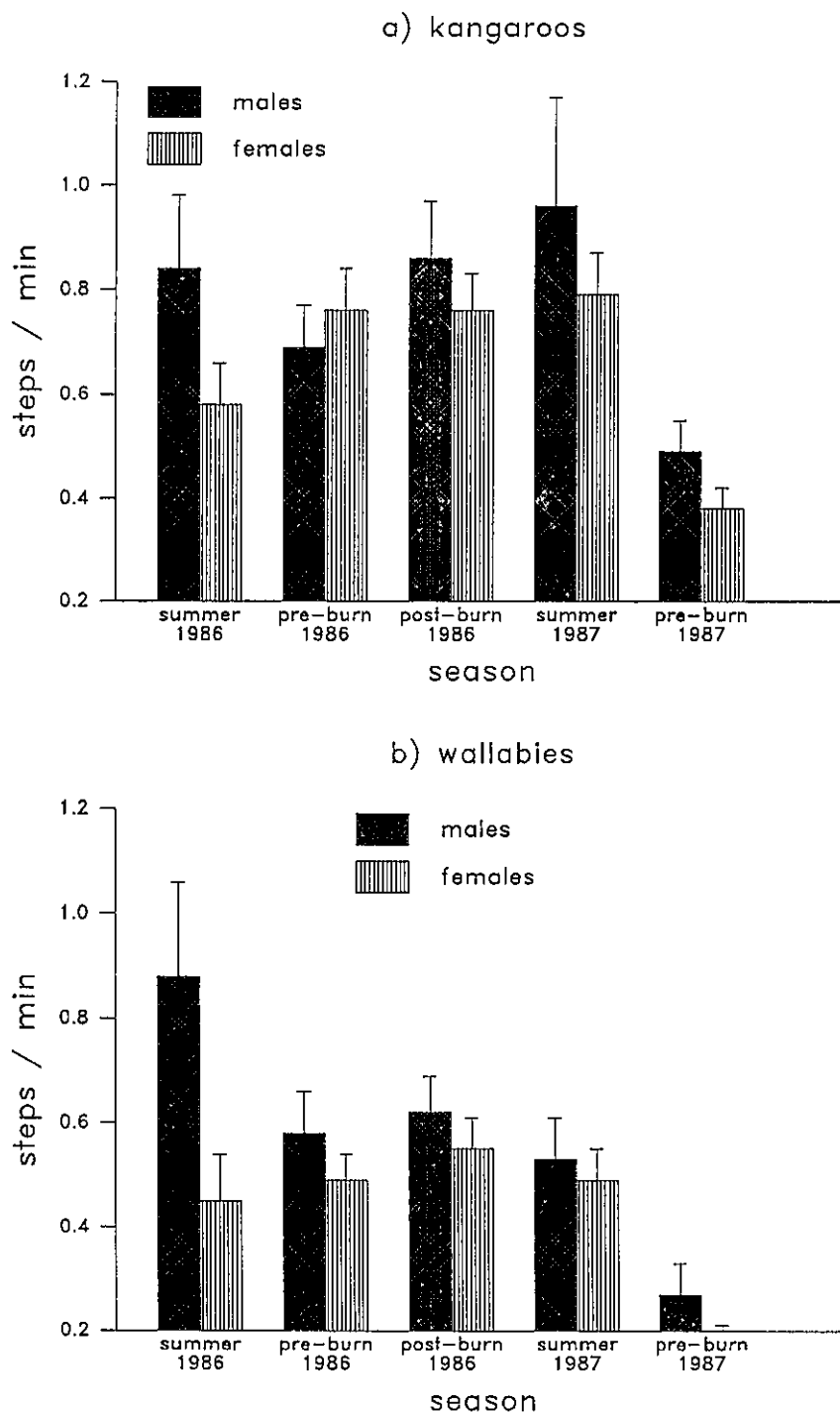


Figure 6.4 The mean number of steps taken per minute (+ s.e.m.) by male and female a) kangaroos and b) wallabies, during 15-minute continuous observations, in each of five seasons. Data from morning and afternoon time periods are combined. Data are from 15-minute continuous observations of a sub-set of each population, with approximately 4 observations per individual per season. The number of observations per season are given in Table 6.2.

movement differed between the species. Both species did show high step rates in the post-burn season of 1986 which included the months at the peak of the drought.

Male and female kangaroos took the same number of steps per minute but in each season male wallabies took more steps than their female counterparts. A greater step rate may result from longer stepping sequences, or a shorter time spent feeding in each patch, and therefore more frequent movement. These possibilities will be considered in later sections.

6.3.6 Displacement during 15-minute observations

The position of the focal animal was recorded at the start and end of each observation allowing the displacement during the 15-minute watch to be estimated to the nearest 5m. The distance used was measured 'as the crow flies' and did not necessarily represent the total displacement on the ground (which could be estimated from the total step and hop number). The displacements of kangaroos and wallabies in 15-minutes were not normally distributed and could not be analysed by AOV. The median displacements of kangaroos and wallabies are compared with a Mann-Whitney U test, for each of the five seasons in table 6.7.

Table 6.7. A comparison of the median and mean 15-minute displacements of kangaroos and wallabies in five seasons between summer 1986 and pre-burn 1987. Mann-Whitney U tests compare the medians for species in each each season.

		Sum 1	Pre 1	Pos 1	Sum 2	Pre 2
kangaroo	median	10.0	10.0	10.0	10.0	10.0
	mean	24.6	23.2	25.5	29.0	19.8
		(82)	(88)	(99)	(47)	(119)
wallaby	median	15.0	10.0	10.0	15.0	15.0
	mean	31.2	28.3	14.7	32.3	19.1
		(75)	(90)	(80)	(49)	(91)
W		3531	5308	6576	1902	7636
p		0.03	0.83	0.07	0.07	0.45

There were no differences between the displacements of kangaroos and wallabies in four seasons but in summer 1986 wallabies moved further than kangaroos. There were no differences between males and females of either species in the total displacements. Considering that kangaroos took more steps than wallabies and that a kangaroo step is larger than a wallaby step one would expect that wallabies must move further by hopping than kangaroos, or move more directly than them.

6.3.7 Number of hops taken during 15-minute observations

The total hop number for many observations was zero, the data were not normally distributed and the medians for each season and species were zero. The data did not lend themselves to analysis of variance or Mann-Whitney U tests so the frequencies of kangaroos and wallabies taking no hops, less than 10 hops and more than 10 hops were compared by fitting a three-way log-linear model to the frequency data (Table 6.8).

Table 6.8. A comparison of the percentages of kangaroos and wallabies taking no hops, less than 10 hops and more than 10 hops in a 15-minute period. The best fitting 3-way log-linear model for the data grouped by hops (H), species (S) and season (M) is given with G-test statistic and significance.

		number of hops							
		kangaroos				wallabies			
season		n	0	<10	>10	n	0	<10	>10
summer	1986	82	63.0	22.2	14.8	75	33.3	23.8	42.9
pre-burn	1986	88	53.4	20.5	26.1	90	54.4	14.0	31.1
post-burn	1986	99	65.7	11.1	23.2	80	59.5	20.3	20.3
summer	1987	47	61.7	17.0	21.2	49	40.8	12.2	46.9
pre-burn	1987	<u>119</u>	<u>58.0</u>	<u>15.1</u>	<u>26.9</u>	<u>91</u>	<u>53.3</u>	<u>17.8</u>	<u>28.9</u>
all		435	59.7	16.1	24.2	385	52.0	17.0	31.0

Best fitting model for hop(H), season(M) and species(S):

H,M,S df=22 G=28.60 p=0.16

-

Kangaroos

Best fitting model for hop(H), season(M) and sex(S):

H,MS df=38 G=40.33 p=0.37

Wallabies

Best fitting model for hop(H), season(M) and sex(S):

H,MS df=38 G=49.85 p=0.10

A greater proportion of kangaroos than wallabies did not hop at all during a 15-minute watch and a greater proportion of wallabies took more than 10 hops. However, the best fitting model did not include any interaction between hops and species, suggesting that the number of hops taken by animals was independent of species. Similarly, the interaction between sex and number of hops was not included in the best fitting model for the three-way analyses for both species.

6.3.8 Length of step-sequences during 15-minute observations

I use the term step-sequence length to describe a sequence of uninterrupted steps, which is followed by biting. This variable is equivalent to Novellie's step-set (Novellie, 1978) but differs from Underwood's Feeding step-sets (Underwood, 1983), as I did not

count the length of runs of accepted feeding sites. The results of previous sections suggest that kangaroos took more steps whilst feeding than wallabies did but that in most seasons, in the given period of time (15 minutes), they did not move a greater distance than wallabies. The total number of steps an animal takes does not indicate how frequently it was moving; the same step total could result from a few long step-sequences or many short step-sequences.

Observations of the kangaroos and wallabies whilst feeding suggested that animals usually began stepping in order to move onto a new food patch or to move towards or away from a neighbour. However, often it was not possible to distinguish the motive for a movement as what may have started as a move onto a new feeding patch often turned into a movement away from another animal. Thus although step-sequence length may be explained in part by the distribution of the preferred food items of the grazing animal it also represents the animal's response to other conspecifics and possibly other species (cattle in most cases at Wallaby Creek).

Step-sequence length was calculated for each 15-minute observation as the mean number of steps taken before the animal took a bite from the sward. The variable had a highly skewed distribution (the minimum value of 1 was also the most common) which could not be improved by transformation. The data were therefore divided into classes of step-sequence length and the frequencies for the species were compared for each season using G tests (Table 6.9).

Table 6.9. Percentages of kangaroos and wallabies whose mean step sequence length was 1, greater than 1 but less than 2 ($1 < x < 2$) and greater than 2 ($x > 2$) steps. G statistics and significance are given for tests comparing frequencies for the species in each month.

season	n	Kangaroos			n	Wallabies			G	p
		1	$1 < x < 2$	$x > 2$		1	$1 < x < 2$	$x > 2$		
summer 1986	49	40.8	46.9	12.2	42	50.0	50.0	0.0	7.9	0.02
pre-burn 1986	82	39.0	53.7	7.3	67	43.3	53.7	3.0	1.5	0.46
post-burn 1986	92	43.5	52.2	4.3	59	79.7	20.3	0.0	22.0	0.001
summer 1987	46	50.0	47.8	2.2	42	66.7	31.0	2.4	2.6	0.26
pre-burn 1987	62	49.0	42.2	8.8	62	75.8	22.6	1.6	13.1	0.001

In summer and post-burn 1986, and in pre-burn 1987 kangaroos took more steps in a sequence than wallabies did. Fewer than 5% of wallabies had a mean step-sequence length greater than 2 in any season and from post-burn 1986 onwards most wallabies had a mean step-sequence length of 1. There appeared to be some difference between the species in the seasonal changes in step-sequence length. There was no seasonal difference in the distribution of step-sequence length for kangaroos but wallabies took longer step-sequences in summer and pre-burn 1987 than in other seasons.

The frequency of different step-sequence lengths was compared for four population classes of kangaroos and wallabies: large males, small males, females with no young or pouch-young and females with young-at-foot. Using the same cutpoints for step-sequence length, the best fitting three-way log-linear model for kangaroos (step-sequence (Q), population class (P) and season (S)) was:

$$QP, SP \text{ df}=32, G=33.2, p=0.41$$

13% of large males and 16% of small males had a mean step-sequence length greater than 2 steps, compared to 3.5% of females with pouch-young and 4% of females with young-at-foot. There was no significant interaction between mean step-sequence length and population class of wallabies, nor was there an interaction between the effects of season and population class for this species.

6.3.9 Feeding time spent in each accepted patch

The amount of time an animal spends feeding in a patch before moving on to another is, in part, an indication of how selective the animal is. Animals which are highly selective of the plant material they eat should abandon a given patch in a shorter time than a less selective feeder (Charnov, 1976). Of course the time will also be dependent on the feeding rate of the animal, and the number of bites taken in each patch is considered in section 6.3.11. Figure 6.5 compares the mean time spent in an accepted patch (between movements) in each of the five seasons. The means were compared with analysis of variance; Brown-Forsythe's method was used because the variances of groups were not equal.

There was no difference between the species in the time spent per patch ($F_{1,473}=0.65$, $p=0.42$) but there was a highly significant seasonal effect ($F_{4,475}=13.05$, $p=0.0001$) and the interaction between season and species was also significant ($F_{4,475}=2.45$, $p=0.04$). In summer 1986 and pre-burn 1986 kangaroos spent more time per patch than wallabies but in the following three seasons the reverse was true. Between summer 1986 and summer 1987 the time spent per patch ranged from 50 to 80 seconds but in pre-burn 1987 the time increased dramatically to 100 secs for kangaroos and 125 secs for wallabies. This was also the season when the number of steps taken was very low (see Figure 6.4).

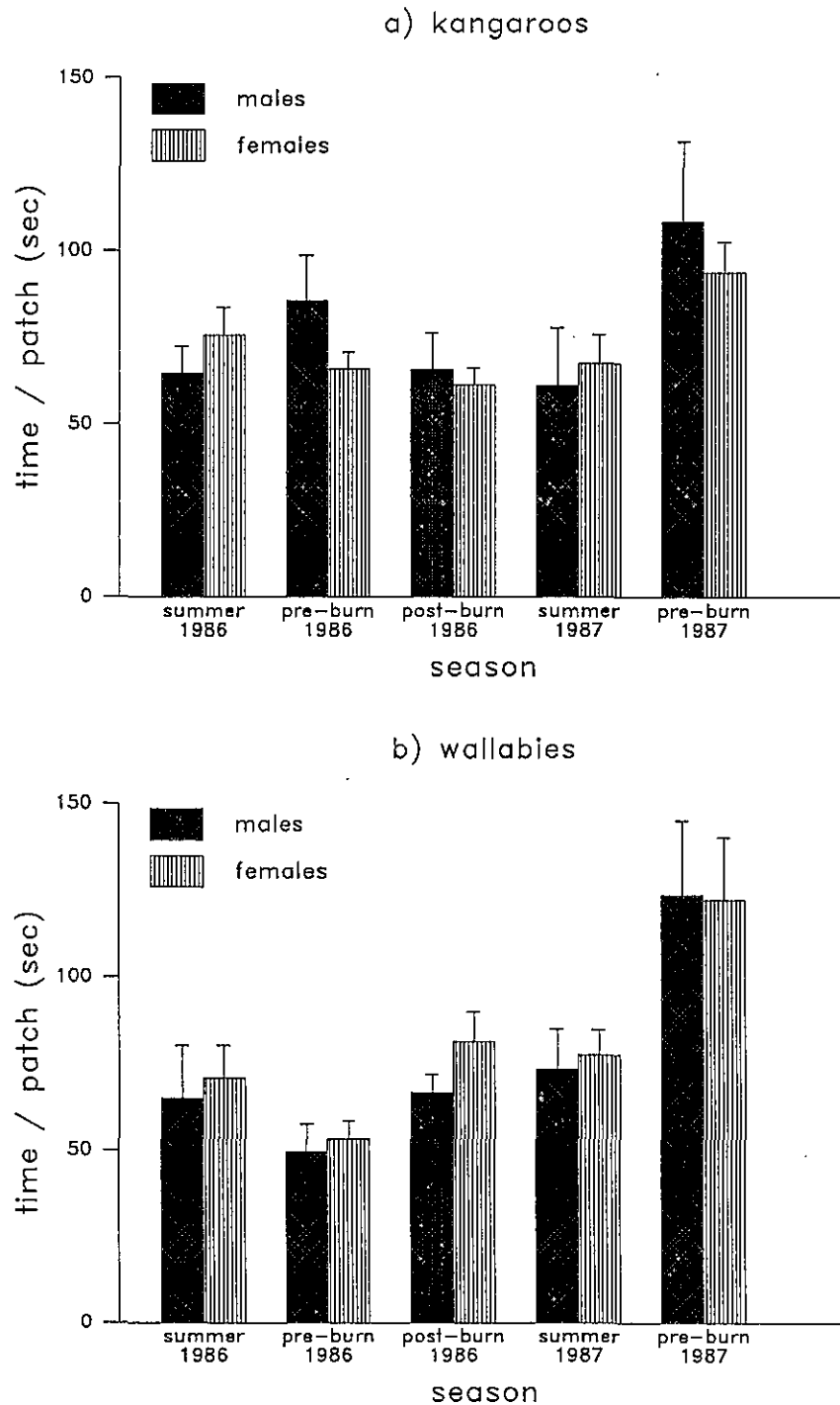


Figure 6.5 The mean length of time (in seconds) spent in each "accepted" patch, by male and female a) kangaroos and b) wallabies, during 15-minute continuous observations, in each of five seasons. Data from morning and afternoon time periods are combined. Data are from 15-minute continuous observations of a sub-set of each population, with approximately 4 observations per individual per season. The number of observations per season are given in Table 6.2.

Large males, small males, females with pouch-young and females with young-at-foot did not differ in the amount of time they spent feeding in each patch. Given that the step-sequence length for male kangaroos was higher than females, and that males also took more steps than females, male kangaroos were moving further between selected patches than females but were spending the same amount of time feeding in each patch. Wallaby males also took more steps than females but they did not move any further than them and did not appear to take more hops than them.

6.3.10 Interactions with other conspecifics

The effect of other conspecifics feeding in the same group as the focal animal were examined in a number of ways (Table 6.10). Observations in which the focal animal was alone for some or all of the observation were excluded from the following analyses. Firstly the number of observations in which some sort of interaction took place was compared between the species and sexes. Interactions which resulted in the focal animal displacing or being displaced by a neighbour were recorded and although the incidences were low I compared the proportion of observations of kangaroos and wallabies, males and females, in different seasons in which such displacements took place. Finally I calculated the proportion of movements (step-sequences as opposed to actual steps) which were taken "away" from the focal animal's nearest neighbour. If an animal took a step or hop in a direction that moved its head further from its nearest neighbour then that movement was considered "away" from its neighbour.

A greater proportion of the observed kangaroos than wallabies interacted at some stage during the 15-minutes. The model which best explained the frequency data for the incidence of interactions (**I**) with species (**S**) and season (**M**) was **M, IS**. This model implies that there was a difference between the species in the proportion of animals which are seen to interact with others; the percentages show that kangaroos are more likely than wallabies to interact with others. The frequency of interaction was so low for wallabies that expected values were too low to compare population classes or the sexes. In most seasons large male kangaroos were more likely to interact with other individuals in the group than small males and females

Table 6.10 The percentage of 15-minute observations in which: the focal animal interacted with another conspecific; the majority of movements were away from the focal animal's nearest neighbour; the focal animal displaced another group member; and the focal animal was displaced itself by another group member. Frequencies for interacting and displacements by another are compared for season and species by fitting a 3-way log-linear model. Frequencies for movements away are compared between the species for each season with G tests. Expected values for the variable displaced by another were too low for a statistical comparison.

	summer 1986	pre-burn 1986	post-burn 1986	summer 1987	post-burn 1987
sample size					
kangaroos	47	81	94	44	114
wallabies	28	58	52	33	40
percentage of observations with interactions					
kangaroos	11.3	18.5	12.0	14.6	24.8
wallabies	4.0	7.6	3.1	2.3	3.5
best fitting model season (M), species (S) and interaction (I) M, IS df=12 G=14.81 p=0.25					
percentage of observations where most movements were away from nearest neighbour					
kangaroos	68.9	63.2	72.7	69.8	67.6
wallabies	52.4	63.8	78.6	82.1	68.8
G	1.66	0.01	0.52	1.42	0.15
p	0.19	0.94	0.47	0.24	0.69
percentage of observations in which focal animal was displaced by another					
kangaroos	5.9	5.7	9.1	2.1	7.6
wallabies	0.0	2.2	2.5	2.1	1.1
best fitting model season (M), species (S) and displaced (D) M, DS df=12 G=15.33 p=0.22					
percentage of observations in which focal animal displaced another					
kangaroos	0.0	6.2	6.4	0.0	1.8
wallabies	0.0	3.4	6.1	0.0	0.0

The percentage of observations in which the majority of movements made by the focal animal were made away from neighbours was independent of season and species. The best fitting model for the three-way data (season(M), species(S) and away (A)) was that of independence and none of the G tests, which compared the species in each season, were significant. However, male kangaroos were much less likely to make movements away from their closest neighbours than females were; 45.2% of large males and 45.3% of small males took more movements away from neighbours (as opposed to towards)

whereas 74.2% of females with pouch-young and 83.2% of females with young-at-foot took more movements away from their neighbours. The values for wallabies were very similar with 43.8% of large males and 64.3% of small males taking more movements away from their nearest neighbours, compared to 82.1% of females with pouch-young and 87.5% of females with young-at-foot.

Frequencies of displacements of other conspecifics were low and therefore expected values for log-linear models were too low for a model to be applied with confidence. The frequencies of displacements of kangaroos were higher than those of wallabies but there was no real evidence for a seasonal difference. The largest number of displacements by kangaroo focal animals took place at the height of the drought in post-burn season of 1986. The numbers of displacements of other animals by the focal animal were even lower, although the majority took place in pre-burn and post-burn seasons of 1986. There were insufficient data for displacements to compare the sexes or population classes.

6.3.11 Feeding Rates

The data from the 15-minute continuous watches presented above were all collected in the morning and afternoon time periods when kangaroos and wallabies were generally active and feeding. However, observations were begun and continued even if an animal was resting, if that animal was on the list to be observed at that time. Thus, the time spent feeding and surveying should be representative of the real time animals spent in these activities (at those times of the day) because observations were made randomly on individuals within a select group (see Chapter 2 for further details of the schedule of observations). The three-minute observations were made only on foraging kangaroos and wallabies and therefore comparisons of foraging parameters such as feeding rates are independent of the amount of time that animals spend foraging.

During a 15-minute observation animals sometimes moved onto a number of different vegetation types. The vegetation type and micro-habitat that an animal occupies is likely to have some influence on its activity but because of the movement of animals to and from different areas during the course of an observation it was often not possible to assign a 15-minute observation to a particular sward type or vegetation area. Feeding rates, movement during feeding and surveying patterns during feeding were therefore compared using the three-minute observation data which could be assigned to a particular vegetation area or a patch type with one dominant grass species.

The foraging behaviours of kangaroos and wallabies were compared in two areas used regularly by both species, in three patch types dominated by different grass species and for animals feeding on new shoots after burning. The Areas 1 and 2 used in Table 6.11 are described in detail in Chapter 5. They are two alluvial paddocks which provide no cover vegetation, and are dominated by *paspalum* and carpet grass. They are used more

heavily by kangaroos than wallabies. The results in Table 6.11 represent the results of species and species x season effects of two-way analyses of variance for each foraging variable. The year was divided into two seasons because there were insufficient data for some comparisons to divide the year into summer, pre-burn and post-burn seasons. The foraging data below were collected for animals feeding on intertussock swards. Figures 2.6 and 2.7 showed that the intertussock vegetation went through only two major changes in the year; the two seasons used here, as in Chapter 5, are winter, April to September and summer, October to March. The foraging behaviours of kangaroos and wallabies feeding on burnt shoots between July and November 1987 were compared with Kruskal-Wallis tests. The results of the analyses and the means of the variables are given in Appendix II. In Table 6.11 I have indicated which macropod species gave the higher value for the variable and, where there was an interaction with season, how the relationship changed with season.

Table 6.11 Significant results for the comparisons of 3-minute feeding observations, between species, on two vegetation areas and three swards dominated by different ground species. Areas 1 and 2 are described in section 5.2.2. Results are for two-way analyses of variance with species and season as grouping factors. Uppercase letters indicate the macropod species which had the higher mean or proportion (K=kangaroo, W=wallaby) and lowercase letters indicate the season in which a difference was significant if there was a species x season interaction (s=summer, w=winter). Results for burnt patches are from Kruskal-Wallis tests for the four months post burning combined. Proportions, means, medians, test statistics and significance levels are given in Appendix II.

Variable	Area 1	Area 2	species dominating sward			burnt shoots
			kikuyu	carpet grass	paspalum	
bite/select	-	-	-	-	-	K
survey/chew	-	-	-	-	K	-
bite rate 1	s: K=W w: K	K	-	-	K	-
bite rate 2	s: K=W w: K	K	-	-	-	W
biting ratio	-	K	-	-	-	K
chew/bite	-	-	-	-	s: W w: W=K	W
bites/patch	K	-	s: W w: K	-	-	-
head up rate	W	W	W	W	W	W
step total	-	-	-	-	-	K

Although most differences between the species were not seen for each sward type, differences were generally consistent across sward types. The most consistent difference was that wallabies raised their heads more often than kangaroos. Like the 15-minute watches, wallabies spent less time biting/selecting whilst feeding than kangaroos when feeding on burnt swards, but less time surveying than kangaroos on paspalum dominated swards.

Kangaroos tended to have higher biting rates than wallabies, especially on the more diverse swards (Area 1, Area 2 and Paspalum), where there was a greater opportunity for selection. In Area 1 the difference in feeding rates between the species was seen only in winter. Biting rates were lower in winter because animals were spending more time searching for green leaves amongst the dead vegetation and wallabies, with a greater requirement for high-quality food, spent more time selecting each bite and had lower biting rates. Other grass species contributed little to the sward in the patches dominated by kikuyu or carpet grass, and on these patches kangaroos and wallabies did not differ in their feeding rates. Wallabies feeding on new shoots after burning had a higher uninterrupted biting rate than kangaroos feeding on the same sward component ($U=783.5$, $p=0.05$, $n=93(k), 43(w)$).

The foraging rates of males and females were compared on Area 3 and Area 4 (see section 5.2 for description) and for kangaroos feeding on burnt shoots. There were no significant differences between the sexes in any of the following foraging parameters that were compared: bite/select time; survey/chew time; uninterrupted biting rates; interrupted biting rates; chews per bite; and bites/patch. There were also no interactions between sex and season for any of the variables tested.

Most of the foraging variables calculated from the three-minute biting observations on wallabies feeding in Areas 1 and 2 were the same for males and females. In Area 2 one of the differences between the sexes was the higher number of chews per bite taken by males compared to females ($F_{1,18}=6.30$, $p=0.02$), even though the proportion of time that males spent survey/chewing tended to be less than that of females. In Area 2 there was also a difference between the sexes in their rates of feeding. Females showed higher interrupted and uninterrupted biting rates in this area (Table 6.12).

Table 6.12. A comparison of the mean ($\pm$ s.e.m.) biting rates (bites/min) of male and female wallabies feeding in Area 1, in summer and winter. Analysis of variance compares means grouped by sex and season.

	summer	winter
interrupted biting rate		
male	31.7 + 2.7	22.2 + 1.1
female	37.6 + 2.7	25.4 + 0.8
season: F1,74=46.04 p=0.0001 sex: F1,74=8.08 p=0.006		
uninterrupted biting rate		
male	41.0 + 1.2	26.7 + 0.8
female	44.5 + 2.8	33.1 + 1.7
season: F1,25=50.64 p=0.0001 sex: F1,26=7.98 p=0.0001 (Brown-Forsythe)		

The difference between males and females in the uninterrupted biting rate suggests that females were either being less selective than males by spending less time selecting each bite or they were taking smaller bites, which allowed them to bite faster. Because the sexes spent the same proportion of time with their heads down, biting and selecting bites, the interrupted biting rate achieved by females was also higher. It is not possible to say whether the females had a higher net intake than males, without knowing the relative bite size of the sexes.

6.4 Discussion

6.4.1 Vigilance behaviour and activity of kangaroos and wallabies

There were a number of important differences in the vigilance behaviours of kangaroos and wallabies, some of which relate to body size and its effect on foraging requirements and anti-predator behaviour, and others which relate to the grouping behaviour of the two species. The relationship between group size and foraging behaviour will be considered in detail in the next chapter. In this chapter I concentrate on differences between the species, given their different grouping behaviours, and consider which differences may be a consequence of their grouping behaviours.

At Wallaby Creek kangaroos spent a greater proportion of the morning and afternoon time periods biting and selecting bites than wallabies, and less time surveying and chewing. Wallabies looked up more frequently, but surveyed for shorter bouts, than kangaroos. In a comparative study of the vigilance behaviour of five African antelope species, Underwood (1982a) found a negative correlations between body size and the proportion of time spent looking, and the rate of looking. Thus, small species, like wallabies in this study, spent more time looking around and looked up from feeding more frequently. He suggested many reasons for the relationship, one being that because large species are more likely to escape predators once a chase has ensued, small species must rely on seeing the predator first so that they can flee and hide, and therefore need to look for predators more frequently. Alternatively, if larger species are in more open habitat, or if the habitat is less likely to conceal predators from their taller vantage point, then larger species can survey less often for the same efficiency of detection, as well as using lower postures (see below).

Differences in surveying time may simply be a result of differences in foraging time, since survey time is often the reciprocal of foraging time. If larger animals have a greater absolute requirement for food which cannot be met by increases in bite size alone they must forage faster and for longer, allowing them less time to survey. This explanation differs from those above in the motive for surveying i.e. whether the time devoted to surveying is decided by the animal's need to survey the environment or whether the time required to forage takes priority and surveying is done in the time that remains. If the latter were the case then I would expect kangaroos to survey in the same manner, or even in a more efficient manner, than wallabies because they are unable to survey for so long.

Wallabies not only surveyed for longer and more frequently than kangaroos, they also spent a greater proportion of that surveying time in a more upright posture. Between animals of the same size, a more upright posture may reflect a greater level of alertness and/or a better scanning performance, but if animals differ greatly in size then smaller ones may need to use a more upright posture just to scan as efficiently as a large one.

Thus, the difference in posture used by the species may simply reflect their difference in height, rather than their perceived danger.

Wallabies also spent a greater proportion of their survey time noticeably alert to disturbances outside the group than kangaroos. Animals that were alert moved their ears to focus on a source of disturbance, they stopped chewing (perhaps to improve their hearing ability) and appeared tense and ready to take flight. The greater survey time, more upright posture and greater alertness of wallabies together suggest that wallabies felt more vulnerable to predators and that they scanned the environment more often to try and reduce their risk of predation by decreasing the amount of time it would take them to detect a predator.

The relationship between body size and vigilance could also be a result of the relationship between body size and group size that has been found for many groups of animals, including macropods; individual kangaroos in large groups tend to spend less time surveying than those in small groups (Southwell, 1981; Jarman, 1987; but see also Chapter 7). The relationship between body size and looking time for the antelopes in Underwood's study was further strengthened when the relationship between group size and body size was accounted for, suggesting that body size was more important than group size in determining vigilance times (Underwood, 1982a). In Jarman's study of grouping and vigilance of eastern grey kangaroos, kangaroos in smaller groups adopted more upright postures. Thus animals may compensate for fewer eyes by standing taller to increase their efficiency of predator detection, in addition to, or instead of, increasing the number of scans they make.

Whilst kangaroos may spend a smaller proportion of their time surveying than wallabies because of their larger group sizes, kangaroos also spend more of their surveying time alert to other group members than wallabies. It appears that there is a cost to grouping as well as a benefit. Kangaroos which did spend some time alert to other group members were in larger groups than those that did not, but this was not the case for wallabies. It may be that the range of group sizes shown by wallabies was too small for the effect of group numbers on alertness within the group to be shown. The suggestion that kangaroos are more affected by other group members is supported by their greater tendency to interact or be actively displaced by others. Although kangaroos may have experienced more interference from group members than wallabies because they are in larger groups, kangaroos still spent less time surveying the environment which gave them more time to forage for food.

Both species appeared to sacrifice surveying time for foraging during the drought of 1986; there was no evidence to suggest that the risk of predation was lower in this season; the proportion of survey time alert was not higher and the number of dingoes sighted by myself and colleagues was no higher than usual (see Chapter 2). When the proportion of green leaf in the sward was low, and sward biomass was low, kangaroos

and wallabies spent more time selecting each bite (see Chapter 5). The smaller time spent surveying the environment in this poor season was probably due to animals placing priority on searching for food items because those items were scarce and hard to find.

The increase in the proportion of surveying time during which animals were alert to disturbances outside their group increased with successive seasons during the course of the study. This change may reflect true differences in alertness of the animals or changes in the degree to which I was able to recognize alert animals over time. If an animal changed from being alert to not alert during the same surveying bout, the transition time was not always obvious. The mean length of surveying bouts also increased over the course of the study, especially for wallabies. This measure is much less likely to be subject to changes in my recording techniques because the start and end of surveying bouts were very obvious. The proportion of time that animals spent surveying, their rate of surveying and the posture they used did not increase over the course of the study, neither did our frequency of dingo sightings. Although sward characteristics varied over the course of the period January 1986 to July 1987 there was no general trend in one direction over this period (e.g. see Fig 2.8). The only possibility I can suggest is that the property owners moved around more often in later seasons in the study and that a working dog was seen and heard in 1987 that had not been there in the previous year.

6.4.2 Comparison of the vigilance behaviour of males and females

There were surprisingly few differences between the sexes in the duration, frequency and mode of surveying behaviour. Despite their larger size and therefore higher absolute energy requirements males did not spend more time biting and less time surveying than females. Even the high costs of lactation for females with large pouch-young and young-at-foot did not cause them to spend a greater proportion of time foraging in those reproductive phases. In section 6.1 I predicted that females at this reproductive stage and their young are more vulnerable to predators and it may be that the two conflicting demands of foraging and vigilance result in females with young-at-foot foraging for the same proportion of time as females with small pouch-young, or males. In Chapter 3 I did record females with young-at-foot and large pouch-young feeding (biting/selecting and surveying/chewing) for more hours in the day than females with small or no pouch-young; perhaps they are spreading their feeding over more hours of the day, instead of reducing their surveying time during foraging.

Similarly, large males experience the conflicting demands of high energy costs (because of a large body mass) and important social interactions which disrupt foraging behaviour. Large male kangaroos did engage in more interactions than other population classes, and were more likely to move towards their neighbours than females were. In an earlier study, the interaction rates of red-necked wallabies at Wallaby Creek were almost three times higher for males and oestrous females than for males and non-oestrous

females (Johnson, 1989b). This result supports the notion that there may be disruptive costs to foraging behaviour for males during the females' oestrus periods; the oestrous female will herself be disturbed but for only one short period during the year. In a review of the activity budgets of male and female herbivores of many species, Bunnell and Gillingham (1985) noted that the males of many species allocated less time to feeding during the breeding season and more time to feeding soon after the end of the breeding season. The kangaroos and wallabies at Wallaby Creek do not have a distinct breeding season and large males may need to alter their allocation of feeding time from day to day instead of season to season. Alpha male kangaroos often lost body condition during periods when many females came into oestrus and one particular male died soon after an unusual week when he achieved five matings. It appears that the energetic costs of following females and keeping other males at bay for long periods can be very high. Comparisons need to be made of the foraging behaviour of males consorting with females and those not, before the effects of such behaviour can be estimated.

The greater tendency of females to move away from, rather than towards, their neighbours suggests that females may have been more likely to disrupt groups than males. Females often moved away from large males that approached to check them, but their behaviour towards females may be more complex depending on the relatedness of the females in a group (R.Stuart-Dick and P.Jarman, pers. comm.). Female eastern grey kangaroos also leave mixed-sex foraging groups more frequently than predicted (Jarman, unpubl. records), perhaps because females are less tolerant of interruptions to their feeding schedules than males are.

Despite females being more vulnerable to predators than large males, and having more to lose at the loss of a young than them, females did not spend more time alert to disturbances outside the group than males. Neither did they survey more frequently or in longer bouts than males. Females did, however, use a more upright posture for surveying than males. As with the kangaroo and wallaby comparison, females may use the more upright posture to improve their surveying capabilities over males, or to achieve the same surveying efficiency as the taller males. Thus, there was little evidence that females adopted a different level of vigilance than males, but they may have expended more energy (in sitting up) to achieve the same.

6.4.3 A comparison between the species of movement during foraging

The differences between the species in their movement during feeding bouts were complex, and not always consistent across seasons. Whilst kangaroos took more steps than wallabies, they tended to shift a shorter linear distance than them over a 15-minute period, especially in the summer of 1986. Kangaroos being larger animals should have a longer gait than wallabies and therefore move further on the ground when they take more steps. That they did not shift a greater linear distance over 15-minutes suggests that a)

wallabies hopped further than kangaroos and/or b) kangaroos moved in a less direct path than wallabies, so that although they may have moved further on the ground, by the end of a 15-minute period they may have progressed less far in one direction.

There was a tendency for wallabies to hop more, and take more sequences of greater than 10 hops, but the variation between seasons was so great that a model of total independence between hop number, species and season fitted the data better than any other. The second possibility, that kangaroos move in more indirect paths than wallabies, seems likely. Kangaroos form larger groups than wallabies (Chapter 7), and in order to maintain group cohesion they must follow other group members or turn back towards the group when they begin to drift away. The advantage of maintaining group cohesion for the individual is that by moving towards other group members it reduces its "domain of danger", making it less likely to be the victim in an attack on the group by a predator (Hamilton, 1971; Vine, 1971).

Jarman (1974) suggested that for antelopes to form prolonged, cohesive and co-ordinated groups they must move at similar speeds, in roughly the same direction and within perceptual range of each other. Observations I have made of feeding groups of macropods and ruminants suggest that members of macropod groups are much less likely to move in one direction whilst feeding. For most groups of eastern grey kangaroos and red-necked wallabies that I observed it was impossible to discern a "front" or "rear" position. Although parallelism is the commonest mutual orientation it is far less predominant than in many bovid groups (Jarman, pers. comm.) and is often obscured by the macropod habit of feeding in wide arc around their bodies. However, there may be some more subtle organization within groups of eastern grey kangaroos at Wallaby Creek since Jarman has found some classes of animals orientate themselves to other classes in a non-random way (Jarman, unpubl. data).

This tendency for kangaroos in a group to move back and forth in an area rather than in one direction could be due partly to the small scale of different vegetation patches at Wallaby Creek. The quality of some areas was so high compared to the surrounding vegetation that animals would be better off remaining in the area, even if it meant more competition between group members. The mode of movement of macropods also allows them to alter the direction of their feeding path more easily than ungulates because when they raise their heads to survey and chew the vegetation in their mouths, they can put their front feet down anywhere in an arc of almost 180°.

According to Charnov's marginal value theorem an animal should leave a patch when its return from that patch falls below the average for the habitat (Charnov, 1976). Kangaroos will accept lower quality food items than wallabies because of their large body size, and are therefore expected to find patches profitable for longer than wallabies. If this were the case then kangaroos may be prepared to move around and feed in one patch for long periods whilst wallabies would prefer to move onto new patches more

frequently. Kangaroos did spend more time feeding per patch than wallabies in summer and pre-burn 1986, but in the following seasons wallabies spent more time feeding in each patch than kangaroos. Post-burn 1986 to pre-burn 1987 included some of the best and worst months as measured by the availability of food, so it is hard explain the difference in time spent per patch on that basis. However, kangaroos also took more bites per patch than wallabies in Area 2 and in winter on kikuyu swards, suggesting that they may find patches acceptable for longer than wallabies.

In the 15-minute observations kangaroos clearly took more steps than wallabies but in the three-minute observations of animals exclusively feeding, kangaroos took more steps than wallabies only when feeding on burnt shoots. Because the sward type was not controlled for in the 15-minute observations the difference between the species in this case may have been due to differences in the vegetation types used by kangaroos and wallabies. When feeding on the same vegetation type, movement whilst feeding was very similar for both species.

Wallabies did not move as far between accepted feeding patches as kangaroos, preferring to take a few bites from many close patches whilst kangaroos took more bites, from fewer patches, that were further apart. This situation is the reverse of that proposed by Jarman (1974) for small and large antelope. He argued that the dispersion of food items of antelopes varied with their quality; high quality food items occurred in patches, but low quality food items were abundant and continuous. Novellie's observations of the springbok, a small selective feeding antelope, and the larger, less selective blesbok, showed the larger species spent more time feeding per feeding station and moved less far between feeding stations, supporting Jarman's proposal. In this study, the high quality food items (such as *Paspalum* leaves and clover) were dispersed in amongst the lower quality food and the strategy of wallabies moving frequently and only taking a few bites per patch could be a response to this dispersion of food items.

The stepping rates of kangaroos in this study were much lower than those found for kangaroos in Southwell's study of the same species on the New England Tablelands (Southwell, 1981). The kangaroos in Southwell's study were feeding on less improved pasture and the step rates must reflect the greater difficulty kangaroos had in finding food items there. At Wallaby Creek, the intertussock sward of introduced grasses provided abundant food which was not noticeably depleted after an animal had been grazing in one patch for a while.

There was evidence from a number of the movement variables that kangaroos and wallabies responded to changes in dispersion of food items with season. The stepping rates and distances moved by both species were at their heighest during the drought of 1986. Southwell (1981) also found an inverse relationship between food abundance and stepping rates for eastern grey kangaroos at another location, and Johnson (1985) reported lower rates of progression in summer for feeding red-necked wallabies at

Wallaby Creek. Greater movement rates during poor seasons have been noted for a number of species e.g. springbok (Novellie, 1978), kudu (Owen-Smith, 1979), impala (Jarman and Jarman, 1979; Dunham, 1982), and are generally attributed to a high dispersion of food items at low availabilities, and a switch from grazing to browsing in dry seasons (Jarman and Sinclair, 1979). In the northern hemisphere, movement during foraging may be restricted in winter, when food availability is low, (red deer, Clutton-Brock *et al.* 1982a; reindeer, Trudell and White, 1981) as animals attempt to conserve energy. In the months preceding the burn in 1987 step-rates were very low and kangaroos and wallabies spent much longer feeding in each patch than in other seasons. Sward heights and the proportions of green leaf in intertussock swards were particularly high in this season (see Chapter 2) so animals did not need to move on to new patches as quickly.

6.4.4 Comparison of the movement of the two sexes

There were more differences between the sexes in movement during foraging than activity. Males had higher stepping rates than females and male kangaroos also had greater step sequence lengths than females. As mentioned above, movement during feeding can reflect the dispersion of preferred food items, or movement in relation to other group members. There was no difference between the sexes of either species in the time spent feeding in each patch, and male and female kangaroos did not differ in their feeding rates, suggesting that social interactions may play a greater role in the difference between the sexes than differences in the dispersion of food items. Given that males interacted with other group members more frequently and were more likely to move towards their neighbours than females, their greater stepping-rates and step-sequences between patches probably reflect their movement around the group to check on females and interact with males.

6.4.5 Comparison of the feeding rates of the species and sexes

On most of the sward types kangaroos had higher biting rates than wallabies. Higher interrupted biting rates are expected on the basis that kangaroos spent less time surveying during feeding than wallabies, yet their uninterrupted biting rates were also higher. Higher biting rates result from a shorter time between bites, time that is spent on selecting the next bite. This suggests that while the difference in diet quality between the species is partly dependent on differences in feeding sites (see Chapter 4), wallabies also spend more time selecting each bite when they are feeding on the same sward type as kangaroos.

The feeding rates of kangaroos and wallabies did not differ on all sward types. There were no differences between their feeding rates on the carpet grass and kikuyu dominated swards. These swards were less diverse than others, with most of the sward comprising the dominant species. In these areas there was little opportunity for selection and kangaroos and wallabies fed at the same rate. Wallabies had higher uninterrupted biting rates on burnt shoots than kangaroos did but they spent a smaller proportion of their feeding time biting/selecting bites and took more chews per bite. Burnt areas were very exposed because of their lack of cover and wallabies may have increased their rate of biting so that they could raise their head from the sward to survey more often.

The foraging parameters of male and female kangaroos were surprisingly similar, especially since differences found between the sexes in diet, feeding site location and foraging time were also very small. However, the similarities of diet and feeding site location may have precluded major differences in foraging behaviour. There can be little doubt that different population classes have different energy requirements on account of their body size or reproductive needs, yet I have been unable to show any foraging parameter in which the sexes differ greatly. The possible constraints on ecological and behavioural differences between the sexes will be considered in the final discussion in Chapter 8.

CHAPTER 7

Group Size and Foraging Behaviour

7.1 Introduction

7.1.1 What are groups?

The eastern grey kangaroos and red-necked wallabies at Wallaby Creek have already been the subjects of separate studies of their grouping behaviour (Jarman and Southwell, 1986, Johnson, 1989a). This study attempts to augment those by comparing the grouping behaviours of the species simultaneously, thus removing possible variation due to season, location and recording techniques. I also look in greater detail at some of the possible costs and benefits of grouping by comparing many foraging parameters, including feeding rates, for animals in groups of different sizes.

Eastern grey kangaroos are more gregarious than red-necked wallabies with typical group sizes at Wallaby Creek of 7.3 and 2.3 respectively, at similar population densities (Jarman and Southwell, 1986; Johnson, 1989a). Both species have a social organization structured around regular associations of certain individuals that may be related (*ibid*, Stuart-Dick, 1987). In the above studies, and in those of other of macropods (e.g. Taylor, 1982), groups have been defined as a gathering of individuals in one place that are within a critical distance of one another (50m for kangaroos and 30m for wallabies), and which are in visual contact with one another. This is a more general definition than some, in that it does not imply that groups persist through time, or that animals interact with one another, although they must have the potential to do so. Stuart-Dick (1987) used the term sub-group to define a set of animals within a group that associate more closely with one another than with the rest of the group. I have followed Southwell, Jarman and Johnson in using the spatial definition of a group. This more general definition does not distinguish groups from aggregations of animals, that is a number of animals drawn together to a spatially concentrated resource (Jarman and Coulson, in press). Although groups and aggregations may form for different reasons, practically they are very difficult to distinguish, especially if 'groups' are recorded on transect counts or searches rather than during prolonged observation.

7.1.2 Why do animals form groups ?

Grouping behaviour is shown in many species of animal, from invertebrates to highly socially organized mammals. The size and constancy of groups varies enormously with their function. Animals may group together to feed, to mate, to roost and to hunt. For example, some bats roost together in huge numbers to conserve the energy required for thermoregulation (Trune and Slobodchikoff, 1976). In this chapter I am concerned mainly with groups that are active and foraging since the selective pressures for feeding and resting groups may be very different. Clearly, there is unlikely to be one evolutionary pressure that has brought about the evolution of grouping behaviour in such diverse circumstances. In the following section I will review some of the reasons given for grouping in vertebrates and discuss how each might have influenced the evolution of grouping behaviour in macropods.

1) Groups as information centres

Animals which forage on patchy and highly unpredictable food supplies may need to spend much time and energy searching for food patches. If, instead, they follow and join other individuals that have already found food supplies, they will not need to spend as much time searching. Ward and Zahavi (1973) suggested that the night-roosting behaviour of some flocking birds is a way of birds exchanging information about where food is located; in the morning those birds which had not found food the previous day will follow other birds that did to a suitable feeding location. Presumably for this behaviour to have evolved, the roles of 'informer' and 'follower' would have to be reversed regularly, otherwise the followers will always benefit by not having to spend time searching and each bird should attempt to be a follower. Krebs and Davies (1981) suggest that the informer might itself benefit from foraging in a group for other reasons, such as anti-predator defence (see later), and therefore tolerate being followed. However, Treisman (1975) has suggested that the exchange of information at the roost may be only a secondary benefit to the birds and not the selective force behind flocking behaviour.

Could this sort of exchange of information apply to large mammalian herbivores? Grazers are surrounded by a large number of potential food items of low quality and there would appear to be little need to follow others to find food. The best quality leaves and plant parts, which make up the diet of selective grazers, are generally dispersed in amongst poorer quality herbage. Again, there would be little advantage in following others to feed because the food items still need to be searched for in the sward.

Following a more experienced forager to gain information about foraging conditions may be of more importance to the continued association of mother and young beyond weaning. Female sub-adults of both the red-necked wallaby and eastern grey kangaroo tend to remain in their mother's home range for a long period after weaning, eventually taking up home ranges overlapping with their mothers, whilst male sub-adults stay in

their mother's home range only until sexual maturity (Johnson, 1986b; Stuart-Dick, 1987). Sub-adults often follow their mother's to feeding sites and it is quite likely that they learn something about the location of good feeding grounds within their mother's home range (*ibid*).

2) Groups as gatherings of animals for reproduction and social interaction

Some special groups are formed only during a particular phase of the reproductive cycle. Harems formed by polygynous species, for example, are groups of females which are herded together and guarded by a male in an attempt to secure his mating rights over each of the females (Wilson, 1975). Despite their polygynous mating system, macropods do not form harems (Caughley, 1964a; Kaufmann, 1974a; Russell, 1984). Eastern grey kangaroos and red-necked wallabies are not highly seasonal breeders, and females may come into oestrus at all times of the year. During the proestrus period, which lasts up to a week in both species (but can be longer for primiparous females), females are attractive to males and are found more often than usual in groups containing males (Jarman and Southwell, 1986; Johnson 1989b), and, in the case of wallabies, are found in larger groups than normal (*ibid*). Usually the alpha male of the population is the most dominant in the group accompanying the female by the time the female is ready to mate; of 35 observed mountings by eastern grey kangaroos at Wallaby Creek, 27 were made by the dominant male of the time (Jarman and Southwell, 1986). Jarman and Southwell (1986) have suggested that synchrony of oestrus might be disadvantageous to females because it would decrease the chances of each female mating with the alpha male. When not involved in following oestrous females males often group together, perhaps to assess each other's dominance status (Johnson, 1983, 1985; Jarman and Coulson, in press).

Female mammals often associate with their kin; in primates these associations can lead to very stable groups of females living together and sharing a home range (Wrangham, 1980). Females have been shown to associate regularly with their independent female young in both eastern grey kangaroos (Stuart-Dick, 1987) and red-necked wallabies (Johnson, 1986d) at Wallaby Creek, and these small matrifocal units may form the basic units of social organization of these species. However, the benefits from associating with kin are far from clear, and in some cases even appear to reduce the reproductive success of the females in the kin group (red deer, Clutton-Brock *et al*, 1982b; red-necked wallabies, Johnson, 1986b). Whilst the associations between mothers and their young (both independent and dependent) may account for some of the basic units of social organization, grouping with kin does not explain why these small groups of interacting individuals coalesce with groups of unrelated animals to form larger groups. Thus, although reproductive activity appears to account for some of the

variations in grouping patterns in many species, it is probably not the major selective force behind grouping.

3) Groups as units to reduce predation risk by dilution of prey

One of the advantages of being in a group is that the chances that any one individual will be taken by a predator decreases with increasing group size (Krebs and Davies, 1981). The actual benefit of this effect will depend on the relative ease that a predator has in detecting a small group as opposed to a large one and the chances the prey species has of escaping attack by fleeing. Underwood (1982b) found no relationship between the distance at which he was able to sight groups and group size, yet there may be a difference between the way predators search for groups (including sound and smell for example) and the ways we do. Jarman (1974) suggested that the smaller species of antelope, which are unable to outrun their predators and rely on hiding to escape predation, would be worse off in a group because a group is more visible to a predator than a solitary individual.

Animals that are different from others in the group in some way, or are vulnerable because of their health or age, are more likely to be the victims in an attack on a group. This effect may account for females with young isolating themselves from a group because their young would be easy targets in an attack on a group (Jarman and Jarman, 1979). However, when numbers of young in a group are very high the dilution effect may still operate for this class, and this may have led to selection for synchronized births amongst females in large herds (Estes, 1966).

When a predator approaches a group each individual in the group is expected to put as many other animals as possible between itself and the predator in order to reduce its own 'domain of danger' (Vine 1971). This behaviour should lead to the formation of tight flocks or groups, with animals on the periphery constantly trying to move into the centre (*ibid*). There is evidence from a number of field studies that animals on the periphery of a group remain more vigilant than those in the centre (pronghorns, Lipetz and Bekoff, 1982; Spanish Ibex, Alados, 1985), presumably because those on the edge are in more danger. However, Underwood (1982a) has suggested that the increased vigilance of antelope at the back of a group was due to these animals attempting to maintain group cohesion.

4) Grouping as a means of improving foraging efficiency by decreasing vigilance time, and increasing effectiveness of predator detection.

One of the most cited reasons for grouping behaviour of birds and mammals is that as group size increases, each individual can allocate less time to vigilance, and hence more time to foraging, whilst at the same time increasing the efficiency of the group as a whole in detecting predators. This benefit of grouping depends on a rapid communication of

alarm between group members when one or more members become aware of a predator (Jarman and Coulson, in press). This point is important when considering the ability of habitat to restrict communication between group members and also the restrictions of darkness.

Evidence of decreased vigilance time and/or increased foraging time with increasing group size has been provided in a number of field studies, and on a variety of species: great-tailed grackles, Smith, 1977; bighorn sheep, Berger, 1978; ostriches, Bertram, 1980; sparrows, Elgar and Catterall, 1981; antelope species, Underwood, 1982a; pronghorn antelope, Lipetz and Bekoff, 1982; Spanish ibex, Alados, 1985; eastern grey kangaroos, Southwell, 1981, Jarman, 1987). However, many of the above studies showed only weak correlations between vigilance time and group size and one other has reported no relationship (Johnson, 1989a).

The hypothesis that grouping behaviour has evolved to improve the foraging efficiency of group members, by allowing them more time to forage, depends on the animal being constrained, to some extent, by their foraging time. Because foraging time is itself dependent on food availability and foraging style (see Chapter 5), selective pressure for grouping should also vary, making time-constrained animals more likely to form groups than energy-constrained ones. Of course, if grouping also improves the efficiency of predator detection for each member of the group, then group members may not need to spend more time feeding to get a benefit from being in the group. One study has demonstrated large groups of harp seals respond more quickly to simulated predator attacks than small groups (da Silva and Terhune, 1988).

In a review of data for 13 species of diurnal primates, Van-Schaik (1983) concluded that predation pressure has been the most important influence on the evolution of grouping behaviour in those species. However, the influence of predation on the evolution of grouping behaviour in macropods has been a matter of controversy in the literature. Russell (1984) concluded that the role of predation in the evolution of gregariousness had not been substantiated for macropods, Lee and Cockburn (1985) suggested that it has had little influence, whilst Jarman and Coulson (in press) suggest that it has played a crucial role. Although the ratio of predator species to herbivore species was comparatively low in the prehistoric mammal fauna of Australia, the ratios of their densities may be a more important measure in determining predation pressure (Jarman and Coulson, in press). A few dingoes can have a significant impact on a kangaroo population in terms of the survival of young (Stuart-Dick, 1987) and it is possible that a few species of generalist carnivores could exert as much pressure as a higher diversity of more specialized species (Jarman and Coulson, in press). As mentioned above, there is some evidence for eastern grey kangaroos that foraging efficiency is increased in larger groups (Southwell, 1981; Jarman, 1987; Heathcote, 1987).

5) Grouping as a result of animals aggregating on a sparse, and patchily distributed resource

Finally there is a non-adaptive cause for grouping behaviour. Groups may arise when animals are drawn onto a spatially concentrated resource such as a water hole or a grassy clearing (Jarman and Coulson, in press). Although groups of this type are better called aggregations (see above) since they do not involve animals choosing to be with others, aggregations and groups may be difficult to distinguish, especially when data collection involves brief contact with groups rather than prolonged observation of them. Animals in groups and aggregations will both experience costs and benefits of grouping behaviour, the size of those costs and benefits depending on the degree of association within the groups.

7.1.3 The costs and benefits of grouping behaviour

I have outlined above some of the possible benefits of grouping which may have been selective forces behind the evolution of the behaviour, or which instead have been beneficial spin-offs. One of the main disadvantages of being in a group is the potential for competition and aggressive interactions between group members. Jarman (1974) has suggested that the abundance and dispersion of preferred food items sets the upper limit on group size, through the effect of competition. The importance of competition in groups depends on the nature of the food resource and how it is depleted. This point is illustrated nicely in a study by Goss-Custard (1976) of the foraging behaviour of red-shanks at night and in the day-time. These wading birds feed alone during the day because their prey, small shrimps on the mud surface, are disturbed by the movement of red-shanks and become unavailable by burrowing into the mud. Individual foragers are more successful when further away from other birds because their prey are less likely to be disturbed. At night, the red-shank switch to feeding on snails found in the mud, and because the snails move too slowly to react to red-shank movement, the birds are able to forage together in flocks.

Jarman (1974) has suggested that browsers increase the dispersion of food items by removing whole plants or food items, requiring the animals that follow to move further to find food, and perhaps making group cohesion more difficult. Grazers remove only parts of individual plants, leaving a distribution of food items of the same density though reduced in biomass. The potential for competition is lower amongst grazers and the even distribution of food items, even after grazing, facilitates group foraging. Besides actually reducing the availability of food, group members may show aggressive behaviour towards other foraging animals (Caraco, 1979; Watts, 1985) or engage in social interactions which disrupt feeding (Berger, 1978; Johnson, 1989b).

Given that grouping behaviour has costs and benefits associated with it, optimality theory predicts that animals should try to maximise the net benefit of the behaviour (Krebs and Davies, 1981) resulting in an optimal group size for a particular set of circumstances. There is some evidence that birds can facultatively change their flock size according to the relative risks of predation and costs of aggressive interactions with other group members (Pulliam, 1976; Caraco, 1979). How they might actually do this in practice is less clear since when a group has reached its optimal group size, the addition of another member will decrease the benefit to the members present, yet will probably greatly benefit the one joining the group. To what extent animals monitor the number of group members or the benefits and costs that they are experiencing is not known.

Other species, including macropods, change their grouping behaviour in accordance with habitat type and food availability (Southwell, 1981; Taylor, 1982; Berger *et al.*, 1983; Jaremovic, 1984). Although winter and dry seasons tend to encourage smaller groups because of the increased costs of competition, this is not always the case (Johnson, 1980; Johnson, 1989a); if a reduction of food availability leaves the remaining food in patches then animals may congregate in these patches, despite the increased possibility of competition there. There may also be a confounding effect in comparisons of group size in different habitats since group size is often correlated with population density in macropod species (Taylor, 1982; Johnson, 1983; Southwell, 1984a).

Since the costs and benefits of grouping are likely to differ between different individuals in a population it is likely that optimal group size will vary for individuals. I have already mentioned the cost of joining groups to females with small and weak young because of the vulnerability of the young in comparison to other group members. In addition, dominance status may affect the amount of aggression received, and feeding disruption incurred (Caraco, 1979; Watts, 1985), leading to differences in the preferred group size of dominants and sub-ordinates.

The aim of this chapter is to compare the typical group sizes of kangaroos and wallabies, in different vegetation types, in different seasons, and between day and night, to try to establish the grouping response of the species to changes in food abundance, foraging ease and predation risk. I look particularly at the night versus day comparison since there has been little comparison of behaviour of animals in daylight and the dark. This is despite the very different problems posed by darkness, in relation to seeing, and being seen by, predators, maintaining visual contact with other group members and selecting food. The timing of changes in group size is used to help interpret the differences in group size between day and night. Finally, I look at the influence of group size on various aspects of foraging behaviour, in an attempt to discover some of the costs and benefits of grouping behaviour in these two species.

7.2 Methods

The data on group size and its variation with habitat and time of year were collected on the regular searches carried out monthly between August 1987 and February 1988. The method of searching and schedule for searches are described in detail in Chapter 4. The searches covered all the study area in every month, both in the afternoon and morning feeding periods. Most areas were also searched at night once in each field trip and every other month the study area was searched in the middle of the day. When referring to the data from these searches winter is defined as August to October and summer as December to February. The period August 1987 to January covered the growth of the grasses that were burnt in July 1987 after which these burnt grasses were indistinguishable from those that were not burnt.

The comparison of group sizes between day and night are made on data that come from the 24-hour watches carried out on 24 kangaroos. Group fluxes and nearest neighbour distances over the 24-hour period were also calculated from the 24-hour data. The comparisons of foraging behaviour of kangaroos and wallabies in groups of different sizes are made on data that come from the 3-minute biting observations collected over the whole study period. The methods of recording feeding rates in these watches are describes in Chapter 2 and the schedules for making the observations are described in Chapter 5.

7.3 Results

7.3.1 Typical group size for kangaroos and wallabies.

The size of group that each sighted individual belonged to was used to calculate the typical group size for each species, in each season and for each time period (Table 7.1). Jarman (1974) has suggested that typical group size more accurately reflects the social experience of the individual than mean or modal group size as it is a measure of the group size in which the average individual occurs. He describes the method for its calculation in Appendix 2 of his paper. The typical group size of each species was compared between seasons and time periods in a two-way analysis of variance. The species are treated separately because variances of group sizes were not equal.

Table 7.1. Typical group size ($\pm$ s.e.m) of kangaroos and wallabies seen on systematic searches of the study area between August 1987 and February 1988. Brown-Forsythe analysis of variance was used, which does not require equal variances between groups (BMDP statistical software), with season and time period as grouping factors.

	morning	midday	afternoon	evening
Kangaroos				
winter	7.6 $\pm$ 0.3 (325)	8.9 $\pm$ 0.5 (137)	8.1 $\pm$ 0.3 (346)	5.6 $\pm$ 0.3 (164)
summer	6.3 $\pm$ 0.2 (346)	6.8 $\pm$ 0.3 (162)	9.3 $\pm$ 0.4 (306)	3.7 $\pm$ 0.3 (99)
Source of variation	d.f.	F	p	
season	1,824	22.04	0.0001	
time	3,820	53.26	0.0001	
season x time	3,821	11.23	0.0001	
Wallabies				
winter	2.6 $\pm$ 0.1 (188)	2.1 $\pm$ 0.1 (47)	2.2 $\pm$ 0.1 (212)	2.0 $\pm$ 0.1 (90)
summer	2.5 $\pm$ 0.1 (192)	1.8 $\pm$ 0.2 (50)	2.0 $\pm$ 0.1 (172)	1.5 $\pm$ 0.1 (75)
Source of variation	d.f.	F	p	
season	1,444	9.61	0.002	
time	3,437	14.68	0.0001	
season x time	3,440	0.58	0.62	

As expected, there were considerable differences between the typical group sizes that kangaroos and wallabies were found in; over all seasons and times typical group size was 7.4 for kangaroos and 2.2 for wallabies. Group sizes were larger in winter than in summer for both species, this difference being apparent in all time periods but the afternoon for kangaroos. However, the typical group size of kangaroos did not differ between summer and winter as greatly as expected, probably because of the confounding effect of pasture type (see later).

Typical group size also differed significantly between time periods. Both species were found in small groups in the evening, especially in summer, although the change to smaller groups in the evening was not a gradual one as both species were found in relatively large groups in the afternoon. Wallabies were found in their largest groups in the morning whereas kangaroos were found in the largest groups in the afternoon in summer and the middle of the day in winter. Wallabies, unlike kangaroos did not aggregate to rest in the middle of the day; they tended to rest alone or with their young in dense vegetation, hence their small typical group sizes in the middle of the day.

7.3.2 Effect of pasture type on within-season variations in group size

The grouping behaviour of kangaroos and wallabies on different pasture types varied between seasons and also within seasons. In Figure 7.1 the grouping behaviour of foraging kangaroos (a) and wallabies (b) are compared on different pasture types in winter only (the midday and evening time periods are excluded). Kangaroos were often found on burnt areas in winter and wallabies on clover-dominated swards, so these pasture types are included. The pasture types are ranked in each group of bars by the nitrogen levels of the dominant plant species, from low on the left to high on the right.

There were more animals belonging to larger groups on better quality swards (the bars on the right of each group), whereas on swards dominated by carpet grass there were more animals in smaller groups. In winter pasture quality is low and there is more likely to be competition between animals grazing together. The larger groups on better quality swards could represent kangaroos and wallabies aggregating on high quality patches or it could represent competition on the poorer quality swards leading to a smaller group size. The two hypotheses do not need to be exclusive.

7.3.3 Effect of pasture type on between-season variations in group size

Group size was compared between seasons for each pasture type separately and with time periods combined. When each individual was sighted, the dominant species in the sward it was feeding or resting on was recorded and Figures 7.2 a-d for kangaroos and Figures 7.3 a-d for wallabies compare the group sizes of individuals sighted on each of the four most common pasture types. Clover could not be included for the wallabies because clover was very scarce in summer and there were no records of wallabies on

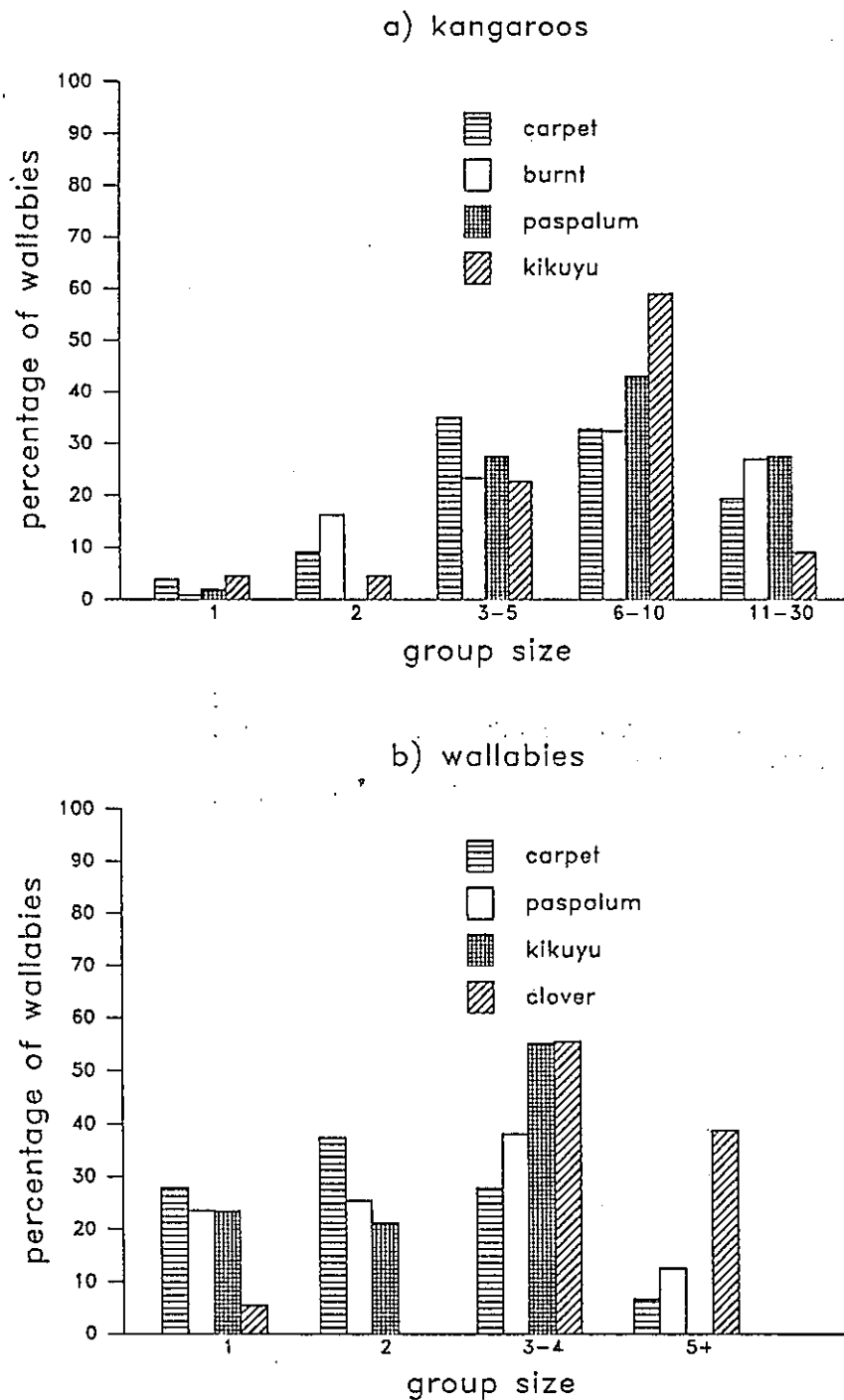


Figure 7.1 Percentages of kangaroos (a) and wallabies (b) sighted on each of four dominant ground types in winter 1987, which were seen in groups of different sizes. The ground species are ranked from left to right in order of increasing nitrogen content. Midday and evening time periods are excluded.

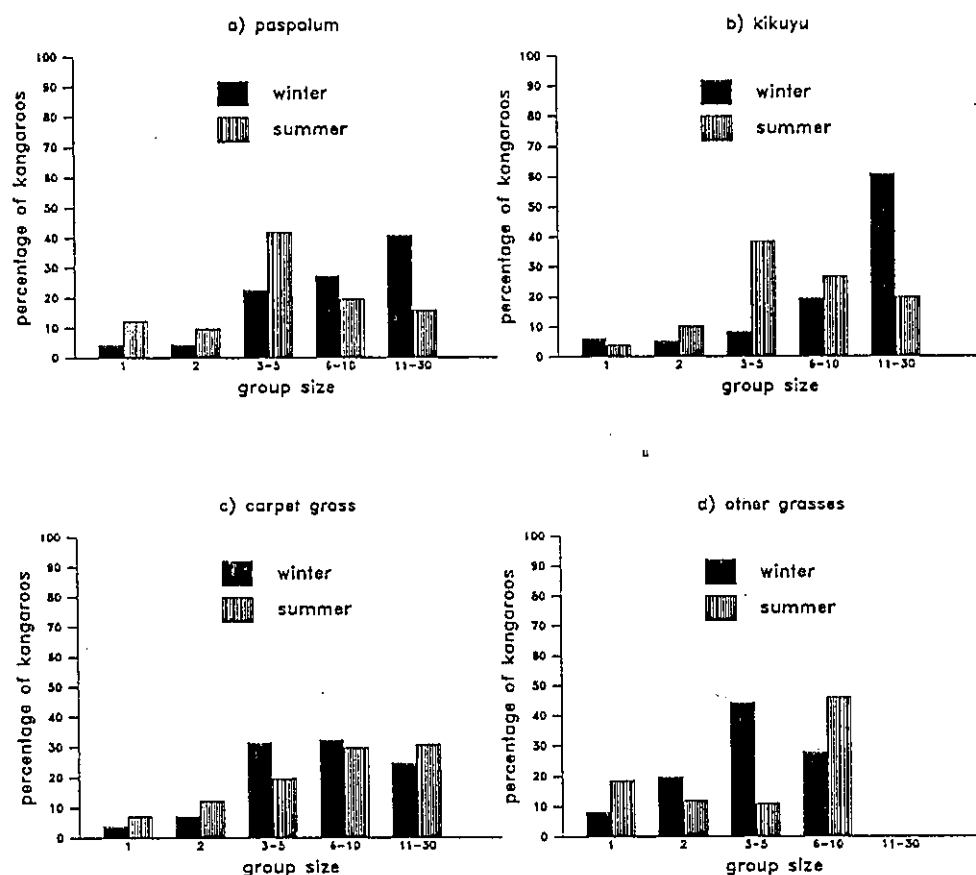


Figure 7.2 Percentages of kangaroos seen in groups of different sizes, on each of four swards dominated by different ground species, in summer and winter. The ground species are: a) paspalum b) kikuyu c) carpet grass d) 'other grasses' (see text for description). Midday and evening time periods are excluded.

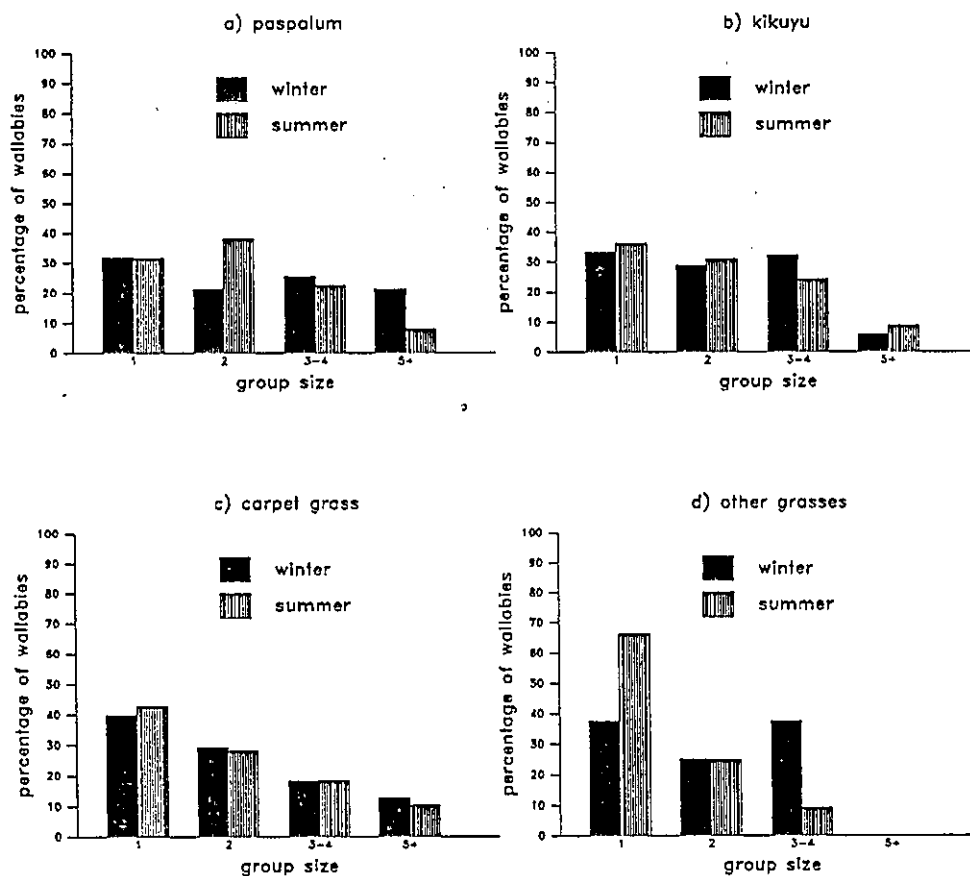


Figure 7.3 Percentages of wallabies seen in groups of different sizes, on each of four swards dominated by different ground species, in summer and winter. The ground species are : a) paspalum b) kikuyu c) carpet grass d) 'other grasses'(see text for description). Midday and evening time periods are excluded.

clover-dominated swards in that season. The data were not normally distributed so group size classes were constructed and the frequencies of animals seen in groups belonging to each group size class were compared with a least-likelihood ratio test.

Table 7.2. Results of two-way G-tests comparing frequencies in group size classes in summer and winter for each of four dominant ground species types.

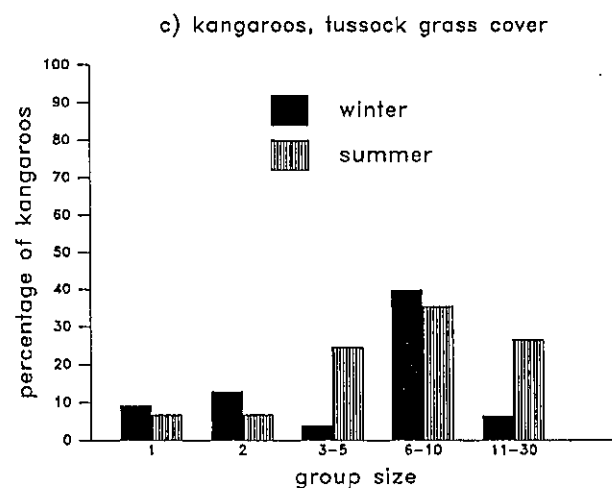
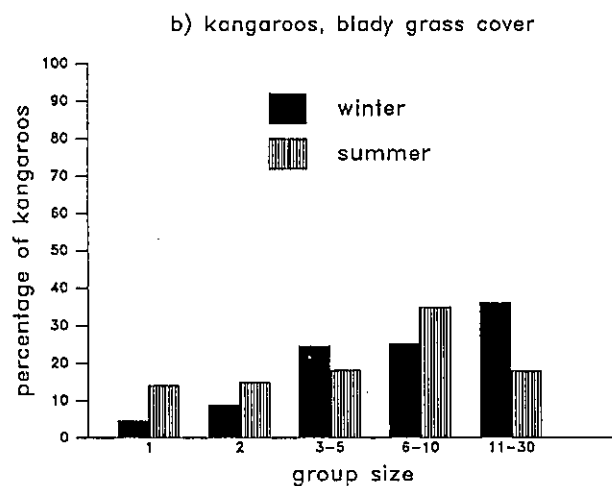
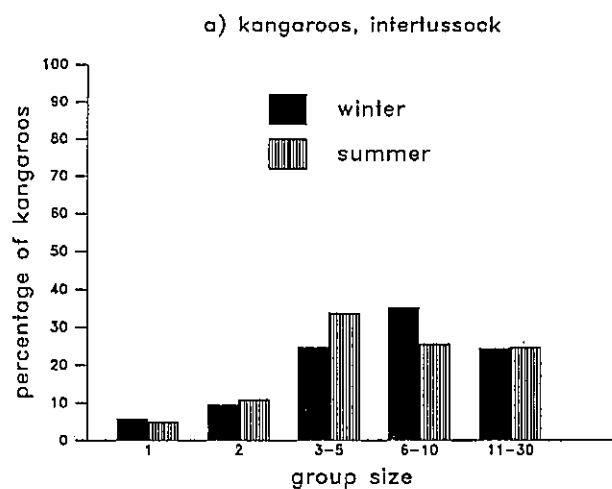
	kangaroos			wallabies		
	G	df	p	G	df	p
carpet grass	27.40	4	0.0001	0.69	3	0.87
paspalum	13.78	4	0.009	7.19	3	0.07
kikuyu	50.59	4	0.0001	1.35	3	0.72
other grasses	28.54	3	0.0001	18.86	2	0.0001

Table 7.2 gives the results of least-likelihood ratio test comparing the frequencies of different group sizes in summer and winter. In the comparison of the nitrogen and fibre levels of the common grass species, paspalum and kikuyu were of consistently higher quality than carpet grass and 'other grasses' (see Chapter 2). Kangaroos on the better quality pastures dominated by kikuyu and paspalum were in larger groups in winter than in summer whereas group sizes were smaller in winter than in summer on the poorer quality swards.

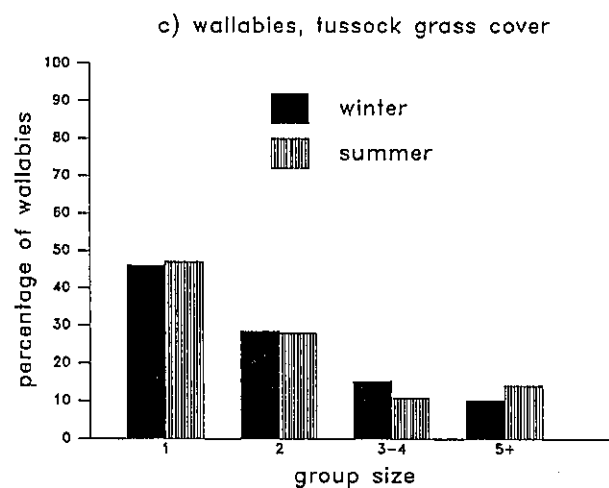
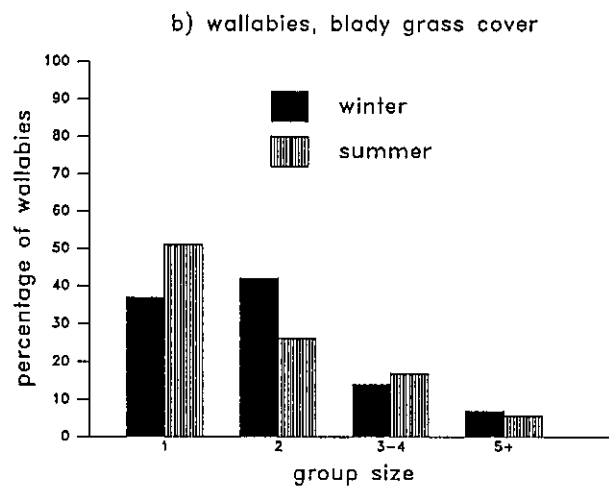
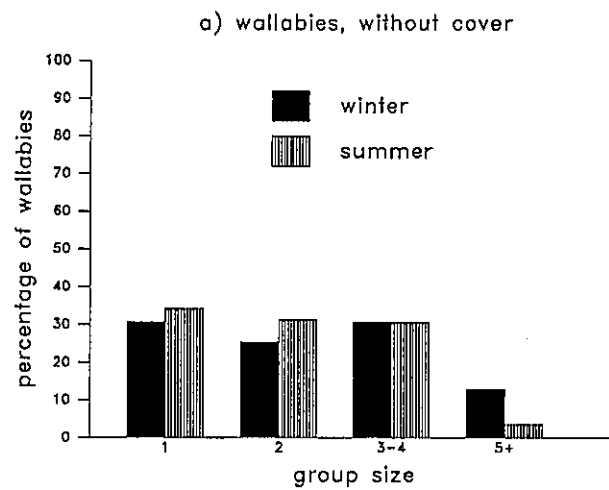
7.3.4 The effect of cover vegetation on group size

If animals groups together in situations where they are more vulnerable then we might expect that when feeding in very open areas, which provide no concealment for grazing animals (or their predators), kangaroos and wallabies would form larger groups. Unfortunately at Wallaby Creek there is some interaction between the quality of a sward, in terms of the species of grass available, and the amount or type of cover provided (see Chapter 4).

Vegetation was classified as providing cover if it was greater than 30cm in height and provided some physical concealment for kangaroos, wallabies and their predators. Stands of blady grass and tussock grasses such as snow grass and swamp foxtail were the most common types of cover vegetation, but cover was also provided by milkweed and other forbs (see section 4.3.2). Blady grass provided much greater concealment than tussock grass. Most of the kikuyu dominated patches had no blady grass or tussock grass and the largest area dominated by paspalum (Area 1, see Chapter 5) was also devoid of cover. Figures 7.4 and 7.5 illustrate the group sizes of kangaroos and wallabies in areas



Figures 7.4 Percentages of kangaroos seen in groups of different size in areas without cover, with blady grass cover and with tussock grass cover, in summer and winter. Morning and afternoon time periods are combined.



Figures 7.5 Percentages of wallabies seen in groups of different size in areas a) without cover, b) with blady grass cover and c) with tussock grass cover, in summer and winter. Morning and afternoon time period combined.

with no cover, with blady grass cover and tussock grass cover. Table 7.3 shows percentage of kangaroos and wallabies seen in each group size class in relation to cover vegetation and season.

Table 7.3 Percentage of kangaroos and wallabies seen in each group size class in areas with and without cover, in summer and winter. Morning and afternoon time periods are combined. Bold figures show the highest frequency of group size for that row. G values in the vertical column compare for each cover type the frequencies of different group sizes seen in each season. Remaining G tests compare for each season the frequencies of group sizes in each cover type.

		group size					
kangaroos		1	2	3-5	10-30	30+	G
without cover	win	5.8	9.6	24.8	35.3	24.4	10.1*
	sum	5.0	10.9	33.7	25.6	24.8	
blady stand	win	4.6	8.9	24.5	25.2	36.1	46.0***
	sum	14.1	15.0	18.2	34.9	17.9	
tussock	win	9.2	12.8	31.9	39.7	6.4	26.9***
	sum	6.8	6.8	24.5	35.3	26.6	
G test: cover type x group size							
winter:	G=19.5*						
summer:	G=50.1***						
		group size					
wallabies		1	2	3-5	5+	G	
without cover	win	30.8	25.4	30.8	12.9	6.6 ns	
	sum	34.3	31.4	30.7	3.6		
blady stand	win	37.0	42.0	14.0	7.0	9.2*	
	sum	51.2	26.2	16.9	5.8		
tussock	win	46.0	28.5	15.3	10.2	4.2 ns	
	sum	47.1	28.0	10.8	14.0		
G test: cover type x group size							
winter	G=29.1***						
summer	G=29.0***						

Kangaroos feeding in areas where there was no cover were more likely to be in small groups (3-5) than kangaroos in areas with blady grass. In summer kangaroos in areas without cover were also in smaller groups than those in tussock grass areas, but in winter the distribution of group sizes was the same with and without tussocks.

Wallabies in areas where there was no cover were more likely to be in large groups (>3) than wallabies in areas which provided cover in the form of blady grass or tussocks. This was the reverse of the pattern shown by kangaroos. In a three-way frequency comparison for the afternoon and morning time periods only, with group-size class (G), cover type (C) and season (S) as grouping factors, the best fitting model included the interaction terms 'group x cover' and 'cover x season' (GC, GS: df=9, G=13.35, p=0.15).

7.3.5 Comparison of the typical group sizes of different population classes

Kangaroos and wallabies form open membership groups which usually contain a mixture of population classes. However, some population classes in particular have been reported as being more solitary than others e.g. large males (Southwell 1984a) and females with young-at-foot (Stuart-Dick 1987). Table 7.4 shows comparative percentage data for kangaroos in each population class, in relation to group size.

Table 7.4 A comparison of the percentages of kangaroos in each population class that were seen in groups of different sizes. The population classes are: large male; small male; females with pouch-young (female py); and females with young-at-foot (female yaf). The most common group-size classes are highlighted for each population class. The best fitting three-way log-linear model is given for the data described by group size, population class and season.

	n	group size				
		1	2	3-5	5-10	10+
winter						
large male	66	10.6	3.0	27.3	31.8	27.3
small male	83	1.2	2.4	31.3	33.7	31.3
female py	247	5.7	11.3	26.3	28.7	27.9
female yaf	70	2.9	18.6	31.4	27.1	20.0
summer						
large male	61	6.6	1.6	24.6	47.5	19.7
small male	116	10.3	3.4	25.0	34.5	26.7
female py	263	8.4	8.4	22.8	29.7	30.8
female yaf	41	0.0	24.4	31.7	26.8	17.1

Best fitting model for group size(G), population class (P) and season(S): PS, GP (df=16; G=18.5; p=0.29)

Group size did differ between the population classes of kangaroos; the best fitting model included the two-way interaction of group size and population class (GP). The most common group size for males, and females with pouch-young was larger than for females with young-at-foot. Females with young-at-foot were more likely to be in group size 2 than other classes i.e. females were likely to be alone with their young-at-foot. In winter large males were more likely to be alone than other males were. Table 7.5 shows similar population class data for wallabies.

Table 7.5 A comparison of the percentages of wallabies in each population class that were seen in groups of different sizes. The population classes are: large male; small male; females with pouch-young (female py); and females with young-at-foot (female yaf). The most common group-size classes are highlighted for each population class. The best fitting three-way log-linear model is given for the data described by group size, population class and season.

	n	1	group size 2	3-4	5+
winter					
large male	100	30.0	21.0	33.0	16.0
small male	23	26.1	26.1	30.4	17.4
female py	141	44.7	24.8	23.4	7.1
female yaf	51	33.3	41.2	11.8	13.7
summer					
large male	63	34.9	19.0	28.6	17.5
small male	26	38.5	26.9	19.2	15.4
female py	103	56.3	23.3	15.5	4.9
female yaf	76	30.3	36.8	23.7	9.2

Best fitting model for group size(G), population class(P) and season(S): GP (df=12; G=9.18; p=0.09)

Female wallabies with young-at-foot were more likely than other population classes to be with one other animal, the other animal often being their own young. However, whereas female kangaroos with young-at-foot were hardly ever seen alone, without their young, female wallabies with young-at-foot were often seen without their young. Female wallabies with pouch-young were more likely to be alone than other classes of wallaby and they were found in groups of 1 or 2 more often than males.

7.3.6 Comparison of grouping behaviour at night and in the day-time

Grouping behaviour has been suggested to be an anti-predator strategy, evolved in those species for which conspecifics do not compete heavily for resources and which live in habitat that allows animals in a group to maintain visual contact (Jarman, 1974).

Darkness may pose a number of problems to animals which use grouping as an anti-predator strategy. Group members need to see one another to benefit from the early detection of predators by a group member. If, as seems likely, predation risk is higher at night because of poor visibility there may be a tendency for animals to form larger groups at night for protection. However, being with others in a group at night may also be a disadvantage because predators are more likely to find a group than an individual at night because the group will have a stronger smell, make more noise and present a larger visual image. In this case it may be better for animals to separate and try, by being cryptic, to avoid detection. The following three hypotheses predict a larger or smaller group size at night compared to the day and are followed by a number of predictions which follow from the hypotheses:

- 1) Group size will be larger at night compared to the day because it is more difficult for animals to spot predators in the dark and the more animals there are in the group the more likely it is that one group member will see, hear or smell the predator. Larger group sizes will only decrease the risk of predation if there is communication between group members. I would expect distances between group members to be smaller at night compared to the day-time to allow group members to maintain good visual and auditory contact.
- 2) Group size will be smaller during the night than in the day because of the difficulties in using grouping as an anti-predator strategy at night; it is easier for the predator to detect a group and difficult for group members to detect predators. If animals use crypsis more at night to escape predators rather than grouping then I would expect animals to be feeding in areas with a greater amount of cover at night. I would also expect quite a sudden change in grouping behaviour at dawn and dusk, rather than a continual change through the night.
- 3) Group size will be smaller at night because of the difficulty of maintaining group cohesion in the dark compared to day-light resulting in animals from groups drifting apart. One would predict greater nearest-neighbour distances at night compared to the day and gradual declines in group size during the night.

To test these hypotheses and the predictions that follow, the grouping behaviour of the kangaroos that were followed for 24 hours (see Chapter 3) was analysed. Every change in the composition of the group that the focal animal belonged to was recorded and hourly rates of changes in group composition were calculated. The mean group-size that each focal animal belonged to was calculated for the hours of daylight and darkness. The mean group size for male and female focal animals in summer and winter are presented in Table 7.6. An analysis of variance with sex and season as grouping factors, and day/night as a within-group factor showed a significant difference between night and day, but not between other factors.

Table 7.6 Comparison of the group sizes of focal animals that were followed for 24 hours (kangaroos only), grouped by sex of focal animal and season of the following. The means ($\pm$ s.e.m.) and are compared by an analysis of variance, with sex and season as grouping factors, and time of day (day/night) as a within-group factor.

	Typical group size			
	male summer	male winter	female summer	female winter
Day	10.4 $\pm$ 2.3	5.7 $\pm$ 1.0	7.4 $\pm$ 2.0	7.4 $\pm$ 1.7
Night	3.5 $\pm$ 1.5	4.1 $\pm$ 1.3	3.9 $\pm$ 1.2	2.6 $\pm$ 0.9
n	5	5	5	4
Source of variation	df		F	p
season	1		0.47	0.50
sex	1		2.20	0.16
sex x season	1		0.62	0.44
time of day	1		19.32	0.0005
sex x time	1		0.00	0.98
season x time	1		1.05	0.32
sex x season x time	1		2.81	0.11

There was a large amount of variation in the group sizes of focal animals, largely because of the small sample sizes. However, there were clear differences in group size between night and day, differences seen for both sexes and in both seasons. The difference in group size between night and day was larger in summer for males, with group sizes of the male focal animals being particularly large in summer.

Given that kangaroos were found in smaller groups at night, at what time did this change in grouping behaviour occur? Did it happen immediately after dark or was the change gradual over the course of the night? Figures 7.6 a-d plot the mean group-sizes of the focal animals, each hour, for the 24-hour period. The plots are the means for the 24 kangaroos which were followed successfully.

In both seasons, and for both male and female focal animals, there was a dramatic drop in mean group size in the hour before dusk. Group sizes were high in the morning and afternoon feeding periods (in the three hours after dawn and three hours before dusk), although in winter females were in larger groups in the middle of the day than at other times. The drop in group size prior to dusk suggests that kangaroos are deliberately breaking up into smaller groups before dark, rather than drifting apart after dark.

The distances to, and identities of, the nearest adult male, adult female, male young and female young were recorded every five minutes. Because kangaroos in groups were closer together when resting than when they were feeding, distances were calculated when kangaroos were feeding and when they were resting. Mean distances were calculated for day-time and night-time separately and the means for each class of neighbour were compared between light and dark using a Wilcoxon matched-pairs test. Table 7.7 presents the differences in distance to nearest neighbours between night and day.

Table 7.7 Differences in distances to the kangaroos of specified class nearest to the focal animals which were followed for 24 hours. Positive numbers indicate neighbours were further apart at night and negative numbers indicate neighbours were nearer at night than in the day. Sub-adults are grouped with adult males and females and young animals are young-at-foot. Asterisks indicate a significant difference ($p < 0.05$) in the distances between night and day using a Wilcoxon matched-pairs test.

sex of focal animal	nearest to focal animal			
	adult male	adult female	young male	young female
<u>Feeding</u>				
male	+3.3 *	+3.3	+0.4	+2.9
female	+2.8	+1.5	-2.0	-2.5 *
<u>Resting</u>				
male	+2.0	+3.8	-0.4	-0.2
female	-6.8 *	+2.4	+0.9	-0.4

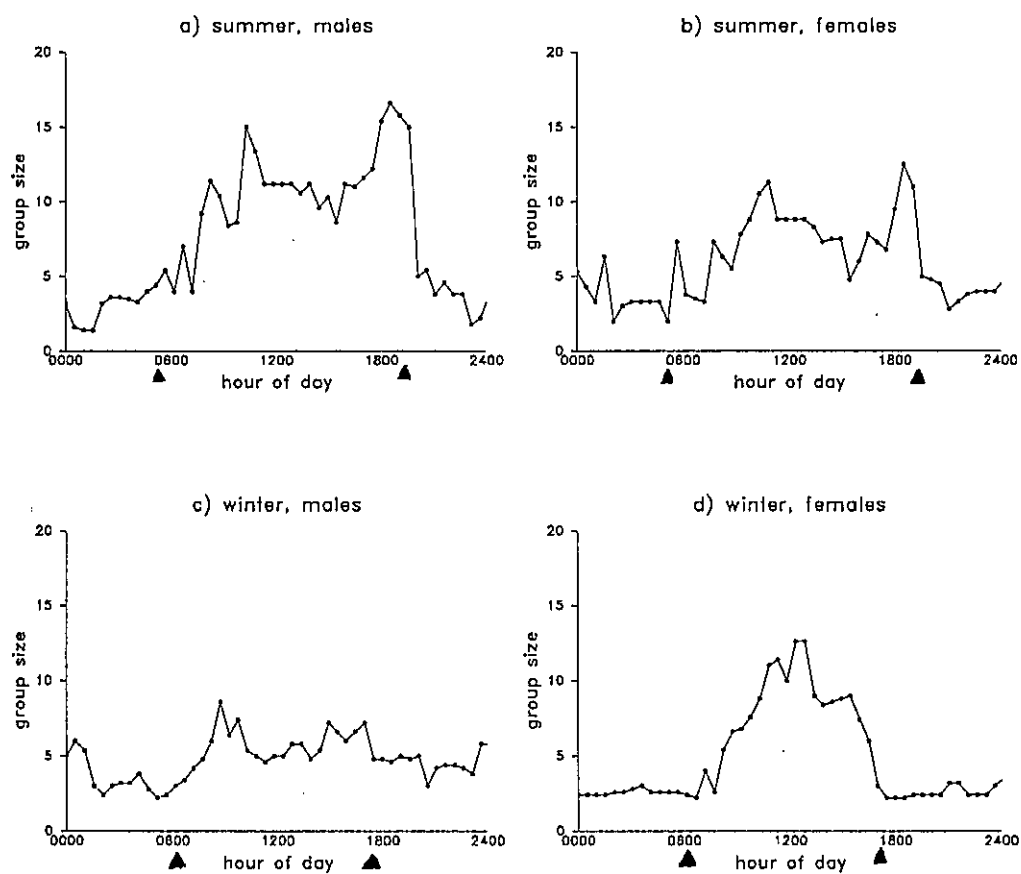


Figure 7.6 Means of the sizes of the groups that focal kangaroos were in recorded at half-hourly intervals over 24 hours. Male focal animals, summer (a) and winter (c), and female focal animals summer (b) and winter (d).

The nearest adult neighbours of resting and feeding focal animals were further away at night than in the day, although the difference was significant only for males and their adult male neighbours. The only exceptions were resting females which were closer to adult male neighbours at night. Female focal animals were closer to female young-at-foot at night than they were in the day-time and the difference, though not significant, was in the same direction for females and male young-at-foot. Thus, there is some evidence that kangaroos may be drifting apart at night compared to the day. The exception is feeding females and their young-at-foot which stay closer together at night compared to the day.

7.3.7 The effect of group size on foraging behaviour

The preceding sections describe how grouping behaviour of kangaroos and wallabies varies with the vegetation available, the cover available and between different times of day. In addition population classes differ in the size of groups they belong to. I have suggested that group size may vary in accordance with the resources available and the risk of predation facing group members. In this section I intend to explore some of the relationships between foraging behaviour and group size in order to consider some of the costs and benefits of grouping behaviour.

In preceding chapters, and in sections of this chapter, feeding behaviour has been shown to differ between seasons and sward types. To look at the effect of group size alone on feeding behaviour, separate analyses were carried out for different vegetation areas and each season for which there were sufficient data. Swards were relatively uniform within the vegetation areas used in this chapter (Areas 1, 3 and 4), although they differed in composition and biomass between areas. Areas 1, 3 and 4 are described in detail in section 5.2.2. Group-size class was used as a grouping factor in an analysis of variance which compared the foraging behaviour of animals in groups of different sizes. The cutpoints for group-size classes were chosen to give a fairly even representation of the data in each group size class, but also to represent the range of group-sizes that were observed.

The foraging parameters which were chosen for the comparison should reflect some of the costs and benefits of grouping. Foraging and surveying time, and feeding rates may alter with group size because animals in larger groups need not spend as much time looking for predators if they can use the vigilance of other group members. Feeding rates and movement rates whilst feeding may alternatively reflect some competition between group members if animals in larger groups are having to move more often and leave food patches more quickly because of the approach of other group members. The following parameters were compared between 3-minute observations of kangaroos and wallabies belonging to each group-size class: proportions of time biting/selecting and surveying/chewing; feeding rates and biting ratio; bites per patch; head-up rate; and total

step number. The majority of parameters did not differ significantly between animals in different sized groups and Table 7.8 presents only the means and tests for cases where differences were significant at the 10% level.

Table 7.8 Means of foraging parameters for kangaroos observed in groups of different sizes in summer and winter in Area 3 and in summer only in Area 4 (there were insufficient data from different group sizes for a winter comparison in this area). Analyses of variance compare the means of each foraging parameter between group-size classes. Only parameters which gave a significant difference between group size classes are included.

	Group Size					F	p
	1-2	3-5	6-8	9-12	13+		
Area 3 in summer							
bite/select	63.4	61.8	71.4	68.2	75.9	2.19	0.07
survey/chew	36.4	32.7	28.4	29.3	21.6	2.61	0.07
head-up rate	6.4	5.6	6.3	5.9	4.3	2.34	0.06
Area 3 in winter							
bite rate 2	36.3	41.4	39.9	34.8	55.9	4.39	0.004
biting ratio	0.66	0.72	0.74	0.85	0.59	3.07	0.03
head-up rate	2.8	5.4	3.9	3.0	2.4	4.87	0.002
step total	4.0	3.0	2.8	3.3	9.2	3.21	0.02
Area 4 in summer							
bite rate 2	67.0	47.8	53.3	49.2	49.0	2.76	0.04

There was some evidence that kangaroos in large groups feeding in Area 3 in summer spent more time biting/selecting bites and less time surveying than kangaroos in smaller groups. However, the differences between the means were not even significant at the 5% level. In winter in Area 3, and in Area 4 in summer there was no evidence that kangaroos in larger groups spent more time biting and less time surveying than those in smaller groups.

Where means for other parameters did differ between group-size classes there was no evidence for a linear response to group size, or a general increase or decrease with group size. The uninterrupted biting rates of kangaroos feeding in Area 3 in winter were highest for kangaroos in the largest groups but in Area 4 in summer this biting rate was highest for kangaroos in groups of 1 or 2.

Although there were some differences in foraging behaviour of kangaroos feeding in groups of different sizes the means for different group-size classes did not show a simple relationship with group size. Changing the cutpoints for group size classes often changed the results, suggesting that the differences may have been obscured or altered by the divisions used. Regression analysis was therefore carried out using each observation as an individual point. Table 7.9 presents the results of regression analyses for Area 3 in each season. There were no significant regressions for Area 4 in summer and there were insufficient data for the area in winter.

Table 7.9 Results of regressions of each foraging variable on group size of the forager, in Area 3 in summer and winter. The direction of the relationship is indicated by (+) for a positive, and (-) for a negative, relationship between group size and the foraging variable.

	R	summer F _{1,62}	p	R	winter F _{1,30}	p
biting/selecting	+0.48	18.45	0.0001	+0.19	1.20	0.28
surveying/chewing	-0.44	15.12	0.0002	-0.19	1.07	0.31
bite rate 1	+0.27	4.89	0.03	-0.01	0.01	0.97
bite rate 2	-0.32	7.15	0.01	-0.10	0.32	0.57
biting ratio	-0.24	3.95	0.05	-0.23	1.72	0.29
head up rate	-0.26	4.43	0.04	-0.35	4.24	0.05
step total	-0.42	13.12	0.001	+0.41	6.11	0.02

In summer 48% of the variation in biting/selecting time and surveying time could be explained by group size but in winter there was no relationship between group size and feeding. As expected, kangaroos in large groups spent more time looking for and collecting their food and less time surveying than did kangaroos in small groups. The rate of kangaroos lifting their heads to survey was related to group size in both seasons, with the rate declining as group size increased.

The uninterrupted biting rate was lower in summer as group size increased, which is the reverse of the pattern shown in the AOV results for winter. The regression of total step number with group size was also negative in summer which means that kangaroos in large groups were moving less whilst feeding. In winter, however, kangaroos feeding in large groups took more steps whilst feeding than those in small groups.

The regression of biting ratio on group size in summer just failed to reach significance at the 5% level but the relationship was negative. Kangaroos feeding in larger groups

took more bites in three minutes than those in smaller groups but took fewer bites per unit time of uninterrupted biting.

The feeding rates of wallabies in different group sizes were compared on Area 1. Group size was divided into four classes: 1,2,3, and greater than three. Table 7.10 gives the regression coefficients, F values and significance for tests of those coefficients.

Table 7.10 Results of regression analyses of foraging parameters with group size, for wallabies feeding in Area 1 in summer and winter. The direction of the relationship is indicated by (+) for a positive, and (-) for a negative, relationship between group size and the foraging variable.

	R	summer F _{1,12}	p	R	winter F _{1,27}	p
biting/selecting	+0.64	6.76	0.03	-0.29	2.28	0.14
survey/chewing	-0.65	7.31	0.02	+0.21	1.16	0.29
bite rate 1	+0.87	30.78	0.0002	-0.30	2.68	0.11
bite rate 2	+0.78	15.85	0.0003	-0.003	0.00	0.98
biting ratio	+0.57	4.93	0.05	-0.01	0.00	0.96

In summer, 65% of the variation in biting/selecting time and survey/chewing time was explained by group size. Like kangaroos, wallabies in larger groups spent more time biting/selecting bites and less time surveying their surroundings. Unlike kangaroos both the interrupted and uninterrupted biting rates also increased with group size. The increase in interrupted biting rates could be partly explained by the higher proportion of feeding time spent biting. The increase in uninterrupted biting rates with group size suggests that wallabies in large groups were either being less selective, were feeding in different patch types to wallabies in small groups or were less disturbed whilst foraging.

7.4 Discussion

7.4.1 Seasonal changes in group size

The typical group sizes of eastern grey kangaroos and red-necked wallabies differed, as expected, by a factor of more than 3. The typical group size for wallabies was the same as Johnson (1989a) found for the same population between 1981 and 1984. Southwell (1984a) has suggested that comparisons of group size between species and populations should take population density into account since group size has been shown to vary with population density (Taylor, 1981; Southwell, 1981). During the seven months that the searches were conducted, the mean density of kangaroos, calculated from the actual number of animals in the 210 ha study area, was 38 km⁻². The majority of my search area fell within the high-density zone of the lower slopes (Jarman and Southwell, 1986) and the density I recorded was similar to that recorded in previous years for the same area of 40 km⁻² (*ibid*). When these figures of population density and typical group size are plotted on Southwell's (1984) graph, for the same species in an open woodland habitat in the New England region, the point lies just within the upper 95% confidence limit for typical group size at a density of 38 km⁻², suggesting that the levels of sociality are similar at the two sites.

Group size was greater in winter in all time periods for red-necked wallabies and all but the afternoon for kangaroos. Larger group sizes in winter have been recorded for a number of species of macropod although different reasons have been proffered. Johnson (1980) found agile wallabies in larger groups in winter and attributed the increase to shortages of food, although he does not comment on the differences in distribution of food items between summer and winter. Johnson (1989a) suggests that larger groups of red-necked wallabies in winter are the result of wallabies aggregating on remaining patches of high quality food, particularly clover. Johnson (1983) suggested that the larger groups of western grey kangaroos in autumn and winter are due to greater intrasexual gregariousness of males at this time, perhaps to enable males to assess each other's dominance status relative to other males in the population. Both Taylor (1981) and Southwell (1984a) found no significant change in group size of eastern grey kangaroos with season, and Jarman and Southwell (1986) report a slightly higher group size in summer compared to winter, although they do say this could be attributed to the larger number of young-at-foot around at this time.

7.4.2 Changes in group size with pasture quality

Changes in group size with season seem likely to be related to the dispersion and abundance of food items. This is supported by the frequencies of different group sizes seen on different sward types in winter. Large groups were seen more frequently on better quality swards and probably represent animals aggregating on high quality patches

and/or large groups being accommodated on these swards because reduced competition leads to a larger optimal group size. If competition brought about smaller groups on poorer quality sward types then I would expect the rates of displacements, interactions and movements to be higher on these swards with a given group size. There was some evidence in Chapter 6 that this was so; those individuals that engaged in displacements or interactions were more likely to be in large groups than those that did not.

The interaction between pasture quality and group size is further illustrated by the different seasonal changes in group size on poor and good quality swards. Swards dominated by carpet grass and annual grasses that made up the majority of 'other grasses' occupied a large part of the study area (see Chapter 4) and had a higher proportion of dead leaf in the sward in winter. Swards dominated by *paspalum* and *kikuyu* were less common and tended to occur in small patches, encouraging an aggregation of foragers. Area 4 (see Chapter 5 for description), which had an almost pure sward of *kikuyu*, often attracted smaller groups from different directions to forage there; they then coalesced into larger groups.

There was less seasonal variation in the typical group size of wallabies but there was a tendency for larger groups to be formed on swards dominated by *paspalum* and 'other grasses'. The grasses which made up the 'other grasses' category for sites used by wallabies included weeping grass and sedges more often, which were of a higher quality than annual grasses in the sites used by kangaroos (see Chapter 2).

7.4.3 Group size and the availability of cover

The species showed different grouping responses to the availability of cover vegetation, with kangaroos tending to be in smaller groups when cover was not available whilst wallabies were in larger groups in this situation. The type of cover appeared to make a difference to the response in winter, with the frequencies of group sizes similar in areas with no cover and with tussock cover but different with blady grass cover; blady grass provided denser and taller cover than tussock grass. In other studies kangaroos have been shown to be in larger groups in open habitats than in closed ones (Southwell, 1981; Heathcote, 1987). Similarly larger group sizes in bovid species have been associated with decreasing cover and increasing openness of habitat (Jarman, 1974). The height of the cover provided at Wallaby Creek is low in comparison to that provided by trees and shrubs, and may not provide any greater protection for the larger kangaroos than no cover. The tendency for wallabies to be in larger groups in open areas could be attributable to their being more vulnerable without the protection of cover vegetation, to a difficulty in maintaining group cohesion or to higher quality sward types being associated with a lack of cover (see Chapter 4).

7.4.4 Group size and population class

Female eastern grey kangaroos were almost never seen apart from their young-at-foot and the probability of females in this class being in groups of two (i.e. with their dependent young) was much higher than for other population classes. This pattern has been demonstrated before for this population (Jarman and Southwell, 1986; Stuart-Dick, 1987), for eastern grey kangaroos in other locations (Taylor, 1982; Southwell, 1984b) and for other *Macropus* species (Croft, 1981; Johnson, 1983; Taylor, 1983b). Various reasons have been proposed including the vulnerability of young animals in a group at the time of an attack (Jarman and Coulson, in press), the poor 'locomotor' ability of the young restricting the pair's movements (Croft, 1981) and the importance of mother-young bonding at the vulnerable stage of pouch-emergence (Stuart-Dick, 1987).

By contrast, whilst female red-necked wallabies also spend a large proportion of their time with only their young-at-foot, they are also often alone. Kangaroo young-at-foot run with their mother from the moment of permanent emergence, and are rarely separated from them, even in the first weeks after weaning (Stuart-Dick, 1987). Female red-necked wallabies hide their young-at-foot in dense vegetation for long periods, especially in the first weeks after permanent emergence, only joining their young to suckle them (Johnson, 1985). The adaptive significance of this behaviour is presumably the same as for small bovid species whose young are too small to flee predators (Jarman, 1974), and whose small groups hold few other young for the dilution of prey to be of benefit.

Large adult male kangaroos tended to be more solitary than other classes in winter and than females in summer. However, large males at Wallaby Creek (see also Jarman and Southwell, 1986) tend to be less solitary than those in other studies of large kangaroos (see Jarman and Coulson for table of figures). This could result from differences in the frequencies of large males in the populations or because the study area included the core area for a mob of kangaroos outside which there is more movement of males between mobs. Some large males did disappear from the study area for days and weeks at a time and it is likely that they spent much of this time alone. The solitary nature of large males has been attributed to their movement between groups of females in search of females in oestrus (Southwell, 1984b; Jarman and Southwell, 1986). As mentioned in Chapter 3, the movement of males between groups need not occur every day, and the more bimodal distribution of group size frequencies for this class (high at group size 1 and 5-10) may result from males alternating being solitary with associating with large numbers of females.

The relatively large group sizes of female eastern grey kangaroos with pouch-young may be explained, in part, by this class of female being the most likely to come into oestrus given continuous breeding. Pro-oestrous females are often accompanied for a week or more prior to oestrus, by a group of males of varying body size which is dominated by the alpha male. Red-necked wallabies come into oestrus about the time

that pouch-young emerge from the pouch permanently (Johnson, 1985) and, unlike female kangaroos, female wallabies with pouch-young were more likely to be alone and less likely to be in large groups than those with young-at-foot.

It appears that differences between population classes in social relationships and predation pressures could adequately account for differences in the group sizes exhibited by them. Of course, differences in energy needs and resulting competition pressures may also play a role. Johnson (1989b) demonstrated that males and females in oestrous groups interact with one another far more frequently than animals in other groups and alpha males which spend the greatest amount of time in such activity may suffer seriously from disruptions to their feeding routines (Jarman and Southwell, 1986). Early in the study at Wallaby Creek alpha male kangaroos appeared to remain in that position for only a year before rapidly deteriorating in condition and eventually dying (*ibid*). More recently at least one alpha male has lost condition, moved out of the study area, regained condition and returned to resume his dominance (Jarman, Stuart-Dick and Clarke, unpubl. records). Thus, the solitary nature of large males may also be a strategy by them to spend periods of time foraging efficiently, without the distraction of other animals, to regain some of the energy lost during energy-expensive movement and interactions.

7.4.5 Group size in the day-time and at night

Both species were found in significantly smaller groups at night than in the daytime, the difference being more pronounced in summer than winter. Kangaroos were in larger groups in the middle of the day in winter, and in the afternoon in summer, than at other times. Taylor (1982) suggested that eastern grey kangaroos were found in larger groups in the afternoon because groups coalesce during the day whilst animals rest in sheltered habitat. He suggested, as Kaufmann (1974a) did for whiptail wallabies, that groups probably break up during the night because group sizes in the morning are smaller. However, they presented no data on group sizes at night to support this claim. Group sizes of wallabies were greatest in the morning, despite their having been relatively solitary at night.

In the introduction I predicted that smaller groups at night could arise from animals attempting to escape detection by predators by being cryptic, and/or from groups breaking up because of the difficulty of maintaining group cohesion in the dark. The dramatic drop in group size prior to dusk suggested that kangaroos were deliberately breaking up into smaller groups before dark, rather than drifting apart after dark. In Chapter 3, I mentioned that in summer kangaroos moved further upslope around dusk, and remain upslope until dawn. This movement of kangaroos could have coincided with the breaking up of groups such that changes in group size were more related to animals

changing their micro-habitat rather than their gregariousness. However, the movement upslope was not significant in winter, whereas the changes in group size were.

If kangaroos are attempting to be more cryptic at night, compared to day, by being in smaller groups then I would expect them also to be found amongst cover vegetation more at night. This did not appear to be the case for either species in winter; in both seasons wallabies were least likely to be in cover at night but in summer kangaroos were more likely to be in areas providing cover at night than at other times (see Table 4.4). As I mentioned in Chapter 4, the distance to cover is probably more important for wallabies than its availability. Wallabies may still benefit by being more solitary at night if predators are less likely to detect single animals than groups. The seasonal differences in night-time grouping behaviour and micro-habitat use of kangaroos are probably related to the availability of burnt swards on the lower slopes in winter, and the lack of cover vegetation in these burnt areas.

Kangaroos tended to be further apart at night compared to the daytime, although the difference for foraging animals was significant only for males and their adult male neighbours, and the differences in distance were small. Females were surprisingly close to their young at night given the difficulties of keeping track of small, young animals in the dark, especially if they are hidden in dense vegetation. There was, therefore, some evidence that adult kangaroos drifted apart in their groups at night whilst females and their accompanying young remained a close unit.

I have been unable to locate other examples of animals being found in smaller groups at night than in the daytime so I am unable to comment on whether this is a general phenomenon, despite the fact that macropods are predominantly nocturnally active. However, in order to record group size at night, animals must be well habituated to spotlights and human observers. Kaufmann (1974b) suggested that the apparent lack of sociality in many macropod species may be attributable to their nocturnal behaviour, and difficulties in maintaining group cohesion and interacting socially in the dark. The consequences of the nocturnal behaviour of kangaroos and wallabies, in terms of their ability to socialize, their foraging efficiency and energy use will be discussed in Chapter 8.

7.4.6 The costs and benefits of grouping behaviour

There was some evidence that kangaroos^{in large groups} spent less time surveying and more time foraging in Area 3 in summer, but there was no evidence of such a relationship in that area in winter, or in Area 4. Similarly, there was some evidence for a relationship between the amount of time wallabies spent surveying or foraging and group size only in summer in Area 1. Although I fitted linear regressions to the data, the plots of the data points did not suggest that the relationship would be better explained by a curvilinear relationship. Jarman (1987) found that Michaelis Menton equations provided the best fit

to his data suggesting an asymptote in the benefits of being in a large group. He found the most change in foraging and surveying time between group size 1 and nine, whilst Southwell (1981) found an asymptotic group size of 3 to 4 for the same species. The highly significant relationship between group size and foraging time in Jarman's study may have been due to his collecting the data in one location and on one day, thus reducing the variability in the sample.

Relationships between group size and vigilance time (and conversely foraging time) have been demonstrated in a number of field studies, on a variety of species (see section 7.1.2). However, a closer examination of these studies shows that many of them were far from conclusive in their support of the relationship between vigilance time and group size. In the study by Berger *et al.* (1983) a relationship was found at only one site. Underwood (1982a) found a relationship for 3 out of the 5 species he studied, and in Smith's (1977) study a weak correlation was found for females but no relationship for males. In the studies by Lipetz and Bekoff (1982) and Poysa (1988) the relationships were weak and in the former, the relationship was due only to the difference between solitary animals and those in all other group sizes. Some authors expressed surprise at the lack of a strong correlation in their data and it is reasonable to expect that many unreported studies have found no relationship at all. I can only add that in this study, in some foraging situations, a relationship was found between vigilance time and group size, but in others it was not.

The interrupted feeding rates of both species increased with increasing group size in summer, but not in winter. This result is expected on the basis of animals spending less time surveying in larger groups in this season. However, the uninterrupted biting rates also changed with group size but in different directions for the two species. Wallabies increased their biting rates with increasing group size whilst kangaroo biting rates declined. The range of group sizes shown by kangaroos was greater than for wallabies and it is possible that at larger group sizes, animals begin to interfere with one another when feeding, depressing feeding rates. However, kangaroos moved less often and raised their heads less often as group size increased, which does not suggest greater interference between animals.

Although the observations of kangaroos feeding described in Table 7.9 were made only in Area 3, there may still have been some variation in the sward between months or parts of the area that could have attracted groups of different sizes and accounted for differences in biting rates. Group size accounted for much more of the variation in uninterrupted biting rates of wallabies in Area 1. As group size increased biting rates also increased, perhaps because wallabies in larger groups were less distracted by the need to survey the environment when there were more wallabies in the group able to contribute to vigilance.

The effect of group size on foraging behaviour of the two species was variable, and even changed for the species in different seasons and locations. The lack of any relationships between group size and the foraging variables in winter may be explained by animals being near the limits of their foraging capacity because of low food availability and therefore there being little opportunity to alter foraging behaviour in accordance with the benefits of grouping. When food items are scarce and of poorer quality increased competition between animals in large groups may balance any benefits in terms of reducing the time that animals need to remain vigilant.

The sward in Area 3 is dominated by carpet grass; in summer kangaroos were found in larger groups on swards dominated by carpet grass which supports the idea that the benefits of grouping were greater in this season than in winter. Wallabies, on the other hand, tended to be found in larger groups on swards dominated by *Paspalum* (as in Area 1), in winter than in summer. This is despite the fact that the benefits of grouping appear to be confined to summer. Johnson (1989a) suggested that the large groups of wallabies seen in winter may have been the result of wallabies aggregating on restricted food patches. He found wallabies were further apart in this season and suggested that groups were also less stable. The lack of a relationship between group size and foraging parameters in winter may be the result of groups being less cohesive in this season.

The benefits and costs of grouping appear to vary for the two species, between seasons and locations. The fact that no clear relationships emerged between foraging time and rate, and group size suggest that kangaroos and wallabies may be doing quite a good job of balancing the costs and benefits of grouping according to the precise foraging conditions they experience. In addition, there were probably other factors in the environment which covaried with group size that I did not measure in this study. A study of the foraging behaviour of groups of animals, in the same location, and at the same time may help to determine which foraging parameters besides surveying time are dependent on group size. Unfortunately, the size of the population and the nature of the terrain did not allow me to make enough observations under identical conditions.

CHAPTER 8

Synthesis and conclusions

8.1 Introduction

In chapter 1 I defined the following aims of the study:

- i) to compare the foraging behaviour of two closely related species of differing body size which live sympatrically and potentially compete for the same resources;
- ii) to compare two species with different social organizations to look at the interaction between foraging behaviour and social organization, with particular emphasis on the role of body size;
- iii) to compare the foraging tactics of the two species on swards with different vegetation characteristics;
- iv) to compare macropod and ruminant species for their tactical foraging responses to changing sward conditions.
- v) to compare the foraging tactics of individuals in different population classes to see whether population classes have different foraging goals depending on their energy demands, social behaviour and risks from predation.

In the following Chapters I discussed the foraging tactics of the study species including: when animals forage; where they feed; what they eat; how fast they eat; how far they move whilst feeding. In this final chapter I summarize the success of the methodological approach adopted. I then discuss the differences in foraging tactics shown for each of the above comparisons, and discuss the causes and implications of the differences. I shall conclude by suggesting how the findings of this study contribute to our understanding of the theory of foraging strategies and the evolution of social organization.

8.2 Appraisal of the methodology used in the study

There have been many dietary studies of macropod species (see Dawson, in press for review) but there have been very few quantitative studies of their foraging behaviour, especially for free-ranging macropods. Measuring the different components of food intake of herbivores requires either habituated animals which allow close observation or remote mechanical and electronic means of measuring foraging time, biting rates, bite size and bite composition. The eastern grey kangaroos and red-necked wallabies at Wallaby Creek were exceptionally habituated to human observers, allowing me to make detailed records of their rates of movement and feeding. There are many advantages of recording foraging rates by observation, one being that I was able to record exactly where animals were feeding and thus relate rates of biting to specific elements of sward structure. I was also able to record events that may have affected the animals' behaviour, such as unusual disturbances, the approach of conspecifics and the appearance of predators.

There were, however, elements of foraging behaviour that I was unable to quantify in the field and future studies may benefit from a combination of field work and captive studies. Both species graze selectively, often plucking complete blades of grass from the sward, and I was not confident that I could measure bite size or determine bite composition from observations of the animals and examination of the sward following biting. My inability to make these measurements meant that I was unable to determine rates of nutrient intake that are necessary to calculate the profitability of food items as a precursor to developing foraging models. Allowing captive animals to bite from pre-measured turves may provide an accurate estimate of bite size and bite selection. However, I was able to observe animals foraging on the same swards, in conditions where I expected there to be little variation in bite size and bite quality, and so compare relative rates of intake of the population classes and species.

I chose to use focal animal sampling methods for the majority of my data collection because I wanted to record foraging behaviour continuously, and in great detail, in order to obtain rates of biting and movement. I had expected to be able to measure some of the costs of grouping behaviour in terms of rates of interactions, displacements and movements. However, the rates of interaction and displacement were so low that I was only able to make a few comparisons with them. Simultaneous observation of each member of a group or subgroup may show that there are subtle competition effects of grouping, such as changes in orientation, and subtle beneficial effects, such as the communication of alarm, that are not immediately noticeable when observing individuals. Analysis of videos of groups of foraging animals should prove useful in identifying these more subtle effects.

Continued observation of individuals over a 24-hour period did provide many interesting insights into the animals' allocation of time to various activities, their changing use of habitat through the day and their association with other animals. There was some evidence from the study that individuals' strategies for foraging and movement change from day to day, and repeated followings of some individuals (large males in particular) could give a greater insight into intra- and inter-individual variation in behaviour. The nocturnal observations demonstrated that kangaroos and wallabies alter many aspects of their foraging behaviour after dark. As equipment for night-time observation becomes more sophisticated, detailed studies of the behaviour of animals at night and the day-time may explain why, and how, some species of macropods have become more diurnal than others. However, we need to know more about how macropods perceive their environment in the dark before we can develop hypotheses to explain their nocturnal behaviour strategies.

One of the major problems with studying foraging behaviour of animals in the wild is that many environmental variables, that have an impact on foraging behaviour, interact with one another. Some of the confounding variables affecting diet selection were eliminated in the experimental trial at Newholme and the results of that study contributed to the interpretation of the field data. Work with captive, or semi-captive animals, under controlled conditions may complement observational field studies by helping to answer more specific questions concerning foraging behaviour. Continued development of multivariate-analysis techniques will also contribute to the interpretation of field studies which involve many environmental variables.

8.3 Ecological overlap between the species and the opportunities for competition

Casual observations of eastern grey kangaroos and red-necked wallabies at Wallaby Creek suggest that they occupy very similar niches in the valley. Both are active during the night but also for a good portion of the daylight hours, setting them apart from the valley's other macropod species which were strictly nocturnal or crepuscular. Both species graze on the open pastures, often utilizing the same patches at the same time. And both species are preyed upon by dingoes, with their young animals being at greatest risk, although red-necked wallaby young are also particularly vulnerable to predation by wedge-tailed eagles. However, closer examination of the activities, behaviours and diets of the species indicated that a number of differences exist which may reduce the level of competition between the species.

8.3.1 Activity schedules

Both the eastern grey kangaroo and the red-necked wallaby are unusual amongst marsupial species in being active during daylight hours as well as at night. Both species were highly active in the few hours after first light and before dusk, but wallabies tended to have a longer daytime resting phase than kangaroos. Unfortunately, our lack of success in following wallabies for 24 hours restricted my ability to compare the species' activities and movements over a 24-hour period. Wallabies appeared to rest longer than kangaroos, both at night and during the day, a difference which may relate to their higher-quality diet (see later) and lower absolute energy requirements.

8.3.2 Resting locations

Wallabies and kangaroos moved a similar distance during a 24-hour period, a distance that was comparatively far for the wallabies given their smaller body size. Movement to and from resting sites accounted for a large portion of the total movement of wallabies but kangaroos often rested in the open, close to where they had been grazing. The difference between the species in their choice of resting sites appeared to reflect different anti-predator strategies while resting. Kangaroos gathered together in large groups in the shade at the end of the morning foraging period and made little effort to conceal themselves whilst resting. Lying was their most common posture for resting but there were usually one or two kangaroos standing crouched or bent in each group at any one time. Wallabies generally moved off to resting sites alone and chose sites with dense vegetation, in gullies or the forest, that concealed them from predators. They preferred to rest in the sitting posture and those individuals that did lie down were usually large males. So whilst kangaroos and wallabies occupy overlapping home ranges at Wallaby Creek they do have different habitat requirements within their home ranges. Wallabies

use open pasture for foraging but, unlike kangaroos, they require the shelter of forests or vegetated gullies nearby for resting or hiding.

8.3.3 Selection of feeding sites and diet

The causes and consequences of feeding style differences between antelope species were discussed by Jarman (1974) and one of the aims of this study was to see if similar relationships might apply to macropods. Jarman suggested that the quality of an antelope's diet is set by the species' body size and digestive capacity and that small species require relatively high quality diets (*ibid.*). Differing distributions of high and low quality food items give rise to a range of feeding styles amongst the species, each adapted to the type of dispersion of the species' preferred food items. Wallabies are approximately a third of the body weight of kangaroos and I predicted that they would have a higher quality diet. Although high-quality food items are rare and dispersed in a natural environment (Jarman, 1974), the introduction of highly digestible pasture species to the Wallaby Creek valley has changed the natural pattern of food dispersal there, creating some large areas of high quality grass. The difference between the dispersal of food items in natural grasslands and the improved pastures of Wallaby Creek had to be accounted for when interpreting the data.

Diet selection is the result of selection at a number of levels: the selection of site, the selection of a plant species within the site and perhaps the further selection of plant part (Bunnell and Gillingham, 1985). Patches of vegetation that had been burnt induced the biggest contrast between the preferences of the species for different feeding sites. Kangaroos showed a strong preference for burned vegetation patches, and the newly exposed shoots and leaves of tussock grasses and blady grass featured prominently in the diets of kangaroos in the few months following the burning event. By contrast, wallabies avoided areas that had been burned and avoided burned grass species in their diets.

The chemical analysis of the leaves of burned grasses showed that they were on average lower in fibre and higher in nitrogen content than leaves sampled prior to burning or later in the season. However, they were higher in fibre and lower in nitrogen content than leaves of most of the introduced grasses in the intertussock sward. The intertussock swards were low in biomass at the time of burning and contained a high proportion of dead vegetation which probably impeded selection of green leaves. Foraging in burned areas allowed kangaroos similar rates of biting as on the intertussock sward and also provided them with a greater bite size.

Whilst kangaroos were foraging on the burned species, wallabies continued to eat carpet grass, the most abundant grass in the study area, and selected the less abundant and more dispersed paspalum. Wallabies also selected clover which was ignored by kangaroos. Their foraging rates were lower than those of kangaroos foraging on the same swards, both because of their increased vigilance (see below) and because of their longer

search time per bite. Over most of the study area paspalum was dispersed amongst the swards of carpet grass or found growing within tussocks, but in vegetation area 1 it dominated the sward. Despite the abundance of paspalum in this large area kangaroos were rarely seen there, except on wet and windy days. There is evidence that sheep make some foraging selections on the basis of sward height (or biomass) and potential rate of intake (Kenney and Black, 1984). A strategy by kangaroos to maintain a rate of intake above a minimum threshold could result in them foraging on higher biomass swards, whilst a strategy by wallabies to maintain a diet of a minimum digestibility could result in them foraging selectively on swards with high quality grasses. Experiments where both sward biomass and quality are manipulated and intake rates are measured would help to predict what the optimal combination of biomass and quality are for each species.

Despite their differences in diet, the eastern grey kangaroos and red-necked wallaby showed a 73% overlap in the grass component of their diet which was the highest degree of overlap for all the combinations of macropod species in the valley (Jarman and Phillips, in press). Jarman and Phillips (*ibid.*) suggested that the dietary separations of the species are due mainly to different habitat selections of the species rather than to selection within the same swards. The similarities between the diets of the two most abundant species, the eastern grey kangaroo and red-necked wallaby, arise from their use of the most abundant resources, the sward-forming grasses like carpet grass (*ibid.*).

8.4 The relationships between body size, sociality and anti-predator behaviour.

There are three main ways in which animals can avoid being eaten: they can try to hide from predators; they can watch out for predators and flee before they are spotted by them; or they can flee or defend themselves once under threat. Increased efficiency of predator detection is thought to be one of the major benefits of grouping behaviour (Vine, 1971; Jarman, 1974) but competition for resources amongst animals in a group is thought to set the upper limit of group size (Jarman, 1974). Jarman (1974) suggested that antelope species use anti-predator strategies that are appropriate to their body size and habitat, with small species tending to be cryptic and solitary and sociality increasing with body size. One of the aims of this study was to examine the anti-predator behaviour of the two species and its effect on foraging behaviour. To do this I looked at group size in relation to sward quality and the provision of cover, and tried to determine the costs and benefits of grouping behaviour. I also compared the vigilance behaviour of the two species to see if there was any evidence that differences in their grouping behaviour and body size affected their relative vulnerability to predation.

8.4.1 Factors affecting group size

Kangaroos and wallabies were found in larger groups on better quality swards which initially suggested that competition on poorer quality swards might have been limiting group size. However, the areas with high quality swards of kikuyu and paspalum were small in comparison to the large areas dominated by carpet grass and tussock grasses. Group size differences on alternative swards may therefore have been the result of aggregation on limited food patches, not a restriction of group size through competition.

This also appeared to be the likely explanation for seasonal differences in group size; over all sward types group sizes were larger in winter than summer but on carpet grass swards they were smaller. In winter wallabies aggregated in the alluvial paddocks to make use of clover growing there and kangaroos aggregated on burnt patches to make use of the new shoots following burning.

The availability of cover vegetation appeared to have differing effects on the grouping behaviour of the two species, although there was an interaction between the availability of cover and sward type which may have accounted for some, or all, of this effect. Kangaroos were found in larger groups when cover vegetation was available, an unexpected result given that the cover probably interferes with group cohesion and makes animals less visible to their predators. Wallabies were found in larger groups when cover was *not* available but the lack of cover on high quality swards was a confounding factor. The difference in body size between the species may have been critical in determining the effects of cover on their visibility and ease of maintaining group cohesion, leading to different grouping responses for the species.

Although I predicted that kangaroos and wallabies might forage in larger groups at night because of the difficulty of detecting predators in the dark, both species foraged in smaller groups at night. The difference was not great for wallabies but was very marked for kangaroos. I suggested that difficulties in maintaining group cohesion may have caused the disruption of groups at night because there was a tendency for foraging kangaroos to be further apart at night than in the daytime. However, dramatic changes in group size occurred shortly before dusk suggesting that kangaroos did not simply drift away from others, but chose to be in smaller groups at night.

Grouping acts as an anti-predator strategy when group members are able to communicate with one another and warn of danger. However, a group is also more likely to be detected by a predator than a solitary individual. Optimal group size should represent a balance between the efficiency of detecting predators and the ease of being detected. The balance may change at night when animals rely more on their senses of smell and hearing to detect their prey or predators, and animals that group during the day may benefit from being more solitary and cryptic at night. There was no evidence that wallabies attempted to be more cryptic at night; wallabies were less likely to be found amongst cover vegetation at night than in the daytime. However, I had insufficient night-time observations of red-necked wallabies to test whether they actively left groups at night or drifted apart.

8.4.2 The costs and benefits of grouping behaviour.

An inverse relationship between group size and the mean surveying time for each member of the group has been demonstrated in a number of studies (e.g. Smith, 1977; Berger *et al.*, 1978; Bertram, 1980; Elgar and Catterall, 1981; Underwood, 1982a; Jarman, 1987) but the results of many of these studies have been far from conclusive. The results of this study were also inconclusive in that relationships between surveying time and group size were only found for summer observations, and then for some vegetation areas or sward types and not for others. However, an increase in the efficiency of detecting predators with increased group size, regardless of changes in surveying time, would be sufficient impetus for grouping behaviour to have evolved.

Optimal foraging theory has been concerned with finding the optimal solution for individual foragers, but many animals forage in groups and interfere and interact with one another whilst foraging. If the effects of grouping on foraging behaviour were simply to change the proportions of time devoted to head-down and head-up foraging behaviour then the effects of group size could be incorporated into foraging models quite easily. However, group size also had an effect on the uninterrupted biting rates of kangaroos and wallabies, and the effect was in a different direction for the two species. Uninterrupted rates of biting for kangaroos were negatively correlated with group size and I suggested that over the large range of group sizes shown by kangaroos, competition

effects may have reduced foraging efficiency in larger groups. The rates of interactions and displacements tended to be higher in large groups of kangaroos than in small groups which also suggested that foraging efficiency may be reduced in large groups. The relationships between group size and foraging variables are unlikely to be linear because of the counter-acting effects of vigilance and competition. Unfortunately, the heterogeneity of vegetation types in the study area and the area's small size did not allow me to remove all the confounding effects of sward structure and quality, as would be necessary to determine more complex relationships between group size and foraging behaviour.

8.4.3 Vigilance behaviour

In this thesis I have suggested and cited a number of reasons why wallabies may be at greater risk from predators than the larger kangaroos:

- i) they are less able to outrun their terrestrial predators and are less able to defend themselves from attack;
- ii) typical group size is smaller for wallabies than for kangaroos and if group size is related to the efficiency of predator detection then wallabies may be at greater risk than the more gregarious kangaroos;
- iii) small species are at risk from a greater number of predator species than large species because there is an upper limit to the body size that each predator can handle (Jarman, 1974);
- iv) whilst cover vegetation may provide more concealment to small species it will also restrict their fields of vision making them more vulnerable to a surprise attack.

Jarman (1974) suggests that because small species are unable to outrun their predators they must detect the predator first in order to escape, whereas large species, which are able to outrun their predators or defend themselves, have less need to detect their predators first. I therefore predicted that wallabies would show a range of behaviours that would decrease their chances of being detected and taken by predators. For example, they may devote more time and energy to predator detection or feed in "safer" areas than kangaroos.

Wallabies did devote a greater proportion of their foraging time to surveying the environment than kangaroos, and did so at the cost of time spent searching for and prehending bites. The partitioning of time to surveillance and the selection of food items may depend on the relative contributions of food and safety to an animal's reproductive success (Pyke *et al.*, 1977). Schoener (1971) suggested that animals could adopt two different optimizing strategies whilst foraging; they could be 'energy maximizers' or 'time minimizers' depending on whether they placed priority on foraging or other

activities. If surveillance is so important to the survival and reproductive success of wallabies then they might be adopting a time-minimizing strategy whilst kangaroos adopt an energy-maximizing one.

The importance of surveying behaviour to wallabies was also confirmed by their greater alertness, use of more upright postures and greater rate of surveying than kangaroos. The species also showed different preferences for foraging sites in relation to the amount of cover provided by the site. Wallabies were found more often in locations that did not provide cover, perhaps because of their need to spot predators before being detected themselves. However, the highly selective foraging behaviour of wallabies is not indicative of a time-minimizing strategy. An alternative hypothesis is that both species adopt an energy-maximizing strategy with different feeding-time constraints. Unfortunately the foraging strategies of the two species cannot be modelled without an accurate measurement of rates of food intake on different food types, data that I was unable to collect.

8.4.4 Why are wallabies less gregarious than kangaroos?

Studies of the gregarious members of the genus *Macropus* have shown that group size and population density are positively correlated (Southwell, 1981, 1984a; Taylor, 1982; Johnson, 1983), suggesting that grouping in these species is the result of random meetings of animals which share overlapping home ranges. However, Johnson (1989a) could find no relationship between group size and density for red-necked wallabies and he suggested that other factors cause grouping behaviour in this species. Wallabies are typically found in groups of one, two or three individuals and Johnson (1989) observed that many of these groups were the result of regular associations of mothers with their young, like-sized males which resolve differences in dominance rank through fighting and display, and oestrous females with parties of consorting males. It appears that social factors may account for many of the small groups of wallabies observed, and oestrus groups may account for some of the larger ones.

Associations between individuals also play a part in the social organization of eastern grey kangaroos (Jarman and Southwell, 1986, Stuart-Dick, 1987) but larger groups of kangaroos consist of a collection of these small sub-groups. Red-necked wallabies gather in larger groups in winter (Johnson, 1989a), but these groups have high rates of group flux, inter-individual distances are relatively large and the groups are relatively unstable (*ibid.*). Johnson (1989a) suggests that these larger groups are aggregations of wallabies concentrated on limited areas of good quality pasture. The results of this study supported this idea because in winter wallabies and kangaroos were found in larger groups on better quality swards, but smaller groups on poorer quality swards. Where declines in food availability lead to dispersion of food items, competition may lead to the breaking up of groups and a limit set on group size (Jarman, 1974; Jarman and Jarman, 1979). However,

when declines in food availability lead to a patchy distribution of resources animals may aggregate on the remaining patches, as appears to be the case for wallabies, and perhaps kangaroos, at Wallaby Creek (Johnson, 1989a, and this study).

The question of the costs and benefits that wallabies derive from aggregations or groups remains unclear. In summer wallabies in large groups did achieve faster biting rates and spent less time vigilant than those in small groups but there were no effects of group size on foraging in winter. There may have been additional benefits in terms of increased efficiency of predator detection that could not be measured in this study. I did not find any evidence that the competition between wallabies foraging together was greater than for kangaroos. To the contrary, wallabies displaced one another less often and interacted less frequently than kangaroos and Johnson (1985) recorded comparatively large inter-individual differences between group members for the species. The vigilance behaviour of wallabies did appear more disruptive to their foraging, in terms of loss of time that could have been devoted to searching for and prehending food items and the rate at which they raised their heads to survey, than any observable competition between group members.

Why then, do wallabies not gather in larger groups to gain benefit from 'many eyes' if they suffer few effects from competition in their smaller groups? One factor may be their small body size which makes communication between group members difficult, especially in their natural habitat. The habitat at Wallaby Creek is more open than the species' natural habitat and wallabies were found in larger groups when no cover vegetation was available. If small wallabies are unable to outrun their predators once detected they may benefit little from being in a group because the group would be more obvious to a predator than an individual.

Evidence from the black-striped wallaby *Macropus dorsalis* suggests that body size can not be the only factor determining the different grouping strategies of the eastern grey kangaroos and red-necked wallabies. The black-striped wallaby, which also lives at Wallaby Creek, is similar in body weight to the red-necked wallaby and is also a grazer (Jarman and Phillips, in press). However, this species is often seen in tight groups which move off together when disturbed (Johnson, pers. comm.). Faecal analysis of samples from Wallaby Creek has shown that they utilize the abundant, poor quality snow grass much more than red-necked wallabies (Jarman and Phillips, in press), which may support the hypothesis that competition sets an upper limit on optimal group size. Clearly a comparative study of the red-necked wallaby and the more gregarious black-striped wallaby would provide some interesting clues to the determinants of social organization, in the absence of body-size differences.

8.5 Comparison between two macropod grazers and large herbivorous mammals on other continents.

Another aim of the study was to compare the foraging behaviours of two grazing macropod species with those of ruminant, and other ungulate, herbivores; in particular to determine how the different constraints operating for the two groups affect their foraging tactics. The study demonstrated a number of interesting differences between the foraging behaviour of macropod species and other large herbivores. Some of the differences related to differing constraints of their mouthparts and gut morphologies and others to the constraints made by the structure of the vegetation communities that they fed upon.

8.5.1 Selection and diet composition

The diets of kangaroos and wallabies in this study contained a very high proportion of monocot species (99% and 88% respectively), suggesting that at this site eastern grey kangaroos are almost pure grazers and red-necked wallabies are predominantly grazers. According to Hofmann's classification of ungulate species into dietary categories, ungulates of the same body weight as wallabies are, with one exception, either intermediate feeders or browsers, and the majority of ungulates of the same weight as kangaroos are also intermediate feeders or browsers (Hofmann, 1973 reproduced in Gordon and Illius, 1988). His classification was based on the natural diets of ungulate species but at Wallaby Creek the pastures have been greatly improved by clearing trees and their understorey, and introducing highly digestible grasses. Thus, the high proportion of grass in the diets of the two macropod species at Wallaby Creek is partly a response to the quantity of high quality grasses available. However, the red-legged pademelon in the same study site had a much higher proportion of dicot in the diet than the similar sized red-necked wallaby (Jarman and Phillips, in press) showing that selection for browse and small dicot plants was possible. Also, eastern grey kangaroos have been shown to be almost pure grazers on unimproved pastures on the New England Tablelands (Taylor, 1983a). It seems that even in the absence of pasture improvement eastern grey kangaroos and red-necked wallabies are predominantly grazers.

Grass leaf made up more than 90% of the monocot proportion of their diets and grass stem and sheath made up the remainder. This proportion of leaf in the monocot portion of the diet was higher than has been demonstrated for ungulate species that are considered pure grazers in the wild (Jarman and Phillips, in press). For example, in one study wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* achieved only 61% and 31% leaf in the grass proportion of their diets (Gwynne and Bell, 1968).

The shape of a herbivore's mouthparts are considered important determinants of their ability to forage selectively (Bell, 1970; Jarman, 1974; Gordon and Illius, 1988), and the narrow muzzle and incisor arcade of macropods, relative to ruminant species of a similar

body weight, enables them to easily grasp and pluck individual food items (Jarman, 1984; Janis, in press). Macropods are also able to use their forepaws to separate grass tussocks and expose the more digestible shoots within. However, diet selection is a function of the preference for different species or plant parts if choice were unlimited, modified by the characteristics of the vegetation canopy which influence the opportunity for selection (Hodgson, 1979). Thus, the structure of the grass sward and the ratios of leaf:stem:sheath are also likely to be important factors determining the proportion of leaf in the diets of grazers (Jarman and Sinclair, 1979).

The diets of domestic grazing animals consistently contain more leaf and less stem than the average of the vegetation to which they have access (Arnold, 1981), but in temperate managed swards the composition of the diet appears to be a consequence of largely unselective grazing in the surface horizons of the sward where leaf:stem ratio is high (Hodgson, 1981). Tropical grasses have a low leaf:stem ratio so that without selection the proportion of leaf in the diet of grazers, in the Serengeti for example, should be lower than in that of grazers feeding on swards with a higher ratio. The introduced grasses at Wallaby Creek all have high leaf:stem ratios (J. Clarke unpubl. data) and correspondingly small proportions of stem and sheath of these species were eaten (Jarman and Phillips, in press). The native kangaroo grass *Themeda triandra* has a lower leaf:stem ratio and there was a higher proportion of stem of this species in the diets of kangaroos in particular (Jarman and Phillips, in press).

Unlike ruminant species, which show isometric scaling of incisor arcade width with body weight (Gordon and Illius, 1988) macropods show negative isometry for the same feature (Janis, in press). Thus, the larger kangaroos have relatively narrow arcades which may restrict their bite size and hence their rate of intake. Selection for feeding sites with a taller sward height may be the kangaroos way of maintaining intake and selectivity and their preference for tussock grasses and blady grass following burning may be evidence of this strategy.

8.5.2 Total foraging time and feeding rate

Kangaroos in this study spent a higher proportion of the 24 hours foraging than has been demonstrated for many ungulate species (see Bunnell and Gillingham, 1985 for review). I have suggested that macropods are less restricted in their total foraging time because they have faster passage rates than ruminant species and because they do not need to allocate time to ruminating (although they may still need to spend some time allowing their stomach contents to be digested).

The highly selected diet of the kangaroos and wallabies in comparison to ungulate grazers (see above) may also require long foraging times to collect. The very slow rate of biting of macropods appears to be the result of their long selection time per bite and, coupled with their comparatively small muzzle width (Janis, in press), their rate of intake

of plant matter is probably much lower than that of ruminant species. A low rate of intake would also allow macropods a longer foraging time because gut fill would take longer to achieve.

The long foraging times of kangaroos in this study may not be unusual for kangaroos on the cool east coast of Australia (see also Osazuwa, 1978; Southwell 1981), but the foraging times of red and western grey kangaroos living in the more arid interior appear to be constrained by the high costs of thermoregulation during daytime foraging (Short, 1986; Priddel, 1986). However, the kangaroos in Priddel's study also rested for long periods at night and it may be that low digestibility of herbage in the arid zone forces macropods there to reduce foraging time in order to digest their stomach contents.

8.5.3 Response of foraging rates to changes in sward height.

The greater selectivity of grazing kangaroos and wallabies compared to ruminant species was also demonstrated by their foraging responses to declines in sward height and biomass. Whilst ruminant species generally show a decrease in biting rate with increasing sward height or biomass (Allden and Whittaker, 1970), in this study there were positive relationships between the biting rates of kangaroos and wallabies and sward height.

The changes in sward height recorded for particular vegetation areas in this study were made over a period of months and years and changes in other sward characteristics, like the proportion of dead vegetation or the proportion of the sward surface obstructed by grass seed heads, may have contributed to the relationships between sward height and biting rates. However, the step-wise regression analysis did indicate that in two vegetation areas sward height was the most important factor affecting biting rate that I had measured. In a study of the foraging behaviour of wallabies in semi-captivity Clarke and Loudon (1985) did find a negative relationship between biting rates (recorded over a period of only two weeks) and sward height, but there were other differences between the compositions of the swards measuring different heights. Thus, the exact role of sward height in the determination of macropod foraging rates will not be decided until the foraging rates of kangaroos and wallabies are recorded on swards of identical composition but varying height.

In a comparative study of the foraging behaviour of two bovid species the blesbok, *Damaliscus dorcas phillipsi* and the springbok, *Antidorcas marsupialis* Novellie (1978) demonstrated that the two species had different foraging strategies to cope with declines in food availability during winter. The blesbok, a large, broad-mouthed grazer, lowered its plane of selection in winter, consumed forage of lower digestibility and reduced its foraging time per day in order to digest the low-quality forage. The smaller bodied springbok, which is an intermediate feeder of a similar body weight to a female eastern grey kangaroo, increased its selectivity in winter and had correspondingly long foraging

times. Lowering selectivity and increasing feeding rates with decreasing food supplies (a generalist's strategy) may, therefore, be a suitable response for large species (rather than all grazers), which can cope with a significant fall in diet digestibility. Increasing selectivity and decreasing feeding rates (a selectivist strategy) may be a response of smaller species which require a minimum diet digestibility, regardless of their feeding style. Sheep may appear to be exceptions to this prediction since they are considered generalists, despite their relatively small body size (Schwartz and Ellis, 1981), although Schwartz and Ellis (1981) have suggested that the sheep's generalist strategy is a result of human selection. Despite this generalist tendency sheep are able to demonstrate a high degree of selectivity on mixed pastures with a very low biomass (Broom and Arnold, 1986). Presumably there is an interaction between grass quality and availability such that these foraging strategies (maintaining diet quality or maintaining intake) are not exclusive but form a continuum. Kangaroos are tolerant of poorer quality vegetation yet have higher absolute energy requirements than wallabies and may, therefore, tend towards maintaining intake, whilst wallabies tend might tend towards maintaining diet quality.

8.6 Foraging strategies and changes in pasture conditions

Many animals experience fluctuations in their food supply, either in time (hours, days, seasons or years) or in space. For herbivorous mammals some fluctuations, such as seasonal flushes of new growth following rain, are predictable whilst others follow unpredictable events such as wildfire. Most models of foraging behaviour are deterministic and assume that the forager has complete knowledge of its environment (Stephens and Charnov, 1982). Although this assumption may be valid in a static experimental environment it is unlikely to be valid in a naturally seasonal and heterogenous environment, where the rules governing the distribution and quality of food items between seasons and years are probably most accurately described by statements of probability (*ibid.*). In this case animals may sample the environment and make foraging decisions on the basis of information gained (*ibid.*).

The intake of energy and other nutrients by herbivores is a product of their foraging time, foraging rate, bite size and bite quality. One or more of these components of intake may be affected by changes in sward conditions and animals may try to compensate by altering one or more of the other intake components. For example, an increase in dispersion of food items due to lack of rain may increase the search time per bite and animals may need to compensate for a reduced rate of intake by increasing total foraging time.

One of the aims of the project was to look at the foraging behaviour of kangaroos and wallabies on different pasture types, to see which factors in the sward were the most important determinants of foraging behaviour, and to try and work out what strategies, or rules of thumb, the animals are using when making foraging decisions. There was evidence, from a number of different foraging actions or decisions, that kangaroos and wallabies did alter their foraging behaviour in response to changes in pasture conditions but there was also some evidence that there were limitations to these foraging responses.

8.6.1 Changes in total foraging time in 24 hours

Kangaroos and wallabies both showed seasonal differences in the proportion of the 24-hour period that they devoted to feeding. In winter animals began feeding earlier in the afternoon and ceased feeding later in the morning, thus increasing the proportion of daylight hours spent foraging, and increasing total foraging time. One explanation for the seasonal difference in activity schedules is that daytime foraging was restricted in the summer because of high ambient temperatures or radiant heat loads. Kangaroos and wallabies were active for longer on cloudy and wet days, providing some support for this explanation. However, whilst red and western grey kangaroos, in the arid zone, foraged very little during the day because of the high costs of thermoregulation (Priddel, 1986),

they also rested during the night suggesting that other factors may help determine foraging bout length.

Physical factors such as stomach fill and chemical factors are known to induce the termination of foraging bouts in herbivores (Bunnell and Gillingham, 1985) and the rate of stomach fill may determine the different foraging times of kangaroos and wallabies in winter and summer. In this study, nutrient requirements would have been met quickly in summer, when the tall, green swards allowed fast feeding rates and probably large bite sizes. In winter green leaves were harder to find in the sward (animals showed a high search time per bite) and a longer foraging time was needed to meet nutrient requirements or gut fill. At the height of the drought in 1986 foraging times reached a maximum of 17 hours a day, longer than has been recorded for most species of herbivore (see Weston 1987 for review). However, even these long hours were insufficient for animals to meet their nutrient requirements (the animals continued to lose body condition), suggesting that the kangaroos had reached their upper limit of foraging time or that all pasture was below a threshold of sustainable quality.

As with ruminant species there appears to be a relationship between rates of intake and total foraging time for macropods, but external and internal constraints may set the upper and lower limits of foraging time. It is often necessary to know the relative importance of different constraints on foraging behaviour when constructing foraging models (Stephens and Krebs, 1986). The results of this study suggest that kangaroos living in the cooler parts of Australia may be less constrained in their daytime foraging hours than those living in the arid centre, and that macropods in general may be less constrained by digestive capacity than ruminant species of a similar body size. Experimental manipulation of factors such as ambient temperature and gut fill would provide more accurate predictions concerning the relative importance of different constraints. Constraints of maximum daily foraging time and daily digestive capacity have both been included in models of herbivore foraging (Belovsky, 1978, 1984; Owen-Smith and Novellie, 1982).

8.6.2 Changing the proportion of foraging time spent surveying the environment

Animals may also vary the proportion of time during foraging bouts that they spend biting and selecting bites by allocating more or less time to other activities, primarily to surveying. The proportion of time devoted to surveying was similar in different seasons except at the height of the drought in the post-burn season of 1986 when the proportion declined. There were no detected changes in the level of danger experienced by animals at this time suggesting that, during the normal seasonal fluctuations in pasture conditions, kangaroos and wallabies maintained a certain level of vigilance (in terms of time devoted to surveying behaviour), but when pasture conditions were very poor they sacrificed some of their vigilance time to spend more time searching for food items.

8.6.3 Pasture conditions and foraging rates

The kangaroos and wallabies in this study altered another component of foraging behaviour (and food intake) when pasture conditions changed or when feeding on different vegetation communities; their biting rate. I have already mentioned that changes of biting rate on the intertussock sward were observed between seasons and that they were related to changes in search time per bite and bite size. Rates of biting also varied considerably between animals foraging on different sward components, with rates highest on the intertussock sward and lowest for foraging within mature tussocks and stands of blade grass.

The rates of biting on the intertussock swards were determined by a number of sward characteristics including sward diversity, obstruction on the sward surface, the proportion of the ground that was bare of vegetation and the sward surface height. However, sward characteristics are not the only determinants of biting rates; depending on their foraging strategy, herbivores may select bites more carefully thus decreasing biting rates, or lower their plane of selection to increase rate of intake, thus increasing biting rates.

When foraging within mature tussocks of snow grass or swamp foxtail kangaroos and wallabies removed leaves of the more palatable grasses from among the coarse tussock leaves. Leaves of kangaroos grass were bitten within tussocks but the chosen leaves were carefully selected from amongst the dead material in the tussock. The interrupted biting rates of kangaroos and wallabies foraging on these components were proportionately lower because the large mouthfuls of grass collected within tussocks took some time to manipulate and chew. I was unable to measure the bite sizes of kangaroos foraging outside and within tussocks so I am unable to say whether the increase in bite size obtained within tussocks compensated for the decrease in bite rate. Trying to predict the rewards that animals gain when foraging on different sward components is further complicated by the fact that leaves growing within tussocks were generally of higher fibre content and lower nitrogen content than leaves of the same species growing outside the tussock. Theoretically there are a number of different solutions to the problem of maximizing nutrient intake through feeding on different sward components, but constraints such as minimum survey time, maximum digestive capacity, maximum foraging time or minimum diet digestibility may be determining which choices animals make.

Rates of biting were recorded on the intertussock swards of a number of different vegetation areas and the sward factors that were most important in determining rates varied from sward to sward. On the more species-rich swards the presence of an obstruction on the sward surface or an increase in the amount of dead vegetation in the sward surface interfered with the process of selection and reduced ^{uninterrupted} biting rates as kangaroos and wallabies spent more time searching for each bite. In some instances

animals compensated for this decline in ^{uninterrupted} bite rate by increasing the proportion of foraging time that they spent searching and biting, such that their ^{interrupted} bite rate over all foraging time was not greatly reduced.

The sward in Area 4 was almost pure kikuyu and offered very little opportunity for selection. Sward height was the most important sward character determining foraging rates in this vegetation area but biting rates were positively correlated with sward height and not negatively correlated as in most studies of domestic grazing herbivores (Aldlen and Whittaker, 1970; Hodgson, 1982). I shall return to the question of the comparative foraging strategies of ruminants and macropods in section 8.8.

Burning of pastures changed the structure and composition of tussocks and stands of blady grass by removing all the dead leaves and exposing the leaves and new shoots of the grasses. The exposure of the burnt shoots appeared to make selection of bites easier for foraging kangaroos and wallabies because following burning their biting rates on tussock grasses and blady grass approached or exceeded those on the intertussock sward.

The biting rates of kangaroos and wallabies varied considerably on different sward types, and on the same sward types at different times of the year. Where there was an opportunity for selection, biting rates appeared to reflect the time required to search for preferred food items but sward height appeared to be more important on swards with low diversity. Ungar and Noy-Meir (1988) have suggested that grazing herbivores may select for bite size rather than bite quality on swards which are quite homogenous in quality, which may explain why bite rates decreased with decreasing sward height on such swards. In general it appears that kangaroos and wallabies respond to declines in forage availability by becoming more selective rather than by increasing their rate of intake.

8.6.4 Changes in bite quality with different pasture conditions

The diets of kangaroos and wallabies did vary with season and their preferences at different times of the year appeared to be related to the abundance or quality of the species or sward components. Carpet grass, the most abundant grass species in the study site was neither selected for nor against by either species, but wallabies showed a strong preference for the high quality leaves of paspalum and kangaroos showed preferences for new leaves of the coarse native grasses which appeared following pasture burning. In section 8.2.3 I suggested that the kangaroos' preference for burnt swards may reflect a tactic of maintaining intake rate when forage availability in the intertussock sward is declining, whilst wallabies' preference for paspalum may represent a strategy of maintaining a minimum diet quality. The cafeteria trials also indicated the importance of sward structure as opposed to bite quality in determining the dietary choices of kangaroos. Kangaroos did not make their selections on the basis of the nitrogen content of species on offer because their preferences were not ranked in the same order as the nitrogen content of the species.

8.7 Changes in foraging behaviour with reproductive class

I have described above the changes in foraging tactics adopted by kangaroos and wallabies in relation to changes in the dispersion and abundance of food items. Animals also experience changes in their energy requirements which may require changes in foraging tactics to meet the increased demands (during pregnancy and lactation for example). Other activities, which are vital to the survival and reproductive success of individuals, may interfere with foraging behaviour and cause different population classes to adopt different foraging tactics. Finally both species are highly sexually dimorphic, leading to large differences between the absolute energy requirements of mature males and females, and differences in the vulnerability of males and females to predators for the same reasons outlined in section 8.3.

8.7.1 Total foraging time

The 24-hour activity schedules for kangaroos did not show any differences in total foraging time between the sexes, but sample sizes were small and variation within the sexes (due to body size or reproductive state) may have obscured differences. Females with young-at-foot or large pouch-young did forage for longer than females with smaller or no pouch-young, as one would predict from the high energy costs of milk production during this reproductive phase.

8.7.2 Vigilance behaviour

Females did not allocate more time to surveying behaviour than males, nor did they spend more time alert to disturbances outside their groups, but they did use more upright postures for surveying than males. Because of their shorter height in comparison to adult males, females may need to use more upright postures to gain the same efficiency of surveillance as males. Thus, there was little evidence that females adopted a different level of vigilance than males but they may have expended more energy (in sitting up) to achieve the same.

8.7.3 Feeding site choice and diet selection

The feeding sites chosen by different population classes did not differ in the amount of cover provided nor in their ground species composition. Given that the sexes are not segregated, but co-existing in mixed-sex groups of open membership, it is perhaps not surprising that the different population classes use the same areas. There was some tendency for females to forage within tussocks and stands of blady grass less often than males, a difference that may have proved significant with larger sample sizes. Selecting a large bite might be one way in which large males could maintain their rate of intake

when foraging in a group with other classes, and foraging within tussocks does provide a large bite.

Sample sizes for the dietary analysis were too small for a comparison between male and female wallabies to be made, and they were still small for the comparison between male and female kangaroos. The data did not indicate any differences in diet between the sexes, but again differences between small and large males, and females of different reproductive class may have obscured general differences between the sexes. A more detailed analysis, with larger sample sizes and the effects of home range location taken into consideration may yield differences in the diets of different population classes.

8.7.4 Foraging rates and movement during foraging

Foraging rate could be one remaining tactic for population classes to compensate for different energy requirements. However, rates of biting for herbivores are greatly dependent on the structure of the sward they feed on (Hodgson, 1981, 1982). Given the similarities of the feeding sites, diets and foraging times of males and females it is, perhaps, not surprising that the sexes did not differ in their feeding rates.

Male kangaroos did take more steps, in longer step-sequences than females, which could reflect differences either in dispersions of their preferred food items or movement in relation to other group members. Given that males interacted with other group members more frequently, and were more likely to move towards their neighbours than were females, the greater movement of males during foraging probably reflects their movement around their groups to check on females and interact with males. Unfortunately I did not have sufficient data on any one sward to compare the movements of solitary males and males in groups.

The 24-hour followings demonstrated that there was great variability in the distances displaced by kangaroos over 24 hours, and that the distances were potentially very large for large male kangaroos. The allocation of time and energy to movements may require different foraging strategies for males compared to females, and perhaps different strategies for the same males at different times. Schmitz *et al.* (1989) have suggested that large male euros may switch from an energy-maximizing strategy to a time-minimizing strategy when they are accompanying oestrous females. The preliminary observations of large male kangaroos at Wallaby Creek suggest that a more detailed studies of individual males may uncover some interesting strategic differences for males of different size and dominance status.

8.7.5 Foraging tactics of males and females

The observations above indicate that the social organizations of the species, but particularly the kangaroo, may restrict the opportunities for individuals of different population classes to vary their foraging tactics. Individuals of both species showed quite dramatic changes in body condition over time, and large males and females with young-at-foot were particularly likely to be in poor condition. If individuals were meeting the fluctuations in their energy demands by the use and deposit of their body reserves then few changes in foraging behaviour would be observed. The use and deposit of body reserves may be important components in the long-term foraging strategies of animals and perhaps should be investigated further when foraging strategies are modelled.

8.8 The contribution of this study to foraging theory

This study is one of many that have been carried out in the last decade on the behavioural ecology of eastern grey kangaroos and red-necked wallabies at Wallaby Creek. Long-term studies of known individuals provide valuable information on life-time reproductive success, and foraging efficiency is an important component of that success (Schoener, 1971). Much of the theory surrounding foraging behaviour has assumed that the fitness associated with an animal's foraging behaviour has been maximized by natural selection (Pyke *et al.*, 1977). Because fitness is extremely difficult to measure for relatively long-lived species, maximization of energy gain is generally considered equivalent to fitness (Schoener, 1971). However, rate of energy gain may not be the most important component of reproductive success and survival, especially for large mammals that are able to store and use metabolite deposits in periods of plenty and scarcity. Kangaroos and wallabies in this study showed marked changes in their deposits of metabolites following dramatic changes in pasture conditions. Some ecologists have recognized that predation often imposes an equal, if not greater risk, than starvation and they have tested the hypothesis that animals are able to balance the conflicting demands of food reward and safety (Sih, 1980; Cerri and Fraser, 1983).

Evidence from this study also suggested that risk from predation may play an important role in deciding where animals feed and how they feed, especially in the case of smaller and more vulnerable wallabies. Furthermore, social interactions may interfere with foraging behaviour whilst contributing significant benefits to the reproductive success of an animal, especially a large male. How can these trade-offs between foraging behaviour and other activities be incorporated into foraging strategies? The most common approach to the problem of trade-offs has been to treat the trade-offs (e.g. anti-predator behaviour and social behaviour) as time constraints and to use energy maximization as the currency, converting the consequences of each behaviour to probabilities of survival (Stephens and Krebs, 1986). However, the costs of the trade-off activities may not be measured solely in terms of time lost to foraging. For example, males may accompany females for many days prior to the female's oestrus, visiting sub-optimal feeding sites as a result. Similarly, the benefits to fitness achieved through the trade-off activities may not relate directly to the time allocated to that activity. The adoption of survival as a currency in foraging models may solve some of these problems, but the effects on survival of variation in time allocation and site choice would be extremely difficult to determine.

Conventional models of foraging behaviour ignore activities or actions that conflict with foraging behaviour and they maximise the net rate of energy gain. The two strategies for achieving this goal, time-minimization and energy-maximization, fall at either ends of a continuum (Belovsky, 1984) and models should predict which strategy an

animal is adopting from the composition of their diet. The question of which dietary component to base diet selection on remains. Some studies have used discrete vegetation components (Belovsky, 1984), others have used species (Westoby, 1974, Owen-Smith and Novellie, 1982), others have suggested that choice of patch type is most important for herbivores (Stephens and Krebs, 1986), whilst others have suggested that choice of bite size is more important for grazing herbivores (Illius, 1986; Ungar and Noy-Meir, 1988).

The observations at Wallaby Creek demonstrated that kangaroos and wallabies selected particular sward components to feed on (e.g. the intertussock sward for wallabies and shoots following burning for kangaroos), but they made further selections within those components. Most optimal foraging studies have concentrated on optimal food selection for food quality and optimal selection for bite size has generally been ignored (Ungar and Noy-Meir, 1988). Variations in sward structure can lead to great variations in the bite size of grazing herbivores (Hodgson, 1981) and the grazing models of Illius (1986) and Ungar and Noy-Meir, (1988) have demonstrated that sward structure can influence rates of intake, and therefore feeding choices of grazers. The cafeteria trials and field observations in this study demonstrated that bite quality was not the most important factor affecting the diet choices of kangaroos, and the need to maintain a minimum threshold of intake may have affected kangaroos' patch choices. However, both species selected a better diet than they could have obtained by foraging unselectively and food items or patches containing items which fell below a certain threshold of digestibility may have been avoided. Illius (1986) included variance in both height and digestibility in his models of cattle grazing behaviour and assumed that herbage below a certain threshold digestibility was rejected. The avoidance by wallabies of snow grass and swamp foxtail suggested that this assumption is probably a valid one, especially for smaller species with a limited digestive capacity.

One of the interesting differences between the grazing behaviour of macropods in this study and those of ruminants in other studies was their different responses to changes in leaf-table height. Sheep and cattle increase their rates of biting with declines in leaf-surface height (Allden and Whittaker, 1970; Hodgson, 1981) but kangaroos and wallabies in this study decreased their rates of biting in the same circumstances. Incisor-arcade width is an important determinant of rate of food intake in grazing mammals (Illius and Gordon, 1987) and on relatively short swards broad-mouthed grazers would have a higher rate of intake than similarly-sized narrow-mouthed grazers or browsers (Gordon and Illius, 1988). If narrow-mouthed grazers were unable to maintain sufficient intake rates of an unselective diet then selection for bite quality may be an alternative strategy for maintaining nutrient intake.

Before too many conclusions can be drawn concerning their responses to changes in sward characteristics, the foraging behaviour of macropods and ruminants need to be compared simultaneously on the same swards. In a grazing trial using red and western grey kangaroos on an arid zone pasture rates of harvesting bites did increase with declining biomass (Short, 1986), as did those of Bennett's wallabies in another study (Clarke and Loudon, 1985). It seems likely that macropods, like many ruminant species, can have differing responses to declines in forage availability depending on the uniformity of abundance and quality on offer and that they will not maximize energy over bite size or bite quality alone, but over both variables.

8.9 The evolution of feeding styles and social organization in macropods

Macropods, like African antelopes (Jarman, 1974), are thought to have radiated from a small, forest dwelling, solitary ancestor (Kaufmann, 1974b). Jarman (1974) suggested that increases in body size allowed African-antelope species to exploit a wider range of habitats as they became less vulnerable to predation and more able to utilize the poorer quality grasses in open habitats. Much of the resource partitioning seen amongst the African ungulates in the Serengeti arises from interspecific variation in body size and accompanying variation of mouthparts (Jarman and Sinclair, 1979). Today, members of the macropod family exhibit a range of body sizes and social organizations, and they occupy a variety of habitats (Norbury et al., in press). Superficially the ecological determinants of evolution in the macropod family appear very similar to those determining evolution in the African bovids. However, there are important differences between the environments of Australia and Africa which may have affected the courses of radiation in these groups.

The Australian continent has supported relatively few species of predator in the past, leading some authors to suggest that predation pressure has been insufficient to encourage the evolution of grouping behaviour as an anti-predator strategy (Caughley, 1964b; Russell, 1984; Lee and Cockburn, 1985). Others have suggested that the densities of predator populations have been high enough to encourage selection for grouping behaviour (Jarman and Coulson, in press). Benefits of grouping in terms of decreasing vigilance time with increasing group size have been demonstrated for kangaroos (Southwell, 1981; Jarman, 1987), and this study provides additional evidence for benefits of grouping behaviour, in summer at least. However, there is little doubt that predation pressures have been lower in Australia than in areas like the Serengeti, and even the most social species of macropod are less gregarious than many African bovids.

The abundance and quality of browse and grasses are also likely to have played a part in the evolution of grouping behaviour. The native grasses of Australia form tussocks which comprise a large proportion of dead vegetation (Norton, 1971). Kangaroos and wallabies are able to extract the young, digestible leaves growing within tussocks by their selective grazing style which is facilitated by their narrow muzzles (Jarman, 1984; Janis, in press). However, their foraging style may restrict communication between group members during foraging bouts and encourage greater inter-individual distances between them to reduce competition. Kangaroos and wallabies did form larger groups on better quality swards indicating that competition may set the upper limits on group size. The swards of matt-forming grasses that cover the Serengeti are less likely to encourage competition and may support much larger feeding aggregations as a result.

With their slow foraging rates and consequent low rates of intake, macropods must forage for long periods in order to ingest their daily food requirements. These long foraging periods are not broken into discrete foraging bouts by periods of digestion and rumination because of the 'tubular flow' of digesta through the macropodine gut (Dellow and Hume, 1982) and probably also because their rates of intake are lower than their rates of passage of digesta. If, as seems likely, changes in group composition occur more frequently in active groups than resting ones then long unbroken foraging bouts may result in many changes in group composition and thereby reduce group stability.

Kaufmann (1974a) has suggested that the evolution of social organization has been restricted in the macropod family because the species are predominantly nocturnal and darkness restricts communication between group members. Kangaroos and wallabies in this study were found in smaller groups at night, but there was evidence that kangaroos were in small groups at night through choice rather than through difficulties of maintaining group cohesion. Kangaroos also surveyed in less upright postures and less frequently at night than in the day-time, suggesting that they were reducing their chances of being detected by predators rather than increasing their chances of detecting predators. African buffalo show the reverse grouping trend at night, as small groups coalesce prior to dusk and forage together in large groups after dark (Prins and Iason, 1989). Buffalo may continue to use grouping as an anti-predator strategy after dark because they are large enough to be able to defend themselves and they spend more time vigilant at night, both to predators and con-specifics (*ibid.*). The results of this study suggest that species are not restricted to one anti-predator strategy determined by their body size. Instead, they may switch strategies according to the ability of group members to communicate with one another, the ability of the animal to conceal itself from predators and the likelihood that the animal could escape capture once detected. More information is required on the sensory abilities of macropods in the dark, and the hunting tactics of their past and present predators before we can determine the exact role of grouping as an anti-predator strategy in the family.

Associations of individuals for social reasons do appear to be the basis for the social organization of the eastern grey kangaroos and red-necked wallabies, but environmental factors such as the density and distribution of food resources and the activity of predators also influence their grouping behaviour. One problem in the study of the evolutionary ecology of macropods is that there have been many changes to their natural environment in recent years; predatory species have disappeared, and native grasslands and woodland have been replaced with improved pasture. These changes in the environment have to be considered when predicting the ecological determinants of foraging behaviour and social organization in the family.

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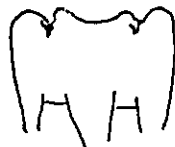
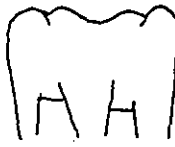
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Appendix I

Schedule for calculating a body condition index for eastern grey kangaroos from a visual assessment of their fat reserves.

The schedule was devised by M.Jones for P.Jarman in 1985. Each animal was observed at close range (from 1 to 5 m) from two angles. The animal had to be in the crouched position, with its fore-feet resting on the ground. The animal was observed from the rear to record the hip and tail-butt scores, and from the side to record the ribs score. The scores for hips and ribs were multiplied by 3 and those for the tail butt by 4 to give equal weight to each parameter. The condition index was the sum of these weighted scores and ranged from a possible 10 to 36.

Parameter	Score	Description	
Hips	1	<i>Rump severely depressed between pelvic bones which are protruding. Very little flesh covering pelvis.</i>	
	2	<i>Rump concave or depressed between hip bones. Pelvic bones protruding.</i>	
	3	<i>Rump flat between hip bones, hip bones may be visible.</i>	
	4	<i>Rump convex between hip bones, hip bones not visible.</i>	

Ribs	1	<i>All of ribs visible or, if coat is long, trailing edges of ribs visible. Area between the processes of the lumbar vertebrae and ribs sunken and strip either side of vertebral column sunken.</i>	
	2	<i>Last 2 to 4 ribs visible. Area between the processes of the lumbar vertebrae and ribs sunken.</i>	
	3	<i>Last 1 to 2 ribs visible. Flank not sunken.</i>	
	4	<i>No ribs visible. Flank not sunken.</i>	
Tail butt	1	<i>Base of tail at 5cm from the body is elliptical in cross section, taller than it is broad.</i>	
	2	<i>Base of tail at 5cm from the body is circular in cross-section.</i>	
	3	<i>Base of tail at 5cm from the body is elliptical in cross section, broader than it is tall.</i>	

Appendix II

Means and statistical tests to accompany Table 6.11

Mean values ($\pm$ s.e.m.) of feeding parameters of kangaroos (EGK) and wallabies (RNW), feeding in Areas 1 and 2, on swards dominated by carpet grass, paspalum and kikuyu, and on burnt shoots. Significant results for two-way analyses of variance are given with species (s) and season (m) as grouping factors. When group variances were not equal the Brown-Forsythe statistic was calculated. Significant species effects are given ($F_{(s)}$) for ease of presentation; and where there is a significant species x season interaction only the interaction is given ($F_{(sm)}$). Significance levels are: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

foraging parameter	EGK summer	EGK winter	RNW summer	RNW winter	
AREA 1					
bite/select	77.4 $\pm$ 2.0	81.6 $\pm$ 2.2	82.3 $\pm$ 2.3	85.2 $\pm$ 1.7	
survey/chew	20.7 $\pm$ 2.0	16.3 $\pm$ 2.2	16.7 $\pm$ 2.5	12.6 $\pm$ 1.4	
interrupted biting rate	33.0 $\pm$ 1.6	29.5 $\pm$ 1.4	35.2 $\pm$ 1.8	24.2 $\pm$ 0.7	$F_{(sm)1,176}=6.4^*$
uninterrupted biting rate	43.4 $\pm$ 1.9	38.2 $\pm$ 1.6	42.9 $\pm$ 1.5	30.3 $\pm$ 1.0	$F_{(sm)1,168}=5.0^*$
biting ratio	0.76 $\pm$ 0.02	0.78 $\pm$ 0.02	0.82 $\pm$ 0.03	0.78 $\pm$ 0.03	
chews/bite	0.54 $\pm$ 0.08	0.43 $\pm$ 0.06	0.53 $\pm$ 0.22	0.36 $\pm$ 0.05	
bites/patch	33.7 $\pm$ 3.0	29.6 $\pm$ 2.5	24.4 $\pm$ 3.3	16.4 $\pm$ 1.2	$F_{(s)1,93}=18.4^{***}$
head-up rate	4.3 $\pm$ 0.4	3.8 $\pm$ 0.4	6.0 $\pm$ 0.7	4.5 $\pm$ 0.4	$F_{(s)1,75}=5.6^*$
step total	3.4 $\pm$ 0.5	5.9 $\pm$ 0.9	5.6 $\pm$ 0.9	6.5 $\pm$ 0.7	

foraging parameter	EGK summer	EGK winter	RNW summer	RNW winter	
AREA 2					
bite/select	78.7 $\pm$ 4.6	80.5 $\pm$ 4.5	66.1 $\pm$ 4.0	81.4 $\pm$ 3.0	
survey/chew	17.4 $\pm$ 4.7	17.7 $\pm$ 4.7	30.2 $\pm$ 3.7	16.9 $\pm$ 2.5	
interrupted biting rate	32.1 $\pm$ 2.2	34.3 $\pm$ 2.7	21.1 $\pm$ 1.5	25.3 $\pm$ 0.9	$F_{(s)1,88}=33.4^{**}$
uninterrupted biting rate	40.9 $\pm$ 1.8	44.0 $\pm$ 1.2	35.6 $\pm$ 1.4	37.8 $\pm$ 1.8	$F_{(s)1,88}=5.6^*$
biting ratio	0.80 $\pm$ 0.04	0.77 $\pm$ 0.05	0.63 $\pm$ 0.05	0.73 $\pm$ 0.03	
bites/patch	23.4 $\pm$ 5.5	24.8 $\pm$ 3.8	19.8 $\pm$ 3.1	19.0 $\pm$ 1.8	
head-up rate	4.5 $\pm$ 0.8	3.3 $\pm$ 0.0	8.1 $\pm$ 0.5	5.2 $\pm$ 0.4	$F_{(s)1,88}=18.0^{***}$
step total	7.3 $\pm$ 1.7	5.1 $\pm$ 1.1	5.8 $\pm$ 1.2	5.4 $\pm$ 0.6	

foraging parameter	EGK summer	EGK winter	RNW summer	RNW winter	
kikuyu-dominated swards					
bite/select	71.7±1.5	77.3±2.3	65.1±4.5	74.3±3.2	
chew/survey	17.2±1.3	16.1±2.0	15.2±4.2	13.0±2.6	
interrupted biting rate	35.9±1.1	33.2±1.5	32.5±3.0	31.9±1.8	
uninterrupted biting rate	52.8±1.5	47.2±1.7	55.3±2.7	46.2±2.8	
biting ratio	0.69±0.01	0.74±0.02	0.65±0.04	0.74±0.03	
chew/bite	0.69±0.07	0.69±0.10	0.99±0.21	0.80±0.14	
bites/patch	36.0±2.6	40.7±3.9	46.3±7.8	31.6±3.8	$F_{(sm)1,172}=3.9^*$
head-up rate	5.4±0.3	4.8±0.4	7.3±0.8	6.3±0.7	$F_{(s)1,182}=10.5^{**}$
step total	2.9±0.3	3.9±0.6	1.9±0.6	3.7±0.6	

foraging parameter	EGK summer	EGK winter	RNW summer	RNW winter
carpet-grass dominated swards				
bite/select	71.3 $\pm$ 2.5	73.7 $\pm$ 2.2	71.2 $\pm$ 3.3	77.3 $\pm$ 2.6
chew/survey	19.3 $\pm$ 2.2	12.5 $\pm$ 1.3	11.7 $\pm$ 1.9	12.7 $\pm$ 2.0
interrupted biting rate	32.1 $\pm$ 1.5	27.5 $\pm$ 1.1	29.7 $\pm$ 1.9	28.4 $\pm$ 1.2
uninterrupted biting rate	46.5 $\pm$ 2.4	39.7 $\pm$ 1.8	45.2 $\pm$ 3.5	37.8 $\pm$ 1.4
biting ratio	0.72 $\pm$ 0.02	0.76 $\pm$ 0.01	0.68 $\pm$ 0.03	0.76 $\pm$ 0.02
bites/patch	28.0 $\pm$ 2.5	29.6 $\pm$ 2.4	23.5 $\pm$ 3.7	29.1 $\pm$ 3.2
head-up rate	4.8 $\pm$ 0.3	4.6 $\pm$ 0.3	7.4 $\pm$ 0.6	6.6 $\pm$ 0.5 $F_{(s)1,167}=31.5^{***}$
step total	3.5 $\pm$ 0.4	3.4 $\pm$ 0.4	3.7 $\pm$ 0.9	3.4 $\pm$ 0.6

foraging parameter	EGK summer	EGK winter	RNW summer	RNW winter	
paspalum-dominated swards					
bite/select	71.7 $\pm$ 3.0	80.5 $\pm$ 3.6	62.7 $\pm$ 3.5	83.4 $\pm$ 3.1	
survey/chew	18.1 $\pm$ 3.3	17.6 $\pm$ 3.3	10.7 $\pm$ 1.7	10.3 $\pm$ 2.5	$F_{(s)1,75}=7.1^{**}$
interrupted biting rate	34.0 $\pm$ 2.4	31.3 $\pm$ 2.4	30.0 $\pm$ 1.7	26.0 $\pm$ 1.2	$F_{(s)1,77}=5.3^*$
uninterrupted biting rate	48.2 $\pm$ 2.3	40.1 $\pm$ 2.6	51.2 $\pm$ 2.6	33.0 $\pm$ 1.9	
biting ratio	0.69 $\pm$ 0.04	0.78 $\pm$ 0.03	0.61 $\pm$ 0.04	0.78 $\pm$ 0.05	
chew/bite	0.67 $\pm$ 0.18	0.47 $\pm$ 0.11	1.27 $\pm$ 0.20	0.41 $\pm$ 0.08	
bites/patch	30.0 $\pm$ 4.4	31.9 $\pm$ 4.1	30.7 $\pm$ 4.6	22.4 $\pm$ 3.6	
head-up rate	5.2 $\pm$ 0.6	4.2 $\pm$ 0.7	8.4 $\pm$ 0.8	4.5 $\pm$ 0.1	$F_{(s)1,70}=6.3^*$
step-total	4.9 $\pm$ 1.1	5.9 $\pm$ 1.8	3.6 $\pm$ 0.8	5.9 $\pm$ 1.1	

Median values of feeding parameters of kangaroos and wallabies, feeding on shoots of blady grass and tussock grasses in the four months following burning. A difference between the medians are compared with Mann-Whitney U tests

foraging parameter	medians kangaroos	medians wallabies	U	p
bite/select	85.0	67.0	8497.0	0.002
chew/survey	9.0	9.0	7959.5	0.80
interrupted bite rate	29.8	24.4	8265.0	0.05
uninterrupted bite rate	36.9	45.8	7398.5	0.006
biting ratio	0.83	0.70	8320.0	0.02
chew/bite	0.5	0.9	7738.0	0.35
bites/patch	20.6	24.8	7698.0	0.25
head-up rate	4.0	7.0	7056.0	0.0001
step total	4.0	3.0	8119.0	0.26

Appendix III

List of scientific names of those plants referred to in this thesis by their common name.

carpet grass	<i>Axonopus affinis</i>
kikuyu	<i>Pennisetum clandestinum</i>
papalum	<i>Paspalum dilatatum</i>
couch	<i>Cynodon dactylon</i>
clover	<i>Trifolium repens</i>
Paddy's lucerne	<i>Sida rhombifolia</i>
blady grass	<i>Imperata cylindrica</i>
snow grass	<i>Poa labillardieri</i>
kangaroo grass	<i>Themeda triandra</i>
swamp foxtail	<i>Pennisetum alopecuroides</i>
balloon cotton	<i>Asclepias physocarpa</i>