CHAPTER 1

Introduction and aims of the study

1.1 The value of comparative studies

"For it is difference in feeding habits that make some animals live in herds and others scattered about; some are carnivorous, some vegetarian, others will eat anything. So in order to make it easier for them to get these nutrients, nature has given them different ways of life."

Aristotle, The Politics

Aristotle's observation of the relationship between a species' social organization and its feeding style was formalized into what we term sociobiological theory only twenty years ago (see Crook, 1970). Since then, many comparative studies have identified relationships between the feeding style, social organization and ecology of species (Geist, 1974; Jarman, 1974; Clutton-Brock and Harvey, 1977; Norbury *et al.*, in press), and in doing so have given us insights into the evolution of behaviour. For example, when unrelated species show a similar behaviour when faced with similar ecological problems we might conclude that the behaviour is an evolutionary adaptation to the problem; the behaviours of the species are analogous. Species that are related through a common ancestor may show homologous behaviours that are derived from the repertoire of the ancestor. However, related species may also show different behavioural solutions to the same problem because interspecific competition has encouraged the evolution of strategies that exploit different resources.

Although Aristotle realised that competition between species was the driving force behind the diversification of feeding styles, it was not until the simultaneous publication by Darwin and Wallace of their Nature papers in Origin of Species that the mechanism for speciation, natural selection, was described. Comparative studies of species living sympatrically, with overlapping ecological niches, have provided further insights into the interspecific competition within communities that may lead to resource partitioning and divergence of niches or behaviour (Jarman and Sinclair, 1979).

This foraging study is a comparative study on many levels. It compares the behaviour of two closely related species, and different age and sex classes of those species, to look for ecological separation between them. It compares the behaviour of two macropod grazers with ecologically similar herbivorous mammals of other suborders and continents to look for analogous behaviours in the two groups. Finally, it compares within species and within class, between times of day, locations and between seasons, seeking evidence of response to temporally and spatially variable facets of the environment.

1.2 What is foraging behaviour?
......tactics and strategies

The term foraging behaviour covers a multitude of behaviours that are directly and indirectly involved with the selection and ingestion of food items. Bunnell and Gillingham (1985) have drawn an analogy between the foraging behaviour of herbivores and the "dynamics of dining out", where a series of decisions and actions made before an animal ingests a food item are compared with choosing when to dine, where to dine and what to select from the menu. A description of foraging behaviour may, therefore, include: what time of day the animal forages; the duration of foraging bouts; where foraging takes place; which food items are ingested; and how the items are ingested. Animals often exhibit other behaviours whilst foraging including grooming, interacting with other individuals, remaining vigilant for predators, thermoregulating and warding off insects. Description of such activities may also be important to the description of foraging behaviour if they influence foraging decisions.

A distinction has been drawn between foraging tactics and foraging strategies (Holling, 1968), both of which contribute to what we observe as foraging behaviour. Foraging tactics are the actual methods by which a forager goes about finding, handling and ingesting food items (*ibid*), whilst foraging strategies have been described as a series of decisions (whether conscious or inherent) which are made with the aim of achieving a particular goal. Continuing with the 'dining out' analogy, foraging strategies of humans could include minimizing the expense of a meal or the time taken to order and eat a meal, satisfying ones hunger with the fewest calories or maximizing the variety of flavours.

Having recognized the link between food intake and reproductive success (see Schoener, 1971 for review) many investigators have treated foraging as a function whose performance could be maximised by natural selection. The selection considered is Darwinian selection coupled with genetic or cultural inheritance (Pyke *et al.*, 1977), and the goal of foraging strategies is to forage in such a way that reproductive success is maximised. Many mathematical models have been developed to simulate foraging strategies and predict behaviour (see Stephens and Krebs, 1986 for review). Because reproductive success is very difficult to measure, especially for long lived species, a shorter-term goal that is assumed commensurate with fitness is generally used, such as maximizing energy yield per unit feeding time (Schoener, 1971). The maximization or minimization of some currency is a problem of optimization and the majority of models used to describe foraging strategies fall into the category of "optimal foraging models". However, the assumptions underlying optimality criteria have been criticized (Pearce and Ollason, 1988) and other approaches have been tried including the use of "satisficing" models (Winter, 1971; Herbers, 1981) and "balancing" the net benefits from two conflicting demands (Sih, 1980; Cerri and Fraser, 1983). The latter may be considered a case of dynamic optimization because a decision about foraging affects the decision concerning anti-predator behaviour (Stephens and Krebs, 1986).

Most foraging models, and optimality models in general, are made up of three components: decision assumptions, currency assumptions and constraint assumptions (Stephens and Krebs, 1986). Decision assumptions decide which of the forager's problems (or choices) are to be analyzed; most models of large mammalian herbivores foraging have been concerned with the choice of diet (Westoby, 1974; Belovsky, 1978; Owen-Smith and Novellie, 1982), but foraging time (Herbers, 1981) and choice of bite weight (Ungar and Noy-Meir, 1988) have also been considered. In section 1.3 I describe each of the foraging choices that kangaroos and wallabies have to make and suggest possible reasons for different foraging decisions being made.

Currency assumptions decide what criterion is used for the various choices to be analysed (Stephens and Krebs, 1986), and for the choice to be analyzed a choice principle (maximization, minimization or stability) must also be assumed. Conventional foraging models maximize the net rate of energy gain while foraging because a relationship between the models' currency (energy) and goal (maximization of fitness) are assumed (Pyke *et al.*, 1977). This strategy is often equivalent to the maximization of some other limiting nutrient, such as nitrogen, since the levels of different nutrients often covary (Stephens and Krebs, 1986). Schoener (1971) described two ways for foragers to acquire more food whilst spending less time foraging. The **time minimizer** minimizes the time required to gain a certain amount of energy and the **energy maximizer** maximizes the amount of energy gained in a fixed time. The dichotomy between the two strategies may be misleading (Stenseth, 1981), and Belovsky (1984) sees them as a continuum, with a mix of the two strategies quite likely. Information concerning the relative importance of time and energy (or other nutrients) to survival may enable us to make realistic assumptions concerning the currency of foraging models.

Constraint assumptions concern the morphological, physiological, behavioural and extrinsic factors which limit and define the relationship between the currency and the decision variable(s) (Stephens and Krebs, 1986). For kangaroos and wallabies extrinsic constraints could include the distribution of food items (e.g. whether food items are encountered sequentially or simultaneously), morphological constraints could include the shape and size of the forager's mouthparts and physiological constraints may include a minimum digestibility for the plant material ingested.

In this study I look at each aspect of foraging behaviour of eastern grey kangaroos *Macropus giganteus* and red-necked wallabies *M. rufogriseus banksianus*, and look at the variation in foraging tactics shown by the two species. I examine the interrelationships between different foraging decisions because these can prove serious impediments to optimality and satisficing functions (Bunnell and Gillingham, 1985). I also examine the relationship between foraging behaviour and other activities that are important to reproductive success e.g. vigilance behaviour and social behaviour. The aim of this thesis is to describe relationships, extract generalities concerning foraging behaviour and to evaluate these against current theory of foraging strategies. I do not seek to propose models of foraging strategies but to test some of the assumptions and predictions of current models using data collected from two large, social, herbivorous mammals.

1.3 Foraging "decisions"

In section 1.4 I outline a number of comparisons where I expected to find differences in foraging behaviour between species or individuals because of different energetic requirements, different nutrient availabilities or differences in the risks of foraging. Before and during a foraging bout an animal must make a series of 'decisions' about when and where to feed. Some of these decisions are predetermined by the animal's size, mouthparts or digestive capability and by certain predictable attributes of the environment. However, foragers also live in a stochastic world where there are unpredictable temporal and spatial variations in their food supplies or predation risks which require the forager to make some assessment of its environment and energy status before making foraging decisions. Foraging behaviour can differ at any stage of the foraging process and often a particular decision at one stage may affect one or more decisions that follow. In this section I deal with each of the decisions in turn and point to the relevant chapters in the thesis where they are considered.

1.3.1 What time of the day to forage?

A number of environmental constraints may make foraging more difficult or dangerous at some times of the day compared to others. For example, in hot climates the amount of energy (or water) required to keep cool during the middle of the day may force some mammals to become nocturnally active (Dawson and Denny, 1969) whilst in cold climates animals may be restricted to sheltering during the night because the cost of thermoregulation would exceed the benefit of foraging after dark (Clutton-Brock *et al.*, 1982a). The predominantly nocturnal activity of some mammals has also been attributed to the danger of foraging during daylight hours (Waser, 1975). In places where many predators are diurnal some species may escape predation by being active (and therefore potentially most conspicuous) at night.

The timing, within 24 hours, of foraging bouts is investigated in Chapter 3 where the results of 24-hour followings of kangaroos and wallabies are presented and the possible reasons for nocturnal behaviour are discussed. Foraging in the dark may pose a number of problems including difficulties of seeing and selecting food items and problems with maintaining social contact. In Chapter 3 I also compare the details of foraging behaviour (biting rates and surveying rates) between day and night to see if darkness has an effect on the way in which kangaroos forage and survey the environment. Kaufmann (1974b) claims that macropods are less social than ruminant species occupying similar ecological niches and he has suggested that this is the result of their nocturnal habit. Changes in grouping behaviour between darkness and daylight are discussed in Chapter 7 where I also consider whether the differences in group size are a result of difficulty in maintaining group cohesion in the dark or whether they are the result of kangaroos choosing to be in groups of different size in the dark.

1.3.2 How long to forage ?

Animals may terminate feeding bouts because of some disturbance, because the animal is satiated or because it needs to move on to some other activity. Both chemical and physical factors act as feed-back mechanisms for grazing animals determining when feeding bouts should end (Weston, 1982). Ruminants may be particularly restricted in their grazing hours by the time they need to spend ruminating (Arnold, 1964). Although Macropods are also foregut fermenters, they lack an omasum at the base of the forestomach to prevent the outflow of digesta (Dellow and Hume, 1982). They therefore have a potentially faster rate of passage and shorter retention times than ruminants (Hume, 1982) which may allow them longer grazing times (Clarke and Loudon, 1985). It may also mean that foraging need not be broken into bouts.

Increasing the duration of foraging time in 24 hours is one possible response to a decline in food availability (Allden and Whittaker, 1970; Hodgson, 1982), although the extent to which animals can do this depends on other constraints on their time (Arnold, 1964). Animals may also increase total foraging time during periods when they have higher energy requirements, such as pregnancy and lactation (Hanwell and Peaker, 1977; Loudon and Kay, 1984; Clarke and Loudon, 1985).

The total time, in 24 hours, that kangaroos and wallabies devote to feeding was investigated in this study by following animals continuously for 24-hour periods and recording their behaviour. These followings are described in Chapter 3, where the differences in total foraging time between seasons and population classes are discussed in relation to food availability. The proportion of active time in daylight that animals spend foraging and surveying are examined in Chapter 6 where activity schedules are compared between the species and sexes.

1.3.3 Where to forage?

The choice of foraging sites will be determined, in part, by the distribution and availability of food items, but other factors also come in to play. Some locations may be rich in food supplies, yet also be dangerous because of predators. The relative importance of food quality and safety to the individual forager will affect the forager's assessment of patch quality and its likelihood of feeding in that patch. Some research has suggested that animals balance the costs and benefits of foraging and anti-predator behaviour such that they do not actually optimize either behaviour (Sih, 1980; Holbrook and Schmitt, 1988), whilst another study has suggested that animals decide where to feed on the basis of food requirements, ignoring the risks of predation (Prins and Iason, 1989).

The latter findings were for the African buffalo *Syncerus caffer* that, because of their size, can probably ignore the risk of predation; the same is unlikely to be true for smaller antelope species.

In Chapter 4 I investigate where kangaroos and wallabies feed and try to identify which attributes of their feeding site locations are important in their choice of site. The factors considered include the dominant plant species in the sward, the proportion of dead vegetation in the sward surface, the cover vegetation available for herbivores and their predators to hide in and time since burning the vegetation. I also tried to remove the confounding effects of predation risk and the different distributions of plant species from the choice of feeding site by conducting 'cafeteria trials' where each plant species was presented in a single species sward in the same paddock (see Chapter 4).

1.3.4 What to ingest?

Beyond choosing where to feed, herbivores may make foraging selections on a finer level by picking which plant and even which plant part to eat. Being highly selective for highly digestible items may bring a high reward for each item eaten but may also incur a high cost in search or handling time. The profitability of a food item is generally considered to be a function of both its nutrient reward and the time and energy required to search for and ingest it (Schoener, 1971). The opposite to being selective is for animals to eat any food items encountered in a food patch, enabling them to achieve a relatively high intake rate but possibly a low diet quality.

In Chapter 4 I look at the proportions of different monocot species in the diets of kangaroos and wallabies in relation to the availability of the plant species in the habitat. I hope to determine the strategies behind their selection choices by comparing their dietary preferences. Chemical analyses of the plant species allowed me to see if animals were selecting items on the basis of their protein or fibre content, whilst feeding rates on different sward components (see Chapter 5) allowed me to see if the potential rate of intake affected diet choice.

1.3.5 How fast to bite and how much to bite?

The mass and structure of vegetation in the sward canopy affect the ingestive behaviour, and hence herbage intake, of grazing herbivores (see Hodgson, 1982 for review). Bite size and biting rate are important components of intake although variations in bite size are generally much greater than variations in biting rate (Hodgson, 1981). Whilst bite size is generally considered to be determined by sward structure and the size and shape of the mouth and buccal cavity, grazing mammals are able to increase their rates of biting in response to increased energy requirements (Loudon and Kay, 1984;

from the sward are constrained by the way the vegetation is presented, foragers may also facultatively alter their biting rates, and perhaps bite sizes, in order to meet their energy requirements.

In Chapter 5 I examine the effect of sward structure on biting rates and other foraging variables. I was unable to measure bite size in this study because accurate measurement of this variable for grazing animals requires the use of fistulated animals. Since incisor arcade width is similar for mature animals of the same species and sex I have assumed that bite size is quite similar for animals belonging to the same class such that variations in intake per unit time are more related to bite rate and bite composition than bite size. Differences in incisor arcade shape and width are very likely to differ between the two species, with the larger species (eastern grey kangaroo) having a proportionately narrower arcade width for the size of its body (Janis, in press).

1.4 Aims of the study

In 1974 Jarman published a paper titled "The social organization of antelope in relation to their ecology" in which he described relationships between body size, social organization, foraging behaviour and behaviour for minimizing predation for a number of related species of antelope. Similar relationships had already been described in comparative studies of birds (Crook, 1965) and primates (Crook and Gartlan, 1966) and have since been suggested for macropods (Kaufmann, 1974a; Jarman, 1984; Norbury *et al.*, in press). Jarman's conclusions relating to the foraging behaviour of antelopes were as follows.

a) Antelope show a wide range of feeding styles, each of which are related to selecting food items of a specific type of dispersion. A species' body size is a major determinant of dietary preference because metabolic rate scales to body weight to the 0.75 power i.e. smaller species require relatively higher quality diets. High-quality food items such as fruits and browse tend to be scarce, widely dispersed and associated with forest or woodland habitat whilst the abundant, poorer quality items are associated with open grasslands.

b) The location, abundance and dispersion of the preferred food items of small and large species are the most important determinants of group size, both directly through the influence of competition, and indirectly through the need for anti-predator behaviour. Thus, large species tend to feed in large groups on open grasslands whilst the smallest species are found in pairs, or singly, in forest and are often territorial.

With increasing body-size macropod species, like the antelope species in Jarman's study (Jarman, 1974), show an increasing tendency to form groups, use open habitat and feed on abundant, relatively poor quality grasses (Norbury *et al.*, in press) and depend less on hiding to avoid predation. However, before conclusions can be drawn concerning the selection forces behind the foraging styles and grouping behaviour of macropod species more information is required in a number of areas:

(i) the choice of preferred food items of a number of species and the distribution of those food items in the environment;

(ii) the risks from predation to species of different size or which use different habitats;

(iii) the costs of grouping behaviour in terms of competition and the benefits of grouping in terms of improving the efficiency of anti-predator behaviour;

(iv) and the foraging strategies of different species which determine which foraging tactics (where and when to feed for example) they employ.

One of the aims of this study was to describe the foraging behaviour of two macropod species which differ greatly in their body size and their tendency to form groups in order to examine the relationship between foraging and grouping behaviour. The eastern grey kangaroo and red-necked wallaby were chosen as the focus for this study because populations of the two species were already completely habituated to human presence at the study site, Wallaby Creek, and were known individually to the investigators there. The species also differed in body size (adult kangaroos ranging in size from 30 to 90 kg and wallabies from 10 to 25 kg) and in grouping behaviour (typical group size of kangaroos 7.4 and wallabies 2.2, see Chapter 7).

The two species live sympatrically over most of their ranges and because the species occupy the same habitat there is opportunity for inter-specific competition to take place. Studies of ungulate species living sympatrically in Africa have demonstrated that the pattern of resource partitioning shown by ungulates in the Serengeti is probably a result of selection for a different feeding strategy for each species in order to reduce competition (Jarman and Sinclair, 1979). Another aim of this study was to identify ecological differences between the two species (e.g. diet and the location of feeding and resting sites), and to see how these differences relate to morphological differences in the species brought about by natural selection to reduce competition.

Eastern grey kangaroos and red-necked wallabies are both primarily grazers at Wallaby Creek (Jarman and Phillips, in press). They provide, therefore, an opportunity to compare the foraging tactics of kangaroos and wallabies on different sward types with those of ruminant species which have been studied in great detail elsewhere. The different mouthparts and digestive capabilities of ruminants and macropods (Janis, in press), means that there are different constraints on foraging behaviour operating for the two groups of species which may demand different foraging strategies. Differing foraging strategies between the two groups (macropods and ruminants) may also result from the distribution and structure of native grasslands in Australia compared with grasslands in other parts of the world. Thus, another aim of this project was to compare the responses of kangaroos and wallabies to changes in sward structure and composition, with the responses shown by ruminant spcies in other studies.

Finally, I also aimed to compare the foraging behaviour of different classes of kangaroos and wallabies, with the major comparison between males and females. Both species are highly sexually dimorphic with differences in body size likely to lead to differences in their energy requirements and risks from predation. The energy requirements of females vary throughout the reproductive cycle and males continue to grow throughout life so there is likely to be a high degree of variation in the intake requirements and vigilance needs of different population classes. By comparing the diet and foraging behaviour of individuals in different population classes I hoped to discover whether the classes used different foraging strategies.

In summary, there are five major comparisons that this study aims to address:

i) to compare the foraging behaviour of two closely related species which live sympatrically, and which 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 the changes in foraging tactics of macropod species on pastures with different sward characteristics with the changes observed for ruminant species, both wild and domestic, which have been studied elsewhere;

v) to compare the foraging tactics of individuals in different population classes to see whether they have different foraging goals depending on their energy demands, social behaviour and risks from predation.

1.5 The study species

The two species that are the subject of this study are members of the family Macropodidae, a family of Australian marsupial herbivores whose species occupy niches equivalent to those of the medium and small ungulates on other continents (Jarman and Southwell, 1986). The eastern grey kangaroo *Macropus giganteus* is one of the largest and most social members of the family with almost all classes mingling freely at all times, in open membership groups, without spatial constraints (*ibid*) (see plates 1+2). By contrast the red-necked wallaby *M. rufogriseus banksianus* is a medium sized, rather solitary macropodid whose individuals spend about 60% of their time alone (Johnson, 1987) (see plates 3+4).

Both species are highly sexually dimorphic as mature adults and males appear to show indeterminate growth by continuing to grow throughout their lifetime (Jarman, 1983). Eastern grey kangaroos are the most sexually dimorphic of all macropodids, and of all terrestrial mammals (Jarman and Southwell, 1986). Differences in body size between the sexes are the result of intrasexual competition among males for mating. Both species have polygynous mating systems with male dominance hierarchies and the alpha male achieving most of the matings (*ibid*, Johnson, 1989b). At the study site at Wallaby Creek both species have year-round matings but there are seasonal peaks in the number of young permanently emerging from the pouch (Jarman *et al.*, 1987).

The females of the species show similar reproductive strategies but differ in their timing of reproductive events. The female eastern grey kangaroo gives birth to a joey of under 1 gram after a gestation period of thirty-six days (Jarman and Southwell, 1987). After four to five months the pouch-young begins to poke its head from the pouch, a month later it may begin to make short exits from the pouch and at about 10.5 months it will permanently emerge from the pouch (Stuart-Dick, 1987). The kangaroo young-at-foot accompany their mothers at all times until they are weaned *(ibid)*, but wallaby young-at-foot remain hidden in cover vegetation for their first weeks following permanent emergence from the pouch (Johnson, 1985). Female kangaroos with dependent young have been shown to be more solitary than other classes of female (Southwell, 1984b; Stuart-Dick, 1987), and may use different habitats as a result of their isolation (Stuart-Dick, 1987).

Females give birth to their next young soon after permanent emergence of the previous young and, provided both young survive, the female will suckle a small pouch-young attached to a teat and a young-at-foot at the same time (Jarman and Southwell, 1986). Female eastern grey kangaroos come into oestrus about the time that their young-at-foot weans. The period of oestrus lasts up to twelve hours for both species (Jarman and Southwell, 1986; Johnson, 1989b), but they have a pro-oestrus period of several days during which the females are accompanied by a group of consorting males. Female

Plate 1 Large male eastern grey kangaroo. Note the large body size, long forearms, large claws and heavy muscle on the chest and shoulders.

Plate 2 Female eastern grey kangaroo with her young-at-foot. Note her paler belly, smaller size, shorter forearms and lighter build in comparison to the male in Plate 1.

Plate 3 Small female red-necked wallaby resting amongst tussock grasses and blady grass. Note the dark forehead stripe, white cheek stripe and red neck which distinguish them from kangaroos.

Plate 4 Female red-necked wallaby with a large pouch-young foraging on weeping grass *Microlaena stipoides* on the floor of a gulley.

during which the females are accompanied by a group of consorting males. Female wallabies come into oestrus at the time their young permanently emerge from the pouch. Females can move great distances during the pro-oestrus period and may do so in order to advertise their oestrus to as many males as possible and thereby encourage inter-male competition (Jarman and Southwell, 1986; Johnson, 1989b).

Both species occupy the higher rainfall area of eastern Australia from Tasmania to Queensland. They avoid dense forest and prefer the more open and dry eucalypt forest (Jarman and Southwell, 1986; Johnson, 1989b). Whilst the eastern grey kangaroo also enjoys the open savanna red-necked wallabies prefer the forest edge where they have easy access to the forest for shelter and the grasslands outside for feeding (Southwell, 1987). Dietary studies of eastern grey kangaroos have shown them to be selective grazers that also take a small proportion of browse in their diet (Griffiths and Barker, 1966, Taylor, 1983a). Red-necked wallabies are also primarily grazers but have been observed eating a mixture of grass and browse (Kaufmann, 1974a). The species are active from a few hours before dusk to a few hours after dawn and as such are among the more diurnally active members of the macropodid family.

The descriptions of the species above suggest that they occupy very similar niches whilst sharing the same habitat over much of their range. In these circumstances one would expect some degree of competition between the species, unless there is a more subtle ecological separation between them. The major contrasts between the species are their body size and degree of sociality.

1.6 The study populations

P.Jarman and his associates have been conducting research in the valley of Wallaby Creek since 1974 and populations of eastern grey kangaroos and red-necked wallabies there have been the subject of intensive study since 1981 (Jarman *et al.*, 1987). Both populations have fluctuated around a mean of 80-100 individuals; each individual is known to the researchers at Wallaby Creek so that the life histories of many of the individuals were known at the start of my study in 1985. The fluctuations in the study populations and the techniques for recognition of individuals are covered in greater detail in Chapter 2. Here I aim to summarize briefly the research that had been conducted on the study animals before my arrival and which provided the background for my study.

Between 1981 and 1984 P.Jarman and C.Southwell collected data on the distributions of each of the herbivore species in the valley in relation to various environmental variables (Southwell, 1987). During this period, and continuing during the period of my study, P.Jarman, C.Southwell and M.Jones studied the dynamics of grouping for the eastern grey kangaroo and the movements of different age and size classes of male in relation to reproductive strategies. In 1981 C.Johnson began a detailed study of the behavioural ecology of the red-necked wallaby and he provided information on the grouping behaviour, male and female reproductive strategies, and home range use of wallabies (Johnson, 1985). The study of red-necked wallabies was continued by K.Higginbottom who explored in more detail the factors affecting female reproductive success. From 1982 to 1986 Stuart-Dick explored many aspects of mother-young relationships in the eastern grey kangaroo, finishing her work in the field shortly before the start of my study (Stuart-Dick, 1987). It was with this background information on the distributions, reproductive strategies and social organization that I began my study of the foraging behaviour of the two species.

CHAPTER 2

The Study Site, Animals and Plant Communities

2.1 Introduction

The scope of this project was partly determined by the unique nature of the study site where I conducted my observations of kangaroos and wallabies. The unusually diverse fauna of the valley known as 'Wallaby Creek' where the study site was located, was first described by Calaby (1966) in a report on the mammal fauna of the Upper Clarence region. Over many decades the land-use practices of the property owners in the valley, including a ban on shooting, partial clearing of the land and control of feral predators, have contributed to the abundance and diversity of the native fauna in the valley. The absence of shooting in the valley since the 1950's has allowed the macropods there to live relatively undisturbed for many years and has allowed them to become habituated to human presence.

The macropods were studied intermittently from 1974 to 1981, and since then have been studied intensively by Jarman and his associates, with studies concentrating on the two most common species: eastern grey kangaroos and red-necked wallabies. Since there was a great deal of information already available on the population dynamics, distributions, home ranges and social organizations of the two populations it was possible for me to direct myself immediately to the main topic of my study, that is the feeding behaviour of the two species. The study site and animals are described in detail by Jarman *et al.* (1987). Here I aim to give the reader an introduction to the study site, and detail the changes in the kangaroo and wallaby populations and the vegetation over the period of this study, to provide a context for discussions of seasonal changes in pasture conditions in later chapters.

2.2 The study site

2.2.1 Location and climate

'Wallaby Creek' is a valley in the northern headwaters of the Clarence River, in north-eastern New South Wales, about one hundred kilometres inland from the eastern coast of Australia (map reference 9341-II-S Koreelah 463485; location 150°27'E.,28°29'S.). Wallaby Creek flows north-south through the valley, with water flowing all year round except during occasional long dry spells (winter 1986 for example), when the Creek ceases to run altogether. The Creek is fed by tributaries running east-west, the largest being Wild Cattle Creek which forms the northern border of the 'intensive study area' described by Jarman *et al.* (1987) and which was also my effective study area. A number of smaller gullies running east-west across the study site contribute water to Wallaby Creek during very wet periods or floods.

Daily weather records in the valley were kept by E.J.Hayes from 1948 to 1988 and the long-term average weather patterns were calculated using the records to 1981 (Jarman *et al.*, 1987). The region's climate is characterized by warm, wet summers and cool, dry winters with poorly defined springs and autumns. The average annual rainfall, for the period 1948-1959 and 1963-1981, is 1023 mm, with a range of 637 (1966) to 1541 mm (1950). Monthly rainfall is highest in January, February and March (summer) and is lowest from April to September (winter) (Figure 2.1). Intensity of rainfall (monthly rainfall divided by monthly raindays) is, however, very low in autumn and spring, and is high in mid-winter and summer.

The rainfall patterns during this study were more erratic. The rainfall in 1985 was close to average but 1986 was the driest year since 1966, with a total fall for the year of 687 mm. March, April and June were particularly dry months in 1986 (Figure 2.1). Although the total rainfall in 1987 was 1043 mm (close to the long-term average of 1023 mm), the rain was unevenly distributed, with alternating wet and dry months in the first half of the year.

The winters at Wallaby Creek are cool, with mean daily maximum temperatures in June and July of 15°C (Figure 2.2) and with an average of 34 frosts a year, most falling in May-September. The mean daily maximum temperatures are highest in December (28°C) and are above 20°C from October to April. On the basis of rainfall and temperature the year could be divided into two major seasons: summer months, October to March; and winter months, April to September. However, changes in pasture conditions do not necessarily reflect these seasonal boundaries because of management practices imposed on the pasture (see section 2.5.2).

The temperatures during the study period were very close to the long term averages, although the mean monthly maxima in the summers of 1985/86 and 1986/87 were a few

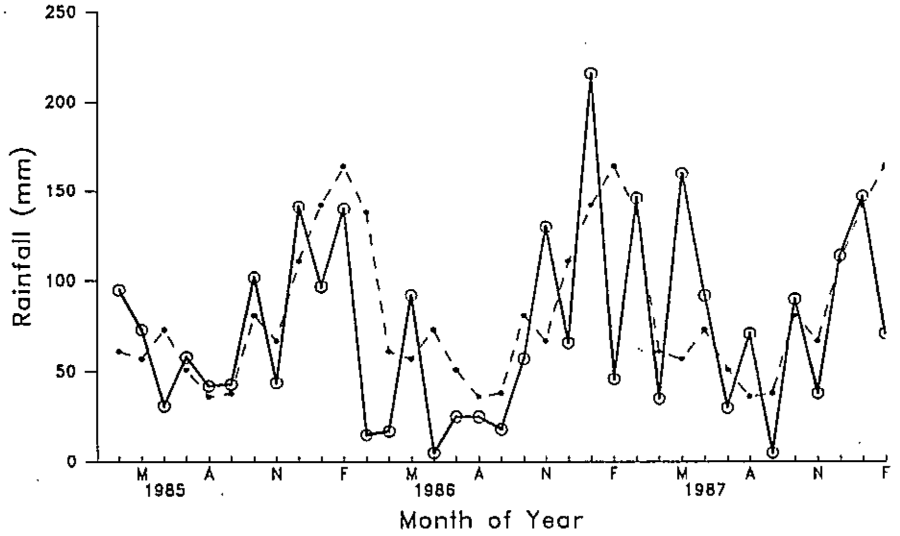


Figure 2.1 Monthly totals of rainfall the during the study period, April 1985 to February 1988. The long-term average monthly totals of rainfall are indicated by the broken line.

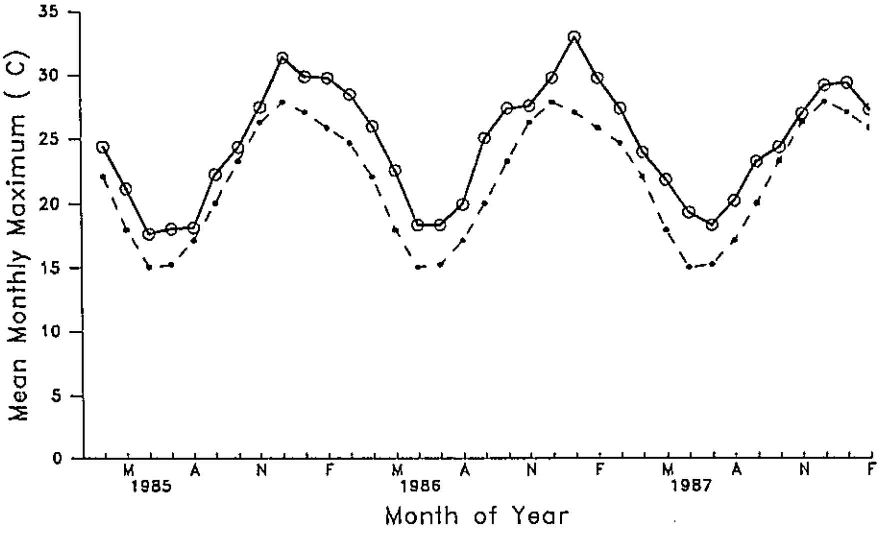


Figure 2.2 Monthly mean daily maximum temperature (°C) during the course of the study period, April 1985 to February 1988. The long-term average monthly mean daily maximum temperature is indicated by the broken line.

maximum temperature equal to or higher than the long term average. The numbers of frost days in 1985 and 1986 were both 35 with slightly fewer (27) in 1987, although July had disproportionately more frosts in that year.

2.2.2 Vegetation and land use

The pattern of land use, and the distribution of the major vegetation types in the valley are illustrated in Figure 2.3. A grid with 1-ha cells was laid out in the intensive study area in 1982, with cell corners being marked on the ground with painted, numbered wooden stakes or tape tied to trees. Some of the grid points also had reflective markers to aid orientation at night. Whenever an animal's location was recorded it was done so to the nearest 10 m, estimated from the distance to the nearest grid markers.

A view of part of the valley is pictured in Plate 5, taken from the eastern slopes looking south-west. The land to the west and north of Wallaby Creek is forested and is owned and managed by the New South Wales Forestry Commission. This forest was last logged in 1950-52 and it was not disturbed during the course of this study. The western area (in the background in Plate 5) was very rarely used by the kangaroos, presumably because it had a very dense understorey, but it was regularly used by the wallabies for resting in the day-time. The forest in the north of the study site, to the south of Wild Cattle Creek, called hereafter 'the northern forest', was leased in 1987 to one of the local property owners who would periodically allow cattle to graze there. The vegetation on the forest floor was dominated by kangaroo grass *Themeda triandra* and snow grass *Poa labillardieri* and both kangaroos and wallabies went to the northern forest to feed and rest. This area provided the most natural habitat in the study area (see Plate 6).

The remainder of the valley is privately owned by local graziers and contains partially cleared, dry sclerophyll forest on the valley slopes (east of Wallaby Creek in the study area) and alluvial flats on the valley floor. The area is fenced into paddocks, although macropods could easily pass through or under the fences and kangaroos could hop over them. Cattle generally had free access to all paddocks but in mid-1987 the cattle on the property in the south of the study site were confined to only a few paddocks. During the study period stocking rates in the valley were low (about one beast per hectare) and the cattle were provided with supplementary feed only during drought years (1986 for example). Macropods did not eat any of this supplement.

Although in the past the southern alluvial paddocks had been sown to clover or lucerne and used for hay making, during the course of this study the paddocks were not managed until mid-1987 when one paddock (later called Area 1) was fertilized with chicken manure, and later in the year was slashed. These southern paddocks were frequently used by the wallabies for feeding, with animals usually moving into the forest on the western edge of the paddocks to rest. The northern paddocks on the valley floor contain natural

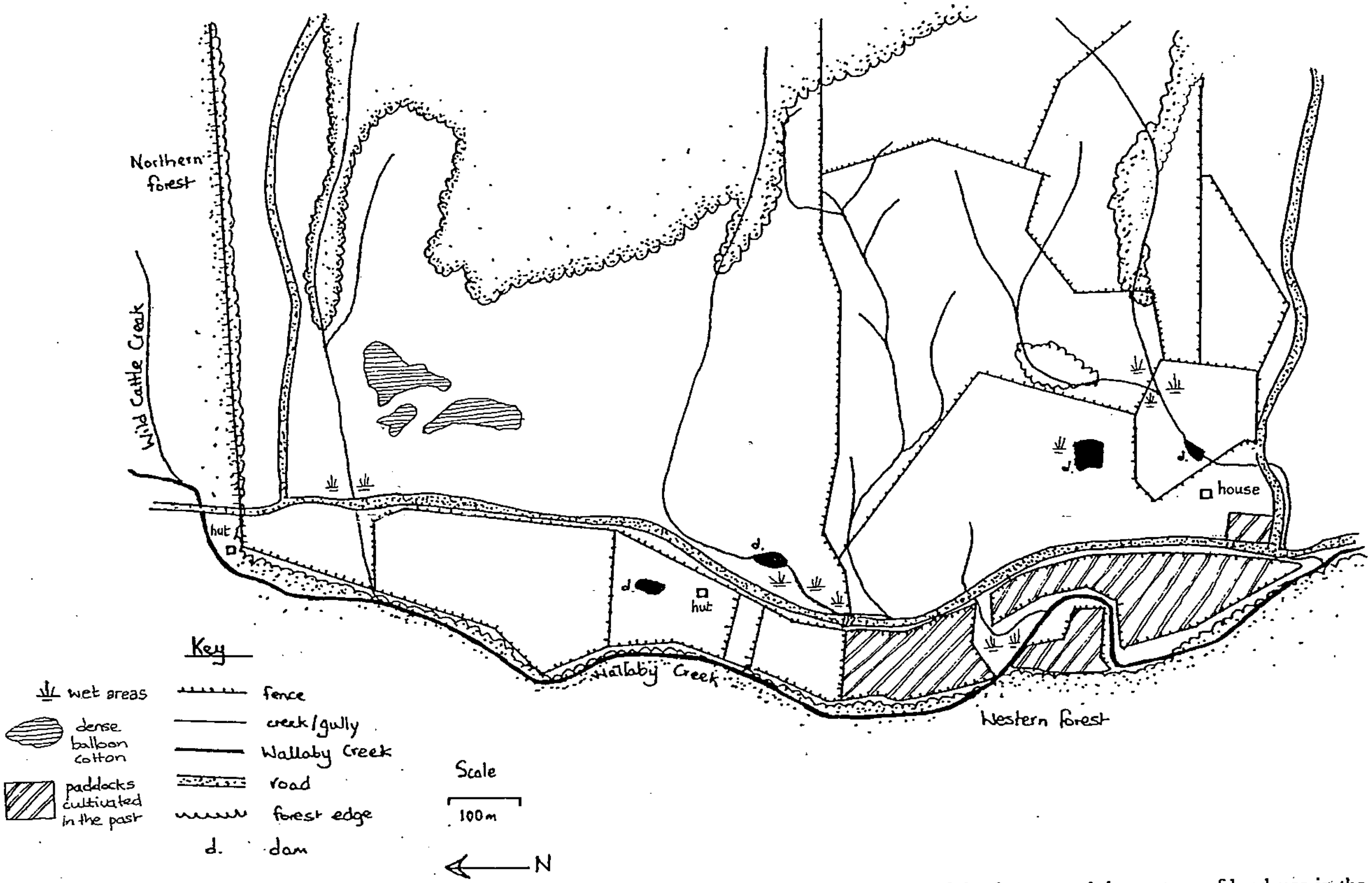


Figure 2.3 Distribution of the forests and the pattern of land-use in the study area.

Plate 5 View of part of the study area, taken from the cleared eastern slopes, facing the valley floor and western forest.

Plate 6 View of the northern forest with its ground vegetation layer dominated by kangaroo grass *Themeda triandra*. The photograph was taken in February 1988, seven months after the forest vegetation was burnt.

tussock grassland dominated by swamp foxtail *Pennisetum alopecuroides* and blady grass *Imperata cylindrica.*

The valley slopes are largely cleared and in early 1987 many of the larger shelter trees were harvested for timber. Tussocks of snow grass and to a lesser extent swamp foxtail cover much of the slopes, with carpet grass *Axonopus affinis*, paspalum *Paspalum dilatatum*, kikuyu *Pennisetum clandestinum*, and various annual grasses dominating between the tussocks (the intertussock sward). Many of the gullies have dense vegetation with ferns, brambles and patches of *Lantana* sp. providing cover for animals.

Dams and the Creek itself provided drinking water for the stock, although macropods were rarely seen to drink, and then only on very hot days.

The major management practice imposed on the cleared pasture is annual burning. Each June or July of the study, areas of the cleared pasture were burnt, with the northern half of the site being burnt more frequently and extensively. Burning in late winter removes dead leaves, and encourages new growth of swamp foxtail, snow grass and blady grass at a time when the availability of the more palatable grasses is low. The grazers in the valley make use of the burnt swards for many months after the burning event. Prior to this study kangaroos, wallabies and cattle at Wallaby Creek were shown to increase utilization of areas following burning, although the magnitude and timing of the response differed between species (Southwell and Jarman, 1987).

2.2.3 Other herbivores in the valley

Besides the eastern grey kangaroo and red-necked wallaby, there are eight other species of macropod living in the valley. The red-necked pademelon *Thylogale thetis* was the most common with up to fifty individuals being counted in one evening search. These small wallabies spent the day-time in the western forest but would come out into the lower paddocks to feed at night. The number seen on a search varied considerably from month to month, and appeared to be related to the burning regime.

The nocturnal rufous bettong or rat-kangaroo *Aepyprymnus rufescens* was also common all over the study area. Other macropodoid species recorded at Wallaby Creek include: common wallaroo (*Macropus robustus*), swamp wallaby (*Wallabia bicolor*), whiptail wallaby (*Macropus parryi*), black-striped wallaby (*Macropus dorsalis*), long-nosed potoroo (*Potorous tridactylus*), and the red-legged pademelon (*Thylogale stigmatica*).

Rabbits *Oryctolagus cuniculus* and brown hares *Lepus capensis* are very uncommon in the valley, with only a couple of sightings in the three years of the study. Rabbits were more common in the southern end of the valley and it may be that the heavy soils in the northern half of the valley prohibit rabbit colonization.

2.2.4 Predators in the valley

The native dingo *Canis familiaris dingo*, feral dog *Canis familiaris familiaris*, fox *Vulpes vulpes*, feral cat *Felis catus* and the Wedge-tailed Eagle *Aquila audax* have all been recorded as predators of kangaroos and wallabies (Russell 1974). Although the individuals of *Canis familiaris subsp.* that we sighted appeared to be dingoes we could not be certain that they were pure-bred. Dingoes were probably the most important predators of kangaroos and wallabies in Wallaby Creek during this study. They were present in moderate numbers throughout the study period although when numbers were such that calves were at risk or being taken, local farmers would reduce their numbers by trapping. Dingoes were sighted in 3 out of 18 field trips between January 1986 and July 1987 and even when not sighted were often heard howling at night, or their footprints or scats were seen on the tracks. Dingoes were sighted foraging during the day and night but in a study of dingoes only 300 km from Wallaby Creek, Robertshaw and Harden (1985) found that dingoes hunted mostly at dawn and dusk.

It was not possible to apportion loss of kangaroo and wallaby pouch-young or young-at-foot to each species of predator and to loss through illness, malnutrition or injury because only two deaths of young were observed during the period of this study, both of them kangaroos. In each case the young was sick and in one case the young was attacked by crows as it was dying. Between 1982 and 1985, in the same population of kangaroos, the proportion of young kangaroos produced each month that disappeared was correlated with the number of dingo sightings per field trip (Stuart-Dick, 1987). K.Higginbottom also found that survival of juvenile wallabies in the valley, between 1981 and 1987, was more dependent on the number of dingoes present than the season of emergence of young from the pouch or prevailing climatic conditions (Higginbottom, pers. comm.).

Dingoes were not only a danger to young animals. On a number of occasions adult wallabies and kangaroos were chased by dingoes and some were probably killed although healthy adult kangaroos appeared to outrun their predators easily. Two adult wallaby carcasses found in gullies had no visible signs of illness or injury and it appeared that the wallabies had been "ambushed" by dingoes.

The importance of the dingo in controlling kangaroo and wallaby numbers appears to vary greatly between geographical regions, depending on the density of dingoes, the presence of dingo-proof fences and the availability of prey species. In a study in eastern Australia, macropods comprised 31-91% of the diet of dingoes (Robertshaw and Harden, 1985).

Wedge-tailed Eagles were also active predators in the valley and on one occasion I found an eagle at the carcass of a newly killed young kangaroo. Even in this case it was not possible to determine whether the eagle had actually killed the young because I had not observed the death. On another occasion I saw an eagle flying off with a small macropodoid but I could not identify the species of prey. An inspection of the ground below the eagles' eyrie by M.Jones in December 1987 did not reveal any macropod bones but inspections by P.Jarman between 1975 and 1982 revealed fur, skulls, jaws etc. of rufous bettong, red-necked wallaby and very young eastern grey kangaroos.

Foxes were also sighted occasionally and almost always at night, but I saw only two interactions between kangaroos and foxes. On one occasion, during one of the 24-hour followings, I noticed two rat-kangaroos feeding close by the kangaroos that I was watching. A fox appeared in my spotlight beam and hid behind a grass tussock. At the moment it pounced on the rat-kangaroos they hopped away but the kangaroos remained where they were and the fox retreated. I sighted a feral cat on only one occasion as it was stalking a wallaby in the day-time; the wallaby escaped.

Kangaroos and wallabies at Wallaby Creek are at risk from predators by day and night, and may be attacked from the ground (dingoes, dogs, foxes *etc.*) or the air (Wedge-tailed eagles). Both species are more active at night than in the daytime, perhaps in an attempt to avoid diurnal predators. The responses of kangaroos and wallabies to the threat of predators will be explored in terms of their activity schedules (Chapter 3), their choice of feeding-site locations (Chapter 4), their vigilance behaviour (Chapter 6) and their grouping behaviour (Chapter 7).

2.3 The Study Populations

2.3.1 Individual recognition

One of the pre-requisites for a study of individual behaviour is the observer's ability to recognise individuals in the population. The studies of eastern grey kangaroos and red-necked wallabies at Wallaby Creek have deliberately involved minimal disturbance of the two populations to keep the animals easy to observe at close range. At the start of this study none of the animals had been captured and we were therefore compelled to learn to identify individuals on the basis of unique markings and features.

C.Southwell and R.Stuart-Dick first identified all the individual adult kangaroos and gave them a unique name and number, passing on their identifications to subsequent observers; C.Johnson did the same for the wallabies. The success of this transfer of identities from one observer to another was tested in a series of trials and approached 100%. The first animals learned were always those with unique identifying marks and injuries. Gradually the new observer would acquire an overall picture of those individuals and those that were not marked in any way.

Each observer used a different list of features to help them learn to identify animals although ultimately animals could be identified from a distance because of their posture, behaviour and overall appearance. Young-at-foot were often identified by their association with their mothers and we had to be careful to learn to recognize them on their own, before they became independent of their mothers. To this end some young animals, and a few adults which were particuarly hard to tell apart, were marked by squirting dye on them from a syringe. The dye marks lasted up to six months and made identification at night much easier. This technique was not suitable for the wallabies because we could not approach them closely enough.

Some wallabies were caught during a tranquiliser darting programme carried out by K.Higginbottom (in press). Those wallabies that were darted were marked with ear notches and reflective ear tags, but all these wallabies were approachable and easy to identify anyway. However, when the ear tags remained in place they were useful for identifying the wallabies at night. It was generally harder to learn to identify wallabies because, although they had more natural markings (e.g. facial stripes, ear borders, neck colouration), we had to observe them from a greater distance and for a shorter time. Also, wallaby young-at-foot were hidden most of the time and were often not seen in the company of their mothers. For this reason I was unable to keep up with the identification of new young wallabies in the last year of the study.

All the observers found it easier to associate animals with a name, especially if that name conveyed some information about the animal's appearance or "character". The young animals were named according to the theme conveyed by their mothers name, making it easier to recall relationships between animals in a group.

When identifying animals, the individuals were first allocated to a population class (see section 2.3.2) thereby greatly reducing the number of possible identities. However, care had to be taken when using the population class to help identify females because they could have lost a class-distinguishing feature (e.g. a pouch-young or a young-at-foot) since they were last identified.

2.3.2 Population classes

Each month an effort was made to find every individual in both populations and to record their population class. These population data were collected for kangaroos by M.Jones until May 1986, and for the wallabies by K.Higginbottom until June 1987; after these times I collected the information.

For the kangaroos I followed the schedule devised by C.Southwell and P.Jarman (see Table 2.1) and continued by M.Jones. Males were categorized on the basis of size and degree of musculature and females were categorized on the basis of the presence and size of their pouch-young or young-at-foot. The schedule for classifying female kangaroos fits within R.Stuart-Dick's finer classification, where 10 classes of female were identified (R.Stuart-Dick 1987). In the case of females with young-at-foot that were close to the age of weaning a number of sightings and some observation time was necessary to ascertain whether the young had been weaned or not. Females with new pouch-young could also be difficult to classify, especially those that were primiparous. Sometimes a female's pouch appeared to have a small bulge in one month, which was not visible the following month. In this case it was not possible to say for certain whether the female had lost the young or whether the bulge had just been a baggy pouch. R.Stuart-Dick estimated that a maximum of 13% of diminutive kangaroo pouch-young were lost (Stuart-Dick, 1987) and the corresponding figure for wallabies was about 5% (K.Higginbottom, pers. com.).

I followed P.Jarman's convention of promoting sub-adults to adults on the basis of size whereas R.Stuart-Dick promoted sub-adults at the age of two years. Although a size criterion could be subject to within- or between-observer variation, there seemed to be merit in using a criterion which allowed some animals to reach adulthood younger than others if they grew faster. For consistency I used the same schedule for wallabies although male wallabies were only divided into small, medium and large categories.

Table 2.1 Descriptions of the 18 population classes identified for eastern grey kangaroos and 15 identified for red-necked wallabies. The abbreviations used for the classes in the text are also given. * indicates which classes are used for wallabies only.

Population Class	Abbreviation	Description
Adult Males		
Large	LM*	*1.5 - 2 times larger than female, heavy muscular development*
1 large, large	LLM	
2 small, large	SLM	
Medium	MM*	*Larger than adult female but smaller than large male. Some muscular development in forearms*
3 large, medium	LMM	
4 small, medium	SMM	
Small	SM*	*Between 2/3 and full adult female size.*
5 large, small	LSM	
6 small, small	SSM	
Adult Females		*Greater than 2/3 adult average female size.*
7 no pouch-young	NPY	*No visible pouch young.*
8 small pouch-young	SPY	*Female has a small pouch young. Young occasionally pokes head from pouch but it never gets entirely out of pouch; head is pink and furless.*
9 medium pouch-young	MPY	*Female has medium pouch-young. Pouch-young often pokes head from pouch and occasionally leaves pouch for brief periods.*
10 large pouch-young	LPY	*Pouch-young has head, tail and/or legs poking out of the pouch most of the time and young spends long periods out of the pouch.*
11 young-at-foot	FYAF	*Female has young-at-foot and no pouch bulge. Young-at-foot never returns to the pouch but still sucks from the mother.*
12 young-at-foot & small pouch-young	FYAF & SPY	*Female has young-at-foot and small pouch-young.*
Sub-adults	SA	*No longer sucking and less than 2/3 of adult female size.*
13 male	SAM	*Sub-adult is male.*
14 female	SAF	*Sub-adult is female.*
15 unknown sex	SAU	*Sex of sub-adult is unknown.*
Young-at-foot	YAF	*Emerged permanently from the pouch, still sucking from mother.*
16 male	YAFM	*Young-at-foot is male.*
17 female	YAFF	*Young-at-foot is female.*
18 unkown sex	YAFU	*Sex of young-at-foot is unkown.*

2.3.3 Population dynamics

During the period May 1985 to February 1988 numbers of adult kangaroos in the population varied between 46 in February 1986 and 68 in September 1987 (see Table 2.2). Numbers of adult males were particuarly low for the first 18 months, due to the recent dispersal of sub-adult males at the start of the study and few male young-at-foot coming through to replace them. Although kangaroos are not seasonal breeders at Wallaby Creek they do show seasonality in the timing of conception and permanent emergence (Stuart-Dick, 1987). The peak period for permanent emergence is September to November, which coincides with good pasture conditions (see section 2.5.2). Hence, there were large numbers of young-at-foot each year between September and March, unless, as in early 1987, many young-at-foot died. The numbers of adult females in the population were boosted in 1987 and 1988 by large numbers of surviving female young.

Table 2.2 Total numbers of adult, sub-adult and young-at-foot eastern grey kangaroos in the study area at Wallaby Creek, each month from May 1985 to February 1988. Numbers were not available for January 1987.

		Adults		Sub-adults		Young-at-foot	
Year	Month	male	female	male	female	male	female
1985	M	16	36	0	3	3	6
	J	17	35	3	3	2	6
	J	17	36	3	6	2	6
	A	17	34	4	5	3	5
	S	17	34	4	5	3	9
	O	14	33	4	5	2	9
	N	16	34	4	6	6	9
	D	13	34	4	7	7	10
1986	J	14	35	3	9	11	8
	F	12	34	3	9	13	8
	M	15	34	2	7	13	8
	A	15	35	4	10	11	5
	M	13	35	7	12	5	4
	J	12	34	8	12	8	4
	J	13	33	3	10	6	6
	A	16	38	10	5	4	6
	S	14	40	8	5	2	11
	O	20	41	5	5	4	9
	N	20	40	6	4	4	15
	D	24	37	5	8	3	10
1987	J	-	-	-	-	-	-
	F	24	39	4	13	2	3
	M	24	42	5	10	4	4
	A	22	38	5	14	7	3
	M	23	38	5	10	3	3
	J	24	37	6	10	4	2
	J	23	41	7	13	5	3
	A	23	42	5	14	7	3
	S	24	44	6	12	7	3
	O	21	40	8	10	5	0
	N	21	40	8	10	5	2
	D	20	39	10	11	5	1
1988	J	21	39	9	8	3	2
	F	22	44	6	3	4	3

The numbers of red-necked wallabies in the population were recorded each month by K.Higginbottom; by the start of my study she could recognize almost all of the adults in the population. The numbers of red-necked wallaby young-at-foot could not be accurately determined each month because this class often hid in dense cover in the first one or two months after permanent emergence. Table 2.3 presents the numbers of adult, and sub-adult, males and females in the red-necked wallaby population between May 1985 and June 1987. K.Higginbottom did not census the population after this date and I was not able to recognize enough individuals to do an accurate census.

The number of adult males in the population remained quite stable over the two-year period but during that time there was a greater exchange of individual males than the figures above might suggest. Large males, in particular, died or disappeared and younger males dispersed into the study area throughout my study period. The large number of sub-adult males in the population from April 1986 onwards resulted from large numbers of male young-at-foot surviving to weaning. Male red-necked wallabies disperse or disappear from their natal ranges at about two years of age (Johnson, 1986a); the age at which they reach sexual maturity. The number of adult females in the population also increased during the two-year period as a result of female sub-adults taking up home-ranges within the study area (i.e. not dispersing) and often overlapping their mother's home range (Johnson, 1986a; Higginbottom, pers.com.).

Table 2.3 Changes in the numbers of adult and sub-adult red-necked wallabies in the study area at Wallaby Creek, each month from May 1985 to June 1987.

		Adult		Sub-adult	
		males	females	males	females
1985	M	19	32	5	8
	J	19	32	5	8
	J	21	32	4	8
	A	21	33	3	7
	S	21	36	1	6
	O	22	37	1	7
	N	22	37	2	7
	D	22	38	3	9
1986	J	23	38	5	8
	F	22	39	8	8
	M	21	40	14	9
	A	19	41	16	9
	M	17	41	17	8
	J	19	41	16	8
	J	19	41	16	9
	A	19	38	17	9
	S	23	38	17	9
	O	24	39	17	11
	N	23	40	18	11
	D	24	40	18	10
1987	J	24	42	18	10
	F	25	44	20	8
	M	25	44	23	7
	A	25	44	22	8
	M	25	44	23	8
	J	25	43	25	8

2.4 Methods

2.4.1 Field schedule

Field trips were conducted once a month for ten days at a time. When possible, dates of field trips were chosen to coincide with the full moon to make night observations easier to conduct. I carried out a similar schedule of work during each field trip from May 1985 to July 1987, except in those months when 24-hour observations were also attempted; the methods used for the collection of 24-hour activity data are described in Chapter 3. In August 1987 some of the data collection procedures were abandoned and some new ones were adopted which were retained until the end of the study in February 1988.

The day was divided into a number of time periods; T1, the first 1.5 hours after first light; T2, from then until 3 hours after first light; T3, from 3 hours after first light to 3 hours before dusk; T4, from then until 1.5 hours before dusk; T5, from then until dusk; and T6, from 1.5 to 3 hours after dusk. Thus, T1 and T2 are called the morning time period, T3 the midday time period and T4 and T5 the afternoon time period. First light was defined as the earliest time at which kangaroos and wallabies could be seen well enough to be identified.

2.4.2 Animal Records

Two types of records were collected on the kangaroos and wallabies: searches were made to determine the distribution of kangaroos and wallabies in relation to environmental variables; and animals were watched for varying lengths of time to record their schedules of activity and movement, and details of their feeding behaviour. Both point-in-time sampling and continuous observations were used. For most of these different data-gathering techniques, the categories of posture and activity were the same; those described below were used unless otherwise stated.

Activities and postures: Seven categories of behaviour were used to describe activity and posture, with up to five states possible for each category. The schedule followed that of C.Southwell and P.Jarman with the additional category of Alertness (Table 2.4).

Table 2.4 Categories and states of behaviour and posture used to describe eastern grey kangaroos and red-necked wallabies.

Activity	State	Description
Feeding	Not feeding	
	Biting	*Head-down biting or selecting bites.*
	Chewing	*Chewing vegetation.*
	Regurgitating	*In the act of mericism.*
	Suckling	*(only applies to YAF)*
Head up	Head up	*Head and eyes facing horizon or higher.*
	Head down	*Head and eyes facing the ground.*
Alertness	Not Alert	*Ears and eyes not focussed on a source of disturbance.*
	Alert in group	*Alert to another group member or approach of new group member.*
	Alert outside group	*Alert to some 'natural' disturbance including cows, dingoes, birds, weather etc.*
	Alert to me, other person, or car	*Ears and eyes focussed towards me, usually after a movement or sound or to the approach of another person, dog or car.*
Posture	Lying	*Lying on one flank, generally resting on forearms.*
	Crouched	*Standing with back horizontal and resting on forepaws.*
	Bent	*Back between horizontal and 60^o to horzontal.*
	Straight	*Back between 60^o - 90^o to horizontal, animal usually alert.*
	Sitting	*Sitting back on haunches with tail forward between legs. Common resting position for wallabies, also the birth position.*
Locomotion	Not moving	*Standing, sitting or lying.*
	Stepping	*Walking by stretching forward, resting on forepaws and tail and bringing hindlegs up.*
	Hopping	*Hopping on hind legs with forepaws off ground.*
Grooming	Not grooming	
	Forepaw	*Grooming with forepaw*
	Mouth	*Grooming with mouth*
	Hindleg	*Grooming with hindleg*
Interact	Not	*Not interacting with any animal.*
	With male	
	With female	
	With own young	
	With other young	

Each of the above activity states was recorded for kangaroos and wallabies in the 15-minute continuous observations described in the following section. A number of variables were calculated from the 15-minute data using combinations of the above activities and states. Results from the 15-minute continuous data are presented in Chapter 6 and the particular variables used in that Chapter are described in Table 6.1.

15-minute continuous watches: From May 1985 to July 1987 the schedule of work on each field trip included 20-40 continuous watches of 15 minutes duration, on consistent subsets of the kangaroo and wallaby populations. Initially the subsets were chosen such that each population class (except young-at-foot) was represented equally in number. The subsets included only those animals that were approachable and not disturbed by close observation. As animals in the subset died or dispersed out of the study area others were chosen to replace them. Every three months from May 1985 to Dec 1986, and every two months from Feb 1987 to July 1987, each animal was watched in each of three time periods. In time periods T2 and T4, animals were beginning or ceasing to rest, whereas in T1 and T5 all animals were active. To balance out active and inactive periods animals were watched in T1, T3 and T4 or in T2, T3 and T5.

During the 15 minutes each change in activity and/or posture state (see above) was recorded. At first these observations were recorded on a tape cassette using a small portable cassette recorder, with reference to a stop watch. They were later transcribed onto data sheets. However, when I had become very familiar with the recording scheme I was able to record behavioural changes directly onto data sheets with as little as two seconds between records.

If the animal was still in sight and still feeding in the same vegetation type that it had been feeding on at the end of the scan, it was watched for a further 3 minutes to collect bite-rate information (see later). The species, density and height of the vegetation patch that the animal was feeding on were also recorded according to a scheme devised by K.Higginbottom for vegetation surveys (see section 4.2.3).

Searches: From August 1987 onwards I undertook thorough searches of the study area with simultaneous recording of kangaroo and wallaby locations. Although C.Southwell recorded sightings of kangaroos and wallabies on transects, he did not record the identity of the wallabies and K.Higginbottom did not record kangaroo locations on her searches for wallabies. Also, wallaby numbers were probably under-recorded by the transect method at certain times of the day because in the middle of the day wallabies tended to hide in gullies and dense vegetation.

The intensive study area was divided into 11 blocks for the purpose of these searches (Figure 2.4). These blocks were of unequal size but took similar amounts of time to search on foot because of their differing densities of vegetation and animals. The boundaries of the blocks were chosen so that each block contained a dominant vegetation

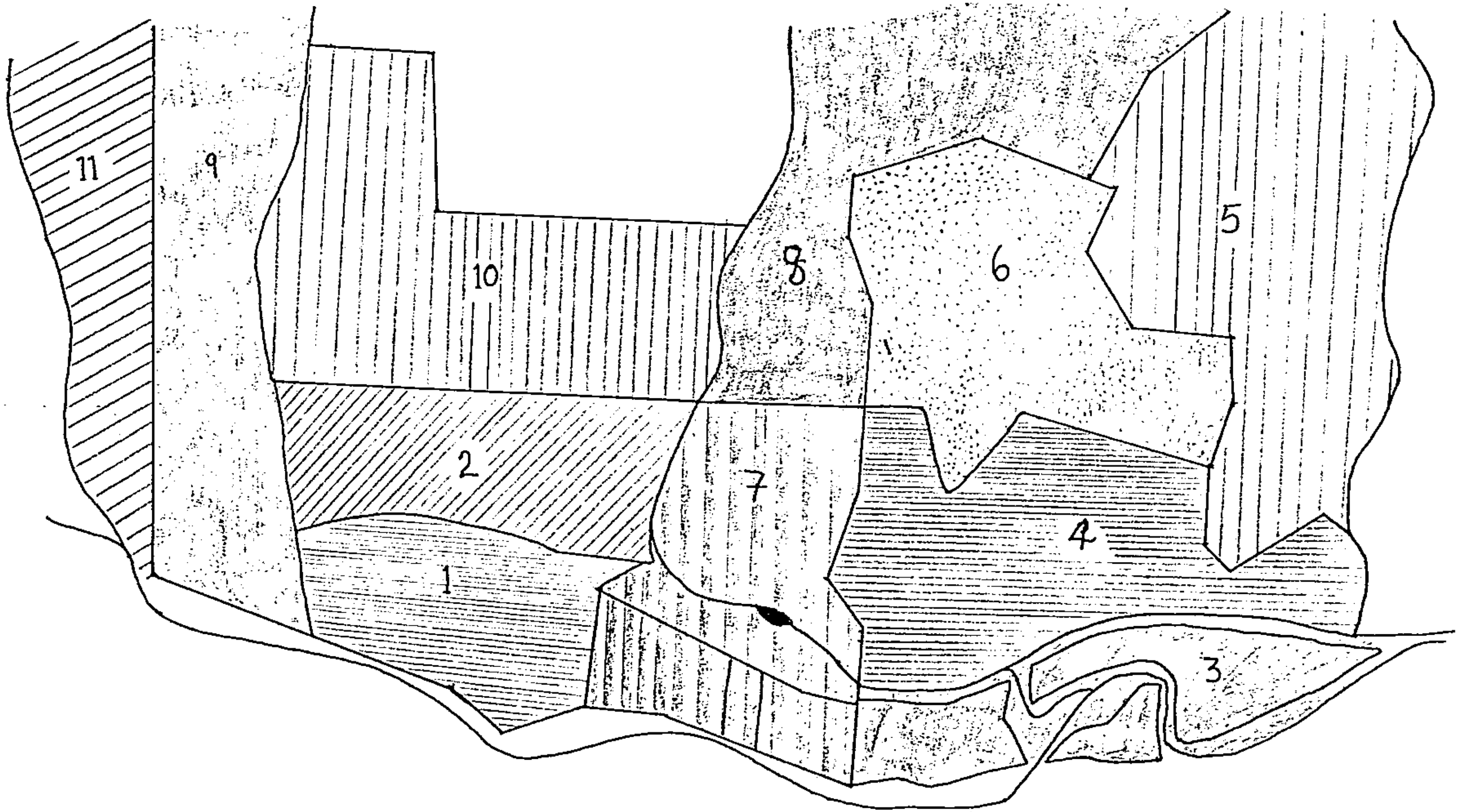


Figure 2.4 Boundaries of the blocks (1-11) that were seached each month between August 1987 and February 1988.

type that was unique to that block and which was important to one or both of the species. All the blocks were searched in each of three time periods (morning, afternoon and night) in each month, and every other month they were also searched in the midday period.

3-minute observations: The six vegetation areas described in 2.4.3 were visited opportunistically, and animals feeding in them were watched for three minutes to record details of feeding behaviour. The 3-minute bite-rate observations involved watching a focal animal continuously for three minutes and recording changes in its activity as well as each incidence of the animal raising or lowering its head, each step and the direction of that step in relation to the location of the focal animal's nearest neighbour, each hop, each bite and where possible each chew.

Bites were characterized by a sharp jerk of the head as herbage was bitten off; when animals were observed at a range of 2 metres there was very good agreement between the number of biting movements observed and the number of bites that were heard. The kangaroos allowed me to approach very closely when they were feeding at night, enabling their bites to be counted by ear. However, I could not determine the bite rates of most wallabies at night. Chews were visible or audible only when I could get very close to the animal and for this reason they were rarely counted for wallabies.

Early in the study these 3-minute observations were described onto a cassette-tape using a small portable cassette recorder and care was taken to announce an action as close as possible to the time it happened. On return to the University the tapes were played and a programmed micro-computer (Epson PX-8) was used to transcribe each action. The internal clock of the computer recorded the time of each action in relation to the start of the scan. At the end of the three minutes, a program was inititated to calculate the variables listed below. The interrupted biting-rate (bites/min) is the total number of bites in three minutes divided by 3. The uninterrupted biting-rate is similar to the 20-bite method of Jamieson and Hodgson (1979) in that it is calculated from the mean time taken for ten bites, without the animal raising its head from the sward. Ten bites were chosen, rather than twenty used by Jamieson and Hodgson for cattle and sheep, because macropods bite more slowly than ruminants and usually raise their head before twenty bites have been taken. The uninterrupted biting-rate reflects the animal's response to sward conditions regardless of the time it spends surveying the surroundings.

The biting ratio is calculated as the ratio of the interrupted biting-rate to the uninterrupted biting-rate and thus indicates feeding "intensity" regardless of total bite number. For example, if an animal spent nearly all its time with its head down, the biting ratio would be close to 1 whereas a smaller ratio would indicate a greater amount of time spent surveying (or at least raising its head from the sward) whilst feeding.

At each step, a kangaroo or wallaby reached a new potential feeding site and if a bite was taken in that patch, the site was considered to have been "accepted" (see Novellie 1978, Underwood 1983). The following variables relating to movement and feeding sites were calculated: the number of accepted sites reached in 3 min; the mean number of bites taken in each accepted site; the total step and hop number; the proportion of steps taken away from the nearest neighbouring animal; the mean step-sequence length between accepted feeding sites; and the frequency of the animal raising its head from the sward. The proportion of time spent in the following activities was also calculated: biting, head-down biting and selecting bites; chewing, head-up surveying and chewing; grooming; and interacting. The variables listed above are described in more detail in Table 5.3.

The 3-minute observations were used in a number of contexts. They were conducted at half-hourly intervals during 24-hour followings of individuals (see Chapter 3), at the end of the 15-minute continuous watches, and opportunistically on searches. They were also conducted during experimental work at the university field station, Newholme (see Chapter 4). Later in the study, when I was able to transcribe the tapes without looking at the keyboard of the micro-computer, I began to use the computer in the field to record behaviour directly. However, in wet conditions and at night the cassette-tape recorder was still used.

Other animal data: Other animal data collected on field trips included the population class of all individuals and the body condition of kangaroos (see section 2.5.4). I could not apply the condition-rating schedule, which was developed for kangaroos, to the wallabies with confidence because I could not get close enough to most of the wallabies to see their ribs, tail and hips clearly. Their shorter-limbed bodies and thick fur also concealed their fat deposits.

Faecal pellets were collected from known individual kangaroos and wallabies (only one pellet per individual, per month), stored in 70% alcohol and brought back to Armidale for diet analysis. The methods used to determine diet are described in more detail in Chapter 4. Opportunistic records were made on oestrous groups, male dominance interactions, injuries, emergence of young from the pouch and predation.

2.4.3 Vegetation records

The grasses at Wallaby Creek could be divided into three main types. Tussock-forming grasses provided cover for animals and for some time after burning provided edible green shoots. At other times more palatable grass species growing within the tussocks were also selected for, especially by kangaroos. Tussock forming species included snow grass, kangaroo grass and swamp foxtail. Grasses which grew, often in a thick mat, between tussocks comprised what is hereafter called the intertussock sward. There were two groups of grasses in the intertussock sward: leafy grasses with a high leaf to stem ratio; and stemmy grasses, with a low leaf to stem ratio. The former were the most palatable species with the highest nitrogen:fibre ratio (see later) and were often stoloniferous. The most common were carpet grass, paspalum, kikuyu, weeping grass

Microlaena stipoides and couch grass *Cynodon dactylon.* The stemmy grasses included many annual species such as blue grass *Bothriochloa decipiens,* slender rat's tail grass *Sporobolous elongatus* and barbed wire grass *Cymbopogon refractus.* Forbs, and clover *Trifolium* sp. in particular, also contributed to the intertussock sward. The third type of grass forms 'stands' which in the mature stage provide cover, but in its young stage after burning also provide edible green shoots. These stands are formed from blady grass *Imperata cylindrica.*

During the period of this study, K.Higginbottom carried out vegetation surveys in a proportion of the study area at six-month intervals. The surveys involved a visual assessment of the proportion, height and density of the different species in 25 quadrats in each 0.25-ha grid cell. I have used these data to confirm my visual classifications of vegetation types and to calculate the area covered by each vegetation type or species (see Chapter 4). I decided to concentrate my vegetation data collection on detailed information on the height, proportion dead, proportion grazed and proportion of different plant components in a few selected sward types that were used in particular by grazing kangaroos and wallabies.

Sward height: During the period May 1985 to February 1988 height data were collected monthly for the swards in each of six vegetation areas. These areas (Areas 1 to 6), illustrated in Figure 2.5, were all heavily used by kangaroos and/or wallabies for some or all of the year and they each represented a different sward type that was fairly homogenous throughout the area. The six areas were used to record details of feeding behaviour in relation to sward types and to compare the foraging behaviour of the species or sexes on uniform sward types. Observations of kangaroos and wallabies are compared in four of these areas (Areas 1 to 4), in Chapters 5 and 6, and the areas are described in detail in section 5.2.2.

Height measurements were made using a 1 metre pole, calibrated at 0.5 cm intervals, with a sliding collar which had a 1 cm^2 horizontal, perspex window. The collar was lowered at each point until it hit some vegetation in the sward surface and the height was recorded. At times of the year when carpet grass stems and seed heads lay over the grass surface and were the first item to be hit by the window, another measure was made using the same point on the ground but beneath the layer of seed heads. The seed heads were excluded from the sward composition calculations and were recorded as a separate layer above the sward surface. At each point I recorded the height of the first item to be "hit", whether it was alive or dead, whether it was grazed or not, whether it was a leaf, stem or flower and whether the point was in a burnt area or not.

Sward composition: Every three months from May 1985 to December 1986 height, species, grazing and plant part were recorded down through the sward at a hundred points in each vegetation area. At each of twenty locations in an area five pins were dropped adjacent to one another using a point-quadrat frame. The perpendicular point-quadrat

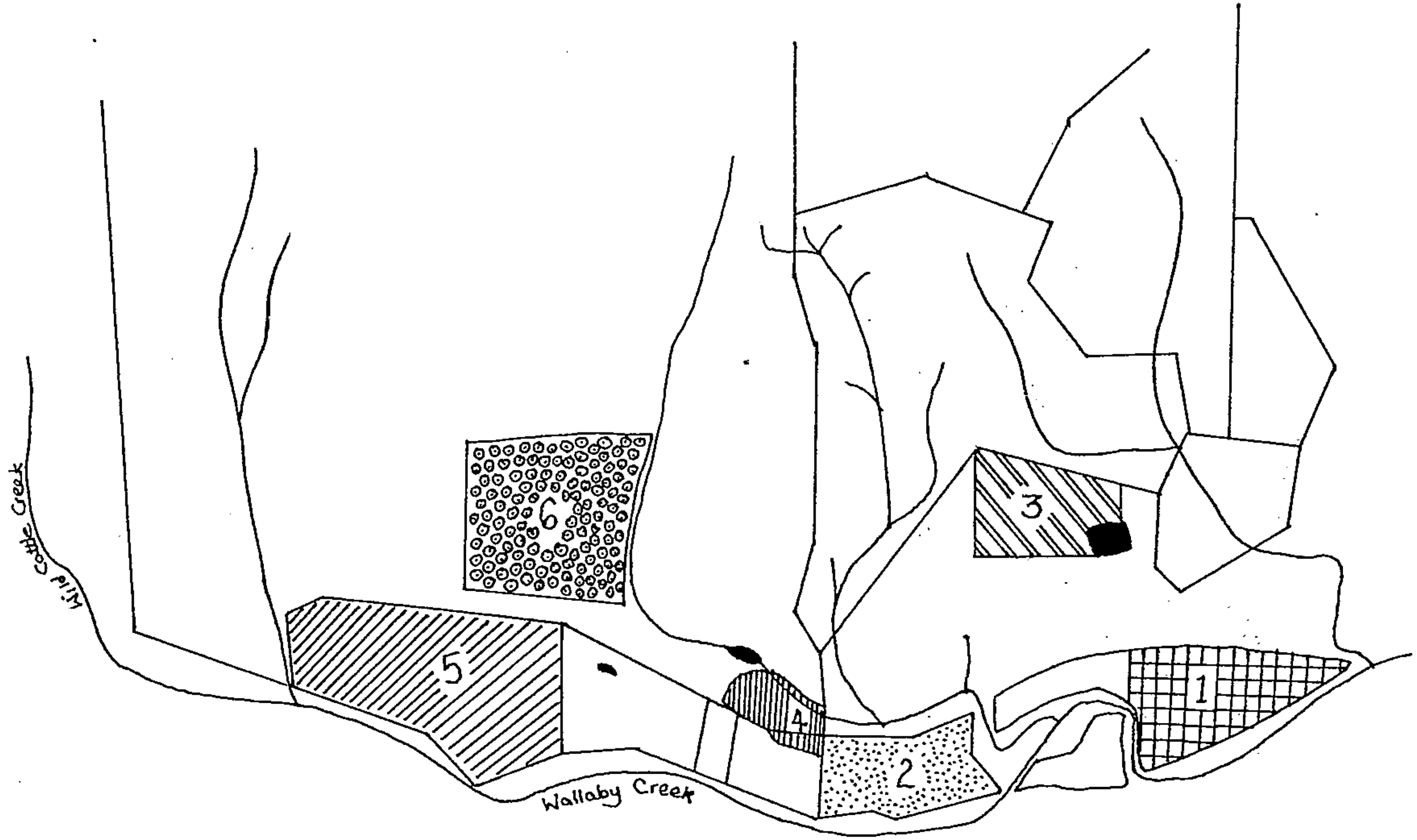


Figure 2.5 Location of the vegetation areas (Areas 1 to 6) where sward measurements and biting observations were made.

frames tend to over-estimate flat, prostrate forms and under-estimate the erect ones so after July 1987 an inclined point quadrat was used (inclined at 45°).

From August 1987, 11 permanent quadrats of 10 X 10 metres were located in each of 11 vegetation types. Each quadrat was marked on a map although a grid marker usually formed one of the corners of the quadrat so that it was easy to relocate. Each month from August 1987 to February 1988, height, species, grazing, and plant part contacted were recorded down through the sward, at each of fifty points, using an inclined point quadrat.

Nutritional composition of sward species: In most months between December 1985 and February 1988 the following samples of grass were collected: swamp foxtail from Area 6; snow grass from Area 6; kikuyu from Area 4 and inside and outside tussocks in Area 3; carpet grass from Area 5 and inside and outside tussocks in Area 3; and paspalum from Area 1 and inside and outside tussocks in Area 3. In addition, samples of kangaroo grass, clover, seed heads, annual grasses and some leafy forbs were collected when they were available or in months when the animals were feeding on them in particular.

Samples were collected on the last day of a field trip and kept under refrigeration until I returned to Armidale when they were frozen until required. Samples were sorted to remove dead material and other species, and leaves were separated from the stems. Both stem and leaf of kikuyu were analysed but generally only leaf was analysed for the other species; this procedure was chosen because wallabies and kangaroos selected heavily for leaf (see later) and it took too long to sort a big enough sample of stem to analyse. Samples were dried in an oven for two days at 50° C and samples were ground to pass through a 1 mm mesh. Kjeldahl digestion and titration were used to determine the nitrogen content of samples and acid detergent fibre fraction, neutral detergent fibre fraction, lignin and ash content were determined for the samples using the methods of Van Soest and Wine (1967). All samples were analysed in duplicate and the average taken; if samples differed by more than 5% the analysis was repeated. Due to a break-down of the portable freezer samples from June and July 1986 were lost as were samples from September 1987.

2.4.4 Statistical analyses

The parametric and non-parametric tests used in this thesis are taken from Sokal and Rohlf (1981) and the BMDP statistical software manual (Dixon and Brown, 1979). Variables measured as a numeric value (e.g. mean step sequence length, step total, biting rates) were first plotted to see if they approximated to a normal distribution. Parametric tests were employed if the condition of normality was satisfied and non-parametric tests or contingency analyses were employed otherwise. The percentages of time allocated to different activities were treated as measured values rather than frequencies to ensure equal weighting for each observation; observations had variable amounts of time missing, and some values were the percentage of another measured time (e.g. biting/selecting as a proportion of feeding time) which varied between observations. Where percentages or proportions covered a wide range of values no transformation was used unless one was particularly suggested by the data. The log of cell standard deviations was regressed on the log of cell means and the value of the regression coefficient (b) was used to determine whether transformation was necessary and which was the best to use (Dixon and Brown, 1979). Percentages and proportions covering a small range of values were given an arcsine transformation (Underwood, 1981).

Student's t tests and analysis of variance were used to test for differences in the means of measured values between seasons, species and population classes. For two-way analyses of variance, the program P7D from BMDP statistical software was used. The advantage of this program is that Levene's test for equal variance and an alternative analysis-of-variance statistic, the Brown-Forsythe statistic, which does not assume equal variances in each group, are provided. Where Levene's test was significant (i.e. variances were not equal) the Brown-Forsythe analysis of variance was used. The P4V program (BMDP statistical software) was used for analyses of variance of a higher order, those using a within-subjects factor or a repeated measure factor and multi-variate analysis of variance. The analyses were weighted by cell sizes (Dixon and Brown, 1979). Levene's test for equal variances within groups was also carried out and if significant, the analysis was reduced to two-way analyses of variance where the Browne-Forsythe statistic could be calculated.

Some variables, particularly those associated with movement (step-sequence length and proportion of steps away from neighbour for example), were highly skewed and could not be improved by transformation. Where one-way analysis of variance was required the non-parametric Kruskall-Wallis test was applied, or the Mann-Whitney U test in the case of only two samples (MINITAB statistical package; Ryan, Joiner and Ryan, 1978). For two-way, or higher order, tests the variable was divided into classes and analysed by multi-way contingency analyses (see later).

Frequency data were analysed by the least-likelihood ratio test which Sokal and Rohlf (1981) suggest has theoretical advantages over the chi-squared statistic. Multi-way contingency tables were analysed by fitting log-linear models to the frequencies to better understand the relationships between factors (Sokal and Rohlf, 1981; Dixon and Brown, 1979). The procedure is analagous to that practiced in anova; progam P4F in the BMDP statistical software package was used for the analysis.

The procedure involves first testing to see which order of effects is required in the model. If, in a three-way analysis, the three-factor interaction term is significant no attempt is made to fit a simpler model, but separate two-way tests of independence are made within each level of one of the factors (Sokal and Rohlf, 1981). If the highest-order interaction term is not siginificant then tests of partial and marginal association are carried out to screen which interaction terms are necessary in the model. For a three-way analysis all models are requested and the model chosen is the simplest one that is non-significant (i.e. provides an adequate fit to the data) and which includes the interaction terms suggested by the association tests. The models are described by their minimal hierarchical form. That is, **GS, AS** represents the model that includes the terms **G, S, A, GS,** and **AS.** I have restricted myself to fitting three-way log-linear models because of the difficulty in interpreting higher order interactions (Vepsalainen *et al.*, 1988).

A variety of regression and correlation techniques were used to look at relationships between two or more variables. The Pearson correlation coefficient was used for normally distributed variables and the Spearman rank coefficient is used otherwise. In Chapter 5 partial correlation analysis and step-wise regression analysis are used to find which sward variables have the most effect on foraging behaviour (program P2R, BMDP statistical software). A forward stepping procedure was used with a minimum acceptable F value to enter the regression of 4.00 and a minimum acceptable F value to leave of 3.90.

In Chapter 4 I used a Cluster analysis to group faecal samples according to the proportions of different monocot species that were identified within them. The CLUSTAN computer package was used and I selected Ward's cluster method and squared euclidian distance as the measure of dissimilarity.

2.5 Seasonal changes in pasture and animals

2.5.1 Changes in intertussock pasture conditions

There was considerable variation in greeness and biomass of vegetation available to the kangaroos and wallabies during, and between, years. Plates 7 - 12 illustrate some of the variation in sward conditions between winter 1986 (at the height of the drought) and the following summer. Availability of grass can be limited by the proportion of green grass in the sward, the ease of selecting this grass and/or the standing crop available. The following section describes some of the changes in sward conditions in the different vegetation areas during the course of the study. The changes in swards after burning are described separately in section 2.5.2.

Seasonal changes in intertussock sward height (height of the sward between tussocks) were similar for each of the vegetation areas (Figure 2.6); all correlations between the heights of different pairs of vegetation areas were positive and significant except for those with Area 5 which approached significance. Heights were low in late winter through to early spring and were lowest at the height of the drought in winter 1986. Intertussock heights were higher in late summer than at other times of the year and were highest in early 1987. On the basis of intertussock sward heights the year could be divided into two periods: June to November and December to May.

The biomass of green leaf available to herbivores is dependent not only on the height of the sward but also on the proportions of green and dead vegetation in the sward. Seasonal changes in the proportion of dead vegetation in the sward surfaces of the six vegetation areas (Figure 2.7) followed the reverse pattern to changes in sward height, such that peaks were in late winter to spring and troughs were in summer. All correlations between the proportions of dead in the six different vegetation areas were positive and significant. On the basis of the proportion of dead in the sward, the year could be divided into two seasons: May to October and November to April.

For most domestic herbivores which graze relatively unselectively, bite size is more important than bite rate or grazing time in determining herbage intake (Hodgson, 1982; Milne *et al.*, 1984). Bite size is itself often correlated with sward height and density (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979; Hodgson, 1982) such that sward height can determine herbage intake. In this study low sward heights were coupled with large amounts of dead vegetation in the swards in the period May to October and this period may be considered to be "poor" in terms of food availability whilst the period November to April may be considered "good". However, in some parts of the study area clover was abundant in winter, often in short swards containing a large proportion of dead vegetation, and in such cases the generalization of short swards in winter being relatively poor may not hold. For seasonal comparisons of the intertussock

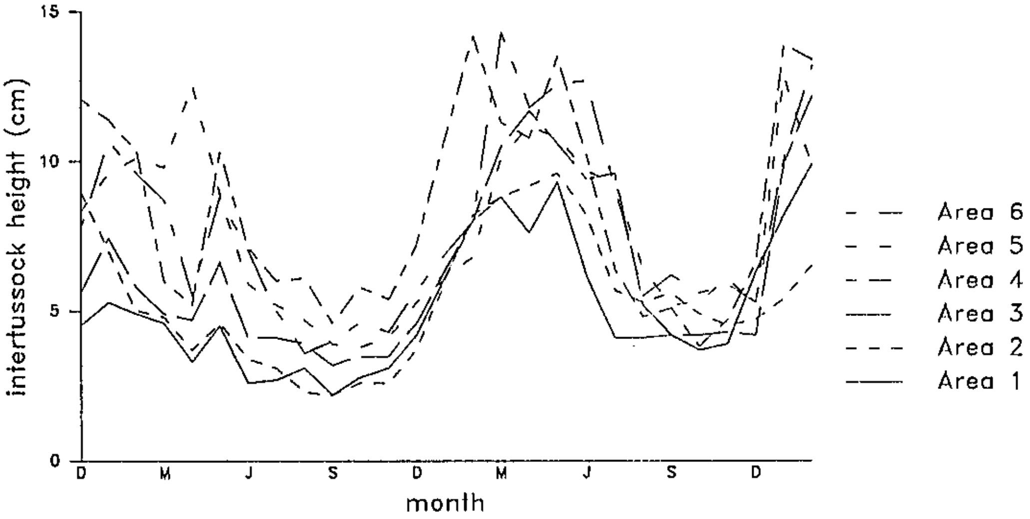


Figure 2.6 Surface height (cm) of the intertussock sward, in Areas 1 to 6, each month from December 1985 to February 1988. No measurements were made in January 1986.

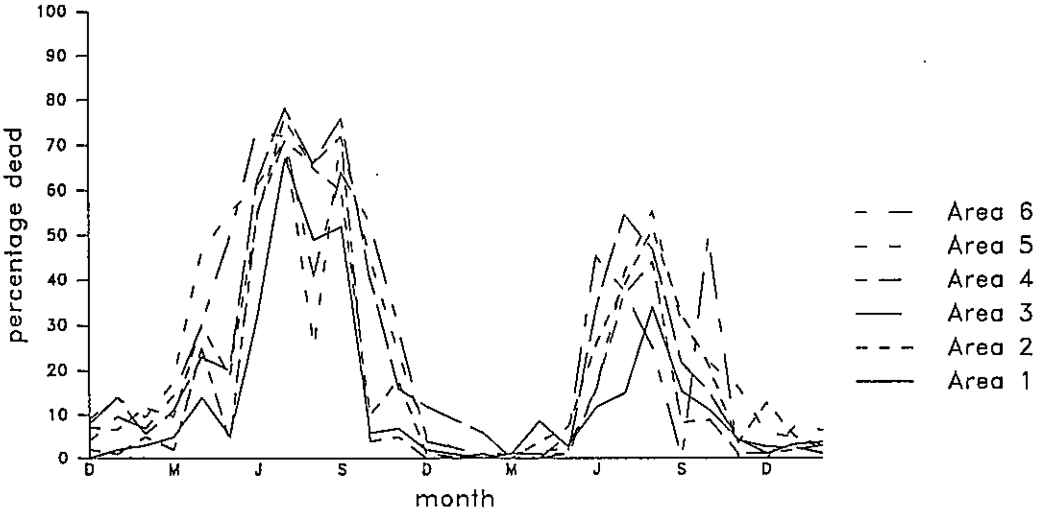


Figure 2.7 Percentages of the sward surfaces in Areas 1 to 6 that were occupied by dead vegetation, each month from December 1985 to February 1988. No measurements were made in January 1986.

Plate 7 View of Area 5 at the height of the drought in August 1986.

Plate 8 View of Area 2 at the height of the drought in August 1986.

Plate 9 View of tussocks and the intertussock sward of Area 5 in August 1986. Note the green shoots in the tussocks and the large proportion of bare ground.

Plate 10 View of the intertussock sward in Area 5 six
months later. Note the carpet grass seed heads on the sward surface.

Plate 11 View of the intertussock sward in Area 2 in August 1986. Clover is the dominant green leaf in the sward.

Plate 12 View of the intertussock sward in Area 2 six months later. Note the leafy forbs and seed heads of paspalum and carpet grass.

swards, or of animals feeding on them, winter is defined as May to October and summer as November to April.

2.5.2 Seasonal changes in the nitrogen levels of the most abundant vegetation species.

Changes in the nitrogen and fibre levels of the grasses did not follow a simple seasonal pattern and samples taken from different parts of the study area in the same month varied widely in their chemical composition. Figure 2.8 illustrates the month by month changes in nitrogen levels of three of the most abundant intertussock species in Area 3, with the levels in clover from Area 2 also indicated. Time constraints did not allow me to analyse samples from every month, and samples from June and July 1986 and September 1987 were lost. Nitrogen levels peaked in May 1986 and were also high in May of the next year. Levels were low in January and February of each year. Levels of nitrogen in clover leaves were higher than for the grass species, often by a factor of 2. There were no siginificant correlations between the nitrogen levels in the grass species from month to month and sward height or rainfall.

Some of the less common grasses that were found in gullies and on the flats by the creek also had high nitrogen levels; these areas were frequented by wallabies more often than kangaroos. Weeping grass contained 3.6% nitrogen in November 1986 and *Bromus* sp. which was common in Area 1, contained 4 - 4.5% nitrogen at different times of the year. Blue grass, a stemmy grass that was found on the valley slopes, contained only 1.4% nitrogen in November 1986.

There was a large degree of variation in the rainfall patterns over the course of this study which makes interpretation of seasonal differences in pasture difficult. However, in the intertussock sward, summer appears to be characterised by a high biomass of grasses, a large proportion of green leaf but relatively poor quality vegetation (in terms of nitrogen content). In winter the intertussock sward is short, with a large proportion of dead vegetation, but with relatively high levels of nitrogen in the green leaf that remains. The rewards of foraging selectively would appear to be higher in winter than in summer.

2.5.3 Burning regimes and changes in burnt pasture

In each of the three years of the study, parts of the study area were burnt in mid-winter. Some areas were burnt each year whilst others were burnt in only one year. The areas burnt in July 1987 are illustrated in Figure 2.9.

On the basis of two intertussock sward characteristics the year was divided into two seasons, which lagged one month behind the two climatic seasons indicated by the temperature and rainfall patterns (April to September and October to March). However, during the winter months, when green biomass in the intertussock sward was very low, burning provided an alternative source of food for the herbivores (macropods and cattle). Although burning did not take place over the whole of the study area kangaroos tended to

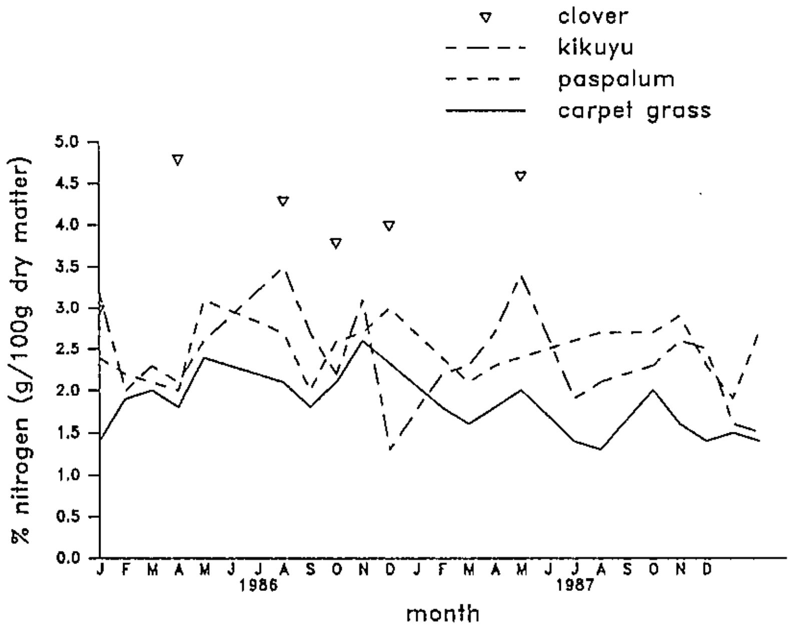


Figure 2.8 Nitrogen levels (g/100g of dry matter) in the leaves of carpet grass, paspalum and kikuyu taken from Area 3, each month between January 1986 and February 1988. The levels of nitrogen in clover leaves are also indicated for the months when samples were collected.

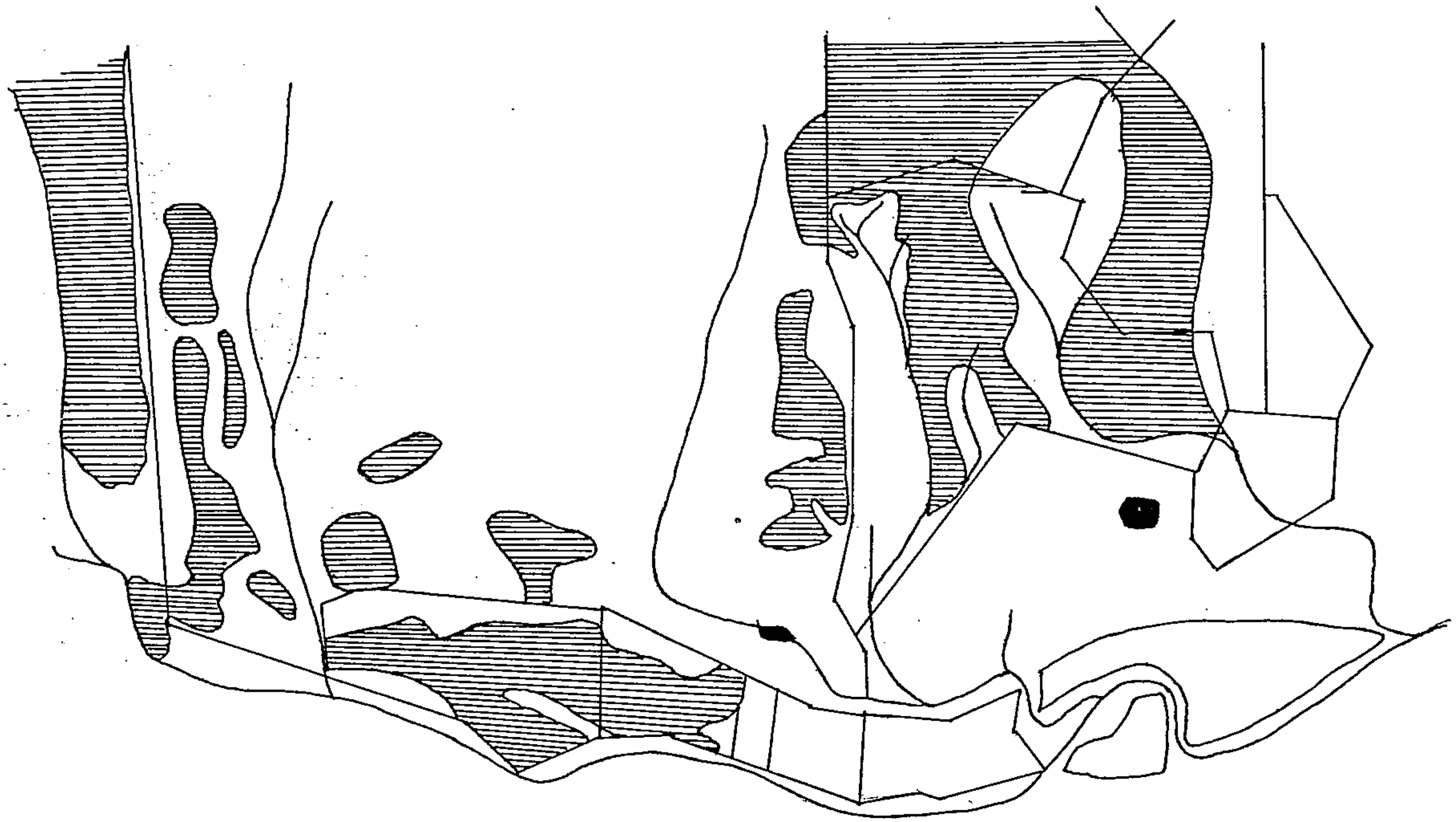


Figure 2.9 Distribution of the burned areas following fire in July 1987. Burned areas are shaded.

feed in burned areas preferentially in winter to spring (see Chapter 4). Thus, for those animals that had access to burnt swards, late winter (after the burn) may not have been the time of most limited food supply. Where comparisons are made of kangaroos and wallabies feeding on areas that were burnt, or where they are not specified as feeding only on the intertussock sward, three seasons are used: summer, November to February; pre-burn, March to June; and post-burn, July to October.

The changes in the availability and quality of grasses through the seasons and burning regimes will be discussed more fully in Chapter 4. I also investigate how the macropods respond to the changes following burning in terms of diet selection and choice of feeding site (Chapter 4) and grazing behaviour (Chapter 5).

2.5.4 Body condition of the study populations

When an animal's food intake exceeds its daily requirements, deposits of protein, fat and other metabolites are built up and body weight increases (Thornton, 1987). As an animal's requirements increase (e.g. during pregnancy and lactation, or periods of movement) or when its food resources decline, its intake may drop below daily requirements and the animal will use up its body reserves, using first the fat and then the protein deposits (*ibid*). Thus changes in body condition reflect surpluses or deficits in the animal's energy balance. Although visual assessments of metabolite deposits are a coarse measure of physical condition, the changes in individuals were noticeable enough to warrant their use. Caution had to be taken when grouping individuals into classes because of the large amount of inter-individual variation.

Between June 1985 and March 1986 M.Jones, for P.Jarman, made a monthly visual assessment of the body condition of the eastern grey kangaroos based on the rating of three characteristics of the animals' morphologies. Appendix I illustrates the criteria which were used to rate the amount of metabolite deposits around the animals' tail base, ribs and hips and it describes how the ratings were combined to give a Body Condition Index.

In May 1986 I began to assess the body condition of the population using the same schedule as M.Jones. Although the same method was used the visual assessment was subjective and despite our close agreement in the ranking of individuals we differed in the range of values we gave. In July 1986 we both independently assessed the body condition of the population and found that although we did not differ significantly in the ratings of adult males (Student's t test: $n=15$, $t=1.34$, $p=0.20$) or adult females (Student's t test: $n=21$, $t=-1.24$, $p=0.25$), I rated young animals higher than M.Jones did (Student's t test: $n=16$, $t=7.82$, $p<0.05$). In October 1986 we did not differ in our ranking of adult females or young but I ranked adult males lower than M.Jones did. Because of the discrepancy in our assessments of body condition I have not combined the data and present only the data that I collected between May 1986 and February 1987.

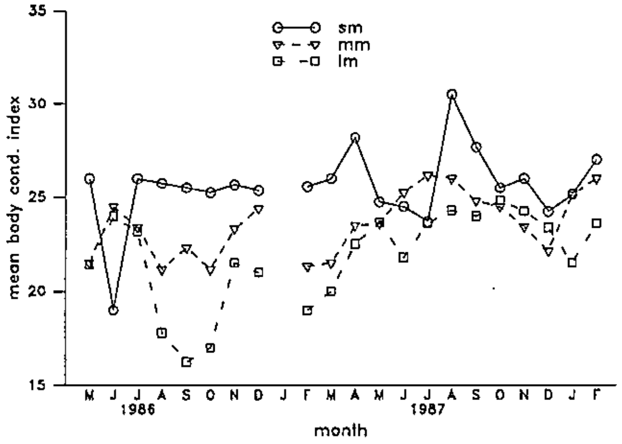
There were consistent differences between population classes in the mean Body Condition Index, with young-at-foot showing the highest condition ratings followed by sub-adults (see Figure 2.10). There was little difference between male population classes although large males generally showed the lowest condition and small males the highest.

Similarly, females with young-at-foot tended to be in poorer condition than those with medium or large pouch-young and poorer still than those females with small or no pouch-young. However, there was considerable variation between individuals and because females were constantly changing from one population class to another this variation may have obscured differences between population classes. In a paired comparison of individual females at different reproductive stages, females were in significantly poorer condition when with young-at-foot than when they had no young or a small pouch-young (Wilcoxon matched-pairs test: T=378.0, n=32, $p<0.04$), or when they had a medium or large pouch-young (T=514.0, n=34, $p<0.001$). The poor condition of females with young-at-foot is not surprising since the late stages of pouch-life represent the most energetically costly time for the mother in terms of milk production (Green 1984) and the weight of carrying a large pouch-young.

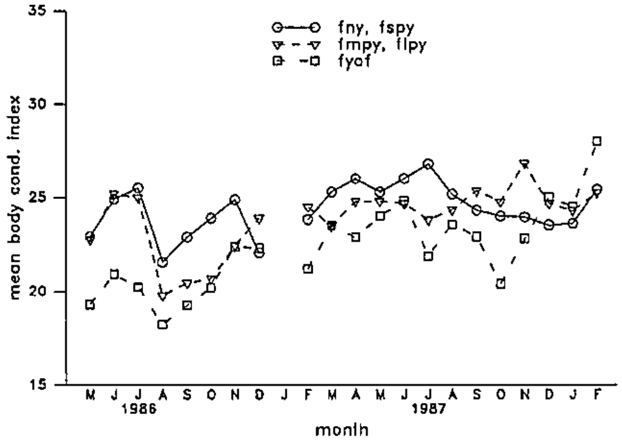
Females with small or no pouch-young were also in poorer condition than females with medium or large pouch-young (Wilcoxon matched-pairs test: T=182.0, n=37, $p<0.02$), despite their lower energetic costs of milk production. The reason for the difference probably lies in the fact that females with no young have usually lost a large pouch-young or young-at-foot recently and that females with a small pouch-young have usually just weaned a young-at-foot or have lost their young-at-foot. Exceptions are females breeding for the first time. When primiparous females were excluded from the Wilcoxon Tests the differences between the female population classes were slightly greater, in the same direction and still significant. Primiparous females did not differ significantly in their body condition rating between different population classes suggesting that the impact of lactation on physical condition may be related to age.

There was no clear seasonal pattern in changes in body condition over the 21 months although all population classes were at their lowest condition in August or September 1986, at the end of the 1986 drought. In 1987, when the total rainfall was close to the long-term average, adult males were in poorer condition in March than in June (Wilcoxon matched-pairs test: T=1.5, n=14, $p<0.05$) but there was no significant difference between their condition in March and September, March and December, June and September, June and December, or September and December.

a) adult males



b) adult females



c) sub-adults and young-at-foot

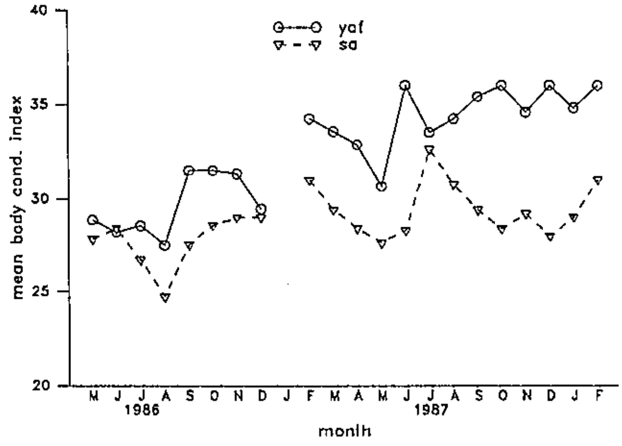


Figure 2.10 Mean body condition indices for a) male b) female and c) young kangaroos in each month between May 1986 and February 1988. The population class categories are: large male (lm); medium male (mm); small male (sm); females with no young (fny); females with a small (fspy), medium pouch-young (fmpy) and large pouch young (flpy); females with young-at-foot (fyaf); sub-adults (sa) and young-at-foot (yaf).

2.6 Summary

The study area at Wallaby Creek is contained within a valley of natural forest and cleared pasture. Most of the area is cleared of trees, with the exception of the northern forest where native kangaroo grass dominates the ground cover. Native tussock-forming grasses and blady grass are common on the cleared valley slopes but introduced grasses such as carpet grass, paspalum and kikuyu dominate the intertussock sward. The valley floor contains a number of paddocks whose pastures vary widely in quality; some contain a high proportion of digestible and nutritious grasses and forbs such as paspalum and clover, whilst others are dominated by the tussock-forming swamp foxtail. Annual burning of the tall, rank tussock grasses and blady grass produces marked seasonal changes in the availability of cover vegetation and new shoots of the burnt grass species.

The weather patterns during the course of the study were variable, with 1986 being an extremely dry year. The growth of grasses in different sward types responded to changes in the rainfall patterns; the availability of green leaf in the swards was particularly low at the height of the drought in late winter 1986. On the basis of changes in intertussock-sward height and the proportion of dead vegetation in the sward surface, the year could be divided into two seasons: May to October (winter) and November to April (summer). The seasons could not necessarily be classed as poor and good because in winter clover availability was higher than at other times and new shoots of tussock grass and blady grass were available after the burn. Nitrogen levels were lowest in mid-summer and highest in May and October. Changes in body condition of the kangaroos reflected severe changes in pasture conditions but there was no regular seasonal change in body condition that matched the changes in pasture conditions.

The populations of kangaroos and wallabies at Wallaby Creek are subject to natural predation, primarily by dingoes with wedge-tailed eagles being a lesser threat. Dingo predation has an important impact on juvenile survival of both the studied macropod species and I consider the threat of predators to be an important component of the habitat at Wallaby Creek. Disturbance of the macropods by man is minimal in the valley and individuals in both populations are approachable and easy to watch.

CHAPTER 3

24-hour Patterns of Activity and Movement

3.1 Introduction

Macropods, like all mammals, divide their time between the essential activities of feeding, resting, reproduction, parental care, and moving. The timing (within the 24 hours) of these activities depends on a number of constraints on the animal, such as its risk from predation, its need to thermoregulate and its method for acquiring food items. While the basic schedule for a species (e.g. predominantly nocturnal or diurnal feeding) may have been established through evolution by selection of those individuals which successfully predicted the best time to feed, there is still scope for individual variation. Individuals will be advantaged if they alter the timing and extent of different activities, to maximise their energy gains, whilst minimizing the costs incurred through movement, thermoregulation and the risk of predation.

If the demands conflict for minimizing the costs, and maximizing the energy gains of foraging, then an animal may try to balance the two (Sih, 1980; Holbrook and Schmitt, 1988). It may still try to maximise energy intake or it may adopt a ‘satisficing’ approach where it feeds only as long as it is ‘hungry’ (Herbers, 1981; Bunnell and Gillingham, 1985). The latter two strategies approximate to Schoener’s energy maximizers and time minimizers (Schoener, 1971), although Herbers (1981) points out that whilst time minimizing and satisficing may give the same result in some cases, the predicted time budgets and position of switch points (the points at which an animal begins and ceases to feed) may differ substantially. A satisficing strategy is likely to lead to animals spending large amounts of time inactive (Herbers, 1981), and is probably applicable to animals which have a very high risk from predation, or which expend more energy whilst foraging through movement or thermoregulation.

Animals following the satisficing strategy will remain foraging until physical constraints force them to stop. Ruminants appear to follow this strategy since they respond to declining food availability by increasing grazing time until physical constraints of the rumen force them to stop feeding, even if they have not met their nutritional needs (Allden and Whittaker, 1970; Hodgson, 1982). Wallabies and kangaroos are also foregut fermenters with microbial fermentation at least as efficient as that of ruminants (Hume, 1977, 1982). Unlike ruminants, however, they lack the omasum of the rumen which limits the outflow of digesta and consequently macropods have what has been described as a 'tubular flow' of digesta (Dellow and Hume, 1982). This gut morphology allows them greater flexibility in the controlled rate of passage of digesta, over a greater range of rates, than a ruminant enjoys. It has been suggested that these differences in gastric anatomy may allow macropods on poor pastures longer foraging times than ruminants (Clarke and Loudon, 1985).

In this chapter I describe the general patterns of activity and movement of eastern grey kangaroos and red-necked wallabies through the day and night and show how those patterns are related to body size. I also explore the degree of variation in these patterns in relation to the animals' energy demands and food availability and discuss whether this variation is adaptive. Although feeding behaviour will be examined in greater detail in later chapters, in this chapter I discuss the total time (in a 24-hour period) that macropods devote to feeding and what limitations there may be to total feeding time.

Like most macropodoids, red-necked wallabies and eastern grey kangaroos are predominantly nocturnally active (Caughley, 1964a; Southwell, 1976, 1981; Johnson, 1985; Jaremovic, 1984), but often start to feed hours before dusk and begin to rest hours after dawn. The habit of nocturnal activity of arid-zone macropods has been attributed to their need to avoid the radiant heat-load of the desert in the day-time (Dawson and Denn y, 1969). The longer hours of activity, extending into the day-time, of macropods in cooler months (e.g. Southwell, 1981) may support this hypothesis, although when cool weather is accompanied by low quality or abundance of vegetation, the extension of feeding activity into the day-time may simply represent a need to spend more time foraging.

The restriction of conspicuous and attention-attracting activities (i.e. feeding) to the hours of darkness has alternatively been proposed as an anti-predator strategy for animals which rely on crypsis to escape predators (Waser, 1975). However, other species may restrict feeding to daylight hours because they rely on visual detection of predators to escape attack (Jarman and Jarman, 1973), especially if they use communication with other group members to aid avoidance of detected predators. In the day-time kangaroos other group members to aid avoidance of detected predators. In the day-time kangaroos appear to adopt the second strategy and group together to gain advantage from many eyes looking for predators (Jarman, 1987) but the benefits of grouping are less clear for wallabies (Johnson, 1985). A comparison of day-time and night-time activities, grouping, posture and feeding behaviour of kangaroos and wallabies may help us decide whether the nocturnal feeding of kangaroos and wallabies is adaptive as an anti-predator strategy or simply the result of avoiding high day-time temperatures.

Little is known about the grouping and anti-predator behaviour of either species at night. Day-time and night-time grouping behaviour will be considered later in Chapter 7; here I shall compare the surveying behaviour and posture whilst surveying of kangaroos feeding in darkness and in daylight. If kangaroos and wallabies used hearing and smell to detect danger at night then they need not spend as much time in upright postures, with their heads raised surveying for predators at night. Indeed, doing so may make them more visible to predators at night by being sillouetted against the horizon.

Darkness can pose a number of problems for animals that are active at night. Darkness reduces the ability of predators to see their prey and animals in danger of predation may have difficulty seeing their predators as well as seeing their own food items. Very little is known about the visual capabilities of kangaroos and wallabies in the dark but it seems likely that, like other mammals, their vision will be less clear at night and that they will rely on smell and sound more at night than in the day-time. If darkness makes selection of food items more difficult macropods at night may spend more time searching for each bite in an attempt to maintain diet quality, or they may become less selective, accepting a lower quality diet and compensating by increasing intake and throughput-rate.

The activity patterns and movements of an animal over a 24-hour period provide us with indirect information on a number of inputs to and outputs from the daily energy budget of that animal. For herbivorous mammals, energy intake is a product of the total time spent feeding (i.e. seeking, processing and ingesting food), feeding (intake) rate, and the assimilable energy content of the food consumed (Allden and Whittaker, 1970). These three components of intake are often related to one another and to the abundance and dispersion of the preferred food items in the environment. Thus, a high proportion of time spent feeding may be the result of animals searching for highly dispersed food items and hence equate with a low feeding (intake) rate. If the cause of the high dispersion of food items is poor climatic conditions then energy content per bite may also be low. Thus, feeding time alone is not a good indicator of an animal's intake of herbage or energy. However, when combined with information on feeding rates and forage quality, foraging times help us to estimate energy and nutrient intake.

Novellie (1978) has suggested that ruminant herbivores respond in two ways to a decline in forage quality. They may accept significantly larger quantities of low-quality forage, and in doing so slow their digestion rate, depress appetite and reduce their daily foraging times because of the extra time they need to spend ruminating and digesting the forage. Alternatively, they may become more selective for the high-quality food that remains, reducing their feeding rate and thus incurring large foraging times. Unselective feeders have been shown to decrease foraging time in response to declining forage availability (cattle: Le Du *et al.*, 1971; Blesbok: Du Plessis, 1972, Novellie, 1978), whereas selective feeders have been shown to become more selective and to increase foraging time in response to declining foraging availability (Impala: Jarman & Jarman, 1973; Springbok: Novellie, 1978; sheep: Arnold, 1972). Changes in foraging times and foraging rates with season should tell us which strategy kangaroos and wallabies adopt.

Movements of animals may be associated with any of the essential activities of food acquisition, thermoregulation, reproduction and predator avoidance. For example, animals which feed in the open may rest in sheltered places in between feeding bouts to reduce their costs of thermoregulation and their risk from predation. Animals must also move to find mates; eastern grey kangaroos and red-necked wallabies are polygynous species, with females coming into oestrus at any time of the year and males competing for access to oestrous females. Males looking for oestrous females are expected to spend more time moving between groups than other males or females (Southwell 1981). Females may be restricted in their movements by the energetic costs of moving with a large pouch-young, or because they risk separation from small young-at-foot (Croft 1981).

The energetic cost of locomotion makes up a substantial component of the extra energy required for free existence (Fancy and White, 1985) although the amount of energy required to move a certain distance depends on the speed and gait of that movement (*ibid.*). The relative cost of quadrupedal movement is less for large animals than small ones (Fancy and White, 1985) because of the greater muscular efficiencies measured for large animals (Heglund *et al.*, 1982). It is interesting then to compare the movements of kangaroos and wallabies, and males and females which also differ greatly in body size.

In this chapter I describe the timing and extent of movement of animals followed for a 24-hour period and make some distinction between feeding and non-feeding movement. In later chapters movement during feeding bouts will be examined in more detail.

3.2 Methods

3.2.1 Introduction

It was possible to follow, on foot, individual kangaroos and wallabies for 24-hour periods because of the small size of the study area, and the confinement of activity to this area by the majority of animals of the two studied populations,. During this time the animals' activities and associations could be recorded in detail. The techniques used relied upon the animals being highly habituated to the observers and upon the ability of the observers to recognize most of the animals in the populations. A focal animal was chosen and followed for a period of 24 hours, by two observers on alternate four-hour shifts in winter and six-hour shifts in summer: M.Jones and I followed the kangaroos; and K.Higginbottom and I followed the wallabies.

Observations began on kangaroos at three hours after first light. This starting time was chosen because by then most animals had moved to their day-time resting spot and were not likely to be disturbed when first approached. The wallabies were generally hard to find when they were resting as they tended to be in the forest, crouching in dense cover or hidden in gullies. We therefore chose to start observations on wallabies 1.5 hours after first light, when they were still feeding, so that we could follow them to their resting place. At the start and end of each shift, the observers located each other using two-way radios; the radios proved useful as we could warn the approaching observer where the macropod group was and which was the best direction for approach without disturbing the animals.

Kangaroos were observed at a distance of 10-20 metres, and wallabies at a distance of 20-30 metres except when they were feeding in open paddocks when observations were made up to 50 metres away. Night observations were made by moonlight or using image-intensifying binoculars; spotlights were used to confirm identification of animals after dark and (if necessary) to relocate animals after a movement. Records were made directly onto recording sheets, then transferred to a micro-computer on return to the University. M.Jones and P.Jarman extracted the movement data used in Tables 3.5 to 3.8 and in the subsequent analyses of variance and two-sample Student's t tests.

3.2.2 Choice of focal animals.

A number of criteria were considered when selecting a kangaroo or wallaby for a 24-hour following. The general aim of the selection procedure was to represent the sexes, population classes, and home range locations (i.e. "south", "central" or "north") as evenly as possible in the samples. However, the following practical considerations were taken into account, especially when selecting wallaby subjects:

Recognition. M.Jones and J.Clarke were able to recognize all the kangaroos in the population by day and night. This theoretically allowed us to choose any animal in the population to follow. Identification of some animals, especially young-at-foot and sub-adults, was aided by squirting dye (Jamar-D) onto their coats at close range using a syringe. This temporary mark made identification at night much quicker as we did not need to see an animal's face to recognize it.

Of the wallabies, 50% were known to myself and about 90% were known to K.B.Higginbottom. We were therefore restricted to choosing only those wallabies that both of us could identify and preferably those which tended to associate with wallabies we both knew. When an observer was unable to identify an animal it was given a temporary name until the second observer arrived. If the unknown animal was still in the group the second observer would try to identify the animal. If this was not possible only the animal's population class was recorded. After K.Higginbottom began darting and capturing some of the wallabies, only those that had been caught and had been given a reflective ear tag were chosen for followings, as the tags made location of animals very much easier at night.

Habituation. At the start of the study, choice of focal animals was limited by the degree of habituation of some individuals. By the end of the study this limitation was minimal for the selection of kangaroos but was always an important factor when selecting wallabies to follow. All the wallabies darted, and therefore all those with ear tags, were well habituated to the observers. Because of the difficulties we experienced following wallabies, a small selection of well-habituated wallabies were followed once or more than once, whereas all the followings of kangaroos were of different individuals. When a kangaroo was lost during a following, another following was attempted on that individual in the same month, so as to reduce bias towards animals that were easy to follow.

Home Range. For both species we attempted to balance the number of followings completed in the northern and southern ends of the study area. However, we had little success at following wallabies that rested in the western forest in the middle of the day because the wallabies were so well concealed there by tall vegetation and they were easily disturbed by our presence. We therefore chose to follow those individuals which rested in a gully instead of the forest. There were no locational constraints in our choice of which kangaroos to follow.

At the start of a field trip we determined which population classes we needed to follow and made a list of those individuals which fulfilled those requirements. An hour before the start of the following we would go in search of one of these animals and begin observations on the first suitable animal that we located.

3.2.3 Recording Methods.

The activities of the focal animal and its nearest neighbours were recorded during scans using "point-in-time" sampling (Dunbar 1976). A 5-minute interval between scans was chosen for the kangaroo watches to allow us time to record bite-rates between scans. A Seiko watch with a repeater alarm was set to emit a noise at the appropriate time interval, indicating when scan should take place. The alarm did not disturb the animals at the distance from which we were watching them and it allowed us to watch the animals continuously without having to keep checking the time.

A shorter time interval of three minutes was used for the wallaby observations in the three hours after dawn, the three hours before dusk and the first hour and half after dusk. The shorter interval was deemed necessary because of the frequency of their changes in location and activity. During the night it was often difficult to see wallabies without a spotlight and since spotlights disturbed the wallabies more than the kangaroos we reduced our rate of scanning wallabies at night to once every ten minutes. Wallabies were also difficult to see from a distance when they were resting in the middle of the day, and a ten-minute time interval between scans was used between three hours after dawn to three hours before dusk to minimize disturbance and because there was little variation in activity during this period.

At each scan the time, grid location of the focal animal and its group size were recorded. The activity states of the focal animal and its nearest neighbours were recorded as well as the identity, population class and distance of each of those neighbours to the focal animal. In addition, for the wallabies the orientation of the focal animal (with respect to north) and the orientations of the neighbours with respect to the focal animal were recorded.

At each scan seven categories of activity were recorded, with up to five states being possible for each category (see Chapter 2). From these records the following activities were defined for kangaroos, for use in this chapter: Feeding, when animals were either biting, selecting bites, chewing or regurgitating; Alert, when they had their ears and eyes focussed on a source of disturbance; Moving, when animals were changing location; Standing, when animals were on their feet, not Moving, and not Feeding or Alert; and Lying, when they were lying down. Biting was a sub-category of feeding and described animals that had their heads down, biting or selecting bites. The last two categories were both considered to be resting activities. The same categories were used for wallabies except that standing included sitting, when the animal sat back on its haunches with its tail forward between its legs. Because the action of taking a complete feeding step may be interrupted by feeding and may therefore span a number of seconds or even minutes, animals were rarely recorded as "stepping" whilst they were feeding, unless they were taking a number of steps in sequence. Animals which were recorded as Moving at a scan were generally hopping.

Although every effort was made to keep the focal animal in sight at all times, in all watches there was a portion of time when the animal could not be seen. This fraction was excluded from the analysis when calculating the time spent in different activities. If any animal was out of sight for more than a period of 1.5 hours the watch was abandoned. Wallabies not visible during the day-time resting period were an exception to this rule. Sometimes during the midday resting period we could not actually see wallabies resting in dense cover. In this case the position where we had seen the wallaby begin to rest was watched and the animal was recorded as "resting" until it was seen to move. These resting periods were included in the Standing category of resting. Unfortunately, on two occasions wallabies left their resting spot without being detected and began to feed at some distance from the observer. In these cases the animal was recorded as resting only up until our last sighting of it, after which time it was recorded as "lost".

If the focal animal was biting at the time of the scan, the vegetation component they were feeding on was recorded as tussock, inter-tussock, stand or single (see Chapter 2). For the last eight kangaroo watches the dominant species of the sward was also recorded. Vegetation-patch information (see Chapter 2) was recorded for the wallabies every time they moved further than 10 metres. Bite-rate observations were recorded verbally onto a cassette tape-recorder at half-hour intervals during feeding bouts (see Chapter 2). These observations were later transferred onto a micro-computer at a later date.

Continuous records were kept of the composition of the group (population class or identity of each group member). The time of any change was recorded along with any observable cause for the change, such as movement of the focal animal or a disturbance which caused the group to break up. Every interaction of the focal animal was recorded with reference to the time and the identity of the other individual involved.

3.3 Success of followings

Between December 1985 and December 1987, 31 followings of eastern grey kangaroos were attempted. Of these, 24 were completed (i.e. the animal was out of sight for no more than 5% of the time and its general activity during that time could be safely inferred). The kangaroos that were "lost" tended to disappear at night, during a phase of movement. The results may therefore under-estimate nocturnal movement.

During the same period 15 followings of red-necked wallabies were attempted but only 4 were considered complete. The main reason for our lack of success in following wallabies was the greater distance from which we had to observe the animals. The kangaroos allowed us to approach much more closely and therefore were more likely to remain within our sight. Many of the wallabies that were "lost" also disappeared at night but some were lost during their midday resting period. Only data from "complete" observations (see above) are included in the analyses unless otherwise stated.

The successful 24 kangaroo followings were evenly divided between adult males and adult females. Nine could be assigned to winter conditions (June to August, all before the burn), ten to summer (December to February) and the remaining 5 were divided between other months in 1986. Pasture conditions were very poor from summer 1986 to late winter 1986 (see Chapter 2), and although sample sizes are small, comparisons between months in this year allow us to look at effects of a short drought on the activity schedules of kangaroos. The small number of completed wallaby followings did not allow us to make comparisons between the seasons or sexes so data have been combined for all completed observations. The completed followings were on: a female with a pouch-young at the point of emerging permanently from the pouch, followed in winter; two females each with a pouch-young and a newly weaned sub-adult, one followed in spring and another in autumn; and the first female again with a large pouch-young followed in autumn.

3.4 Activities and movements of eastern grey kangaroos

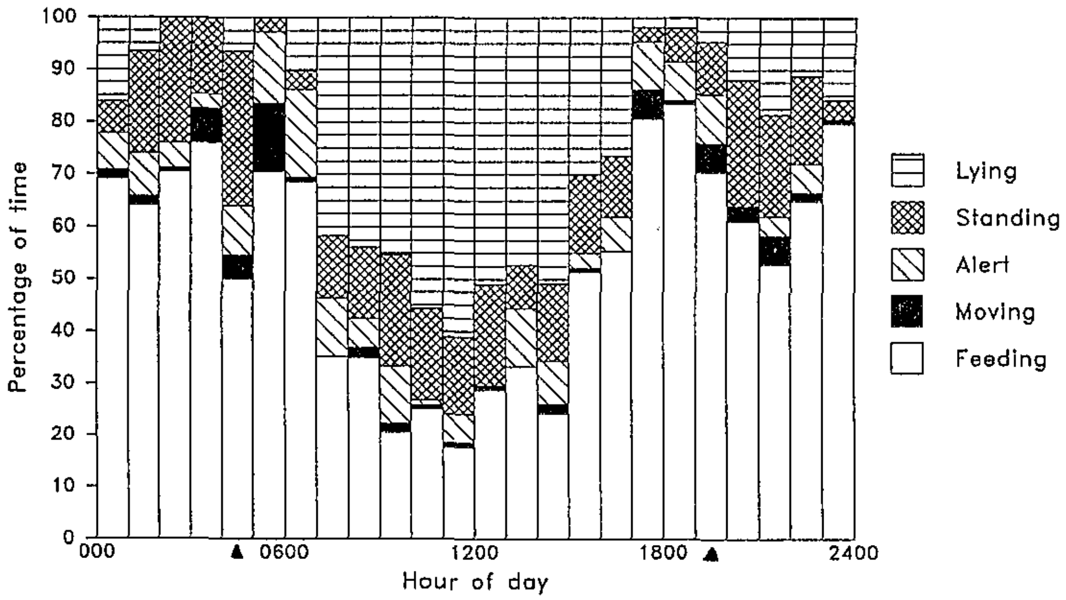
3.4.1 General schedule of activity

Although there was a great deal of variation between kangaroos, a general pattern of activity was distinguishable. Kangaroos were generally resting when we began following them and would lie or crouch in the same location for most of the midday period, occasionally breaking the rest period by feeding for short periods. Two to three hours before dusk one or more kangaroos would begin feeding, often moving to a preferred feeding area if little grass was available at the resting site. Feeding continued through the night, although individuals would often break off from feeding to rest for a period whilst others continued to feed. Around dawn, kangaroos sometimes stood for a while, alert and scanning the environment before moving to join other kangaroos for the morning feeding bout. Kangaroos would usually cease to feed two to three hours after dawn, although when the weather was wet or windy they would often continue to feed later into the day.

Figure 3.1 illustrates the hour by hour activity schedules for kangaroos in summer and winter. As described, activity schedules were flexible with all behaviours being possible at any time of the day or night. Feeding was most common in the two hours before dusk and the hours before and after dawn; these times corresponded to the times when lying was least common. We noted that many individuals rested for periods during the night, but because these resting periods were not synchronised they did not appear in the combined data as a discrete resting period. During followings we had recorded at the end of each minute whether the focal animal had fed during that minute and using these data the time intervals between feeding bouts were calculated. These data were not available for the first three followings. Seventeen out of 21 kangaroos rested for at least one period of greater than 30 minutes during the night and 14 out of 21 rested for over 1 hour. The longest period of resting during the night was 117 minutes.

The major differences between the seasons were the earlier daily onset, and greater amount of, diurnal resting in summer. In summer kangaroos were more likely to be Standing whilst resting in the middle of the day than in winter, although Lying was still preferred over standing. Moving formed only a small proportion of the daily activity and was most common for the first two hours after dawn in summer and three hours after dawn in winter. In winter there was a dramatic drop in feeding in the hour following this morning movement whereas in summer the reduction in feeding time was not seen until two hours following the movement. It may be that in summer kangaroos were forced to seek shade before they had finished their feeding bout. The timing of feeding and non-feeding movement is described in more detail later.

a) summer



b) winter

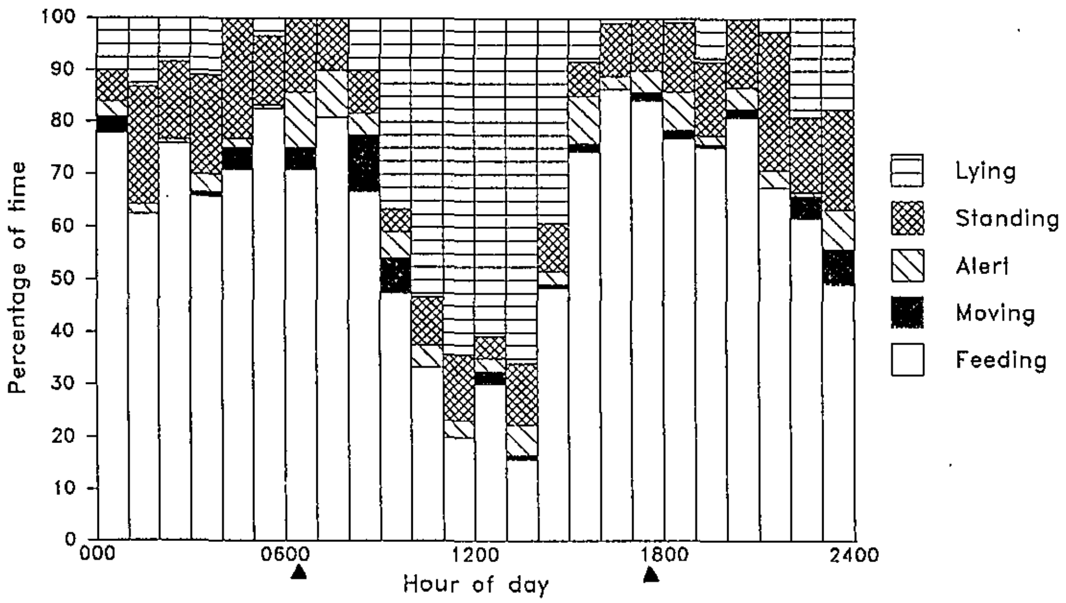


Figure 3.1 Mean percentages of each hour, in 24 hours, spent in different activities by eastern grey kangaroos in a) summer and b) winter. Data are based on 24-hour followings of 9 animals in summer (5 male and 4 female) and 10 in winter (5 male and 5 female). The times of dawn and dusk are indicated by pointers on the x axis.

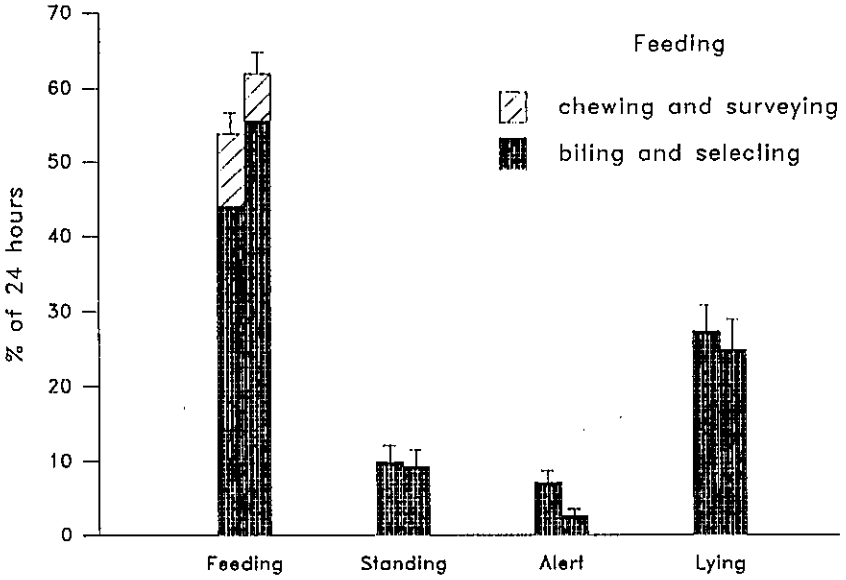
3.4.2 Proportion of time devoted to different activities

The proportions of time spent in different activity states by males and females, in winter and summer, are compared in Figure 3.2. An analysis of variance was carried out on the time spent on each activity, with sex and season as the grouping factors. The significant effects only are presented in Table 3.1

Table 3.1. Significant effects for two-way analyses of variance of the proportion of 24 hours that focal animals spent in each activity, grouped by season and sex. Biting is the proportion of feeding time that the kangaroo was biting or selecting bites.

Test	transformation	F	d.f.	p
Feeding x season	logx	10.47	1,15	< 0.01
Biting x season	none	12.18	1,15	< 0.005
Standing x sex	none	10.62	1,15	< 0.01
Alert x season	logx	5.80	1,15	< 0.05
Lying x sex	logx	9.62	1,15	< 0.05

The proportion of time spent Feeding, the proportion of their feeding time biting or selecting bites (Biting) and the proportion of time spent Alert differed between summer and winter, but not between males and females. The sexes differed significantly in their time spent Standing and Lying. There were no significant interactions between sex and season for any of the activity states.


a) males

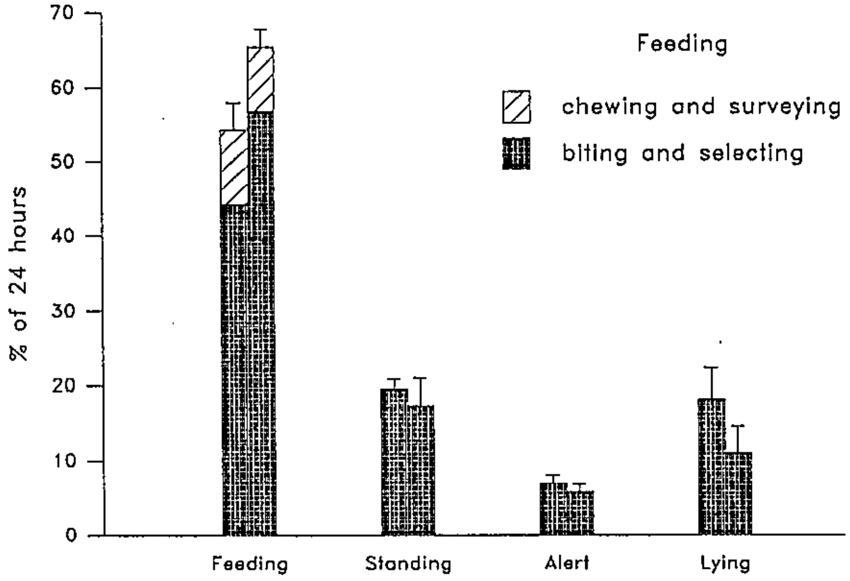

b) females

Figure 3.2 Mean percentages (+ s.e.m) of 24 hours spent in each of four activity states, in summer (left bar) and winter (right bar), by a) male and b) female eastern grey kangaroos. Data are based on 24-hour followings of 9 animals in summer (5 male and 4 female) and 10 in winter (5 male and 5 female). Note that Feeding is further divided by the proportion of time spent biting or selecting bites and chewing while surveying.

Table 3.2. Mean percentage of time spent in different activity states by males and females, in summer and winter. Superscripts indicate significant differences between pairs of values from Student's t tests (superscripts 1-6, $p<0.05$). Population class categories are large male (lm) and large-medium male (lmm), small-medium male and small male (smm, sm), female with small pouch-young (fspy) or medium pouch-young (fmpy) and female with large pouch-young (flpy) or young-at-foot (fyaf).

Records	n	Feeding	Biting	Standing	Alert	Lying
male						
summer	5	53.8	81.7^{1}	9.9^{6}	7.1^{2}	27.4
winter	5	61.9	89.9^{1}	9.3^{7}	2.6^{2}	24.9^{8}
lm,lmm	6	58.3	83.8	9.3	5.2	25.1
smm,sm	6	56.5	88.4	9.7	5.5	26.1
female						
summer	4	54.2^{3}	81.4	19.5^{6}	7.0	18.2
winter	5	65.4^{3}	87.0	17.3^{7}	5.9	11.1^{8}
fspy ,fmpy	6	52.3^{4}	86.8	18.6	5.3	23.3^{5}
flpy, fyaf	6	62.9^{4}	84.5	18.9	6.3	11.2^{5}

Table 3.2 presents a break-down of the same data with the significance of Student's t tests between pairs of values being indicated. In summer and winter females spent more time Standing, not alert, than males and spent less time Lying than males. These differences reflected a difference between the sexes in their preferred posture for resting. Females fed for longer in winter than in summer, and and tended to be biting or selecting bites for a greater proportion of that time in winter compared to summer. Males tended to follow the same pattern, but because of the greater variation in the data the differences in feeding time were significant at only the 10% level. A higher proportion of feeding time spent biting or selecting bites may reflect a difficulty in selecting food items, a need to increase food intake and/or a lesser need to survey whilst feeding.

There were no significant differences between large males (large and large-medium males) and small males (small-medium and small males) in their time spent in different activities. Females with large pouch-young or young-at-foot fed for 16% more of the time than females with smaller or no pouch-young, and spent less time resting than the latter.

3.4.3. Posture whilst surveying, at night and in the day-time

The posture was compared for kangaroos surveying (animals with their heads up but excluding animals that were lying down) in the day and night. In a preliminary analysis there was no significant interaction between population class and season for posture used so the observations were then divided by population class alone. For each class night and day proportions were compared (a night and day pair for each individual) using a Wilcoxon signed-rank test.

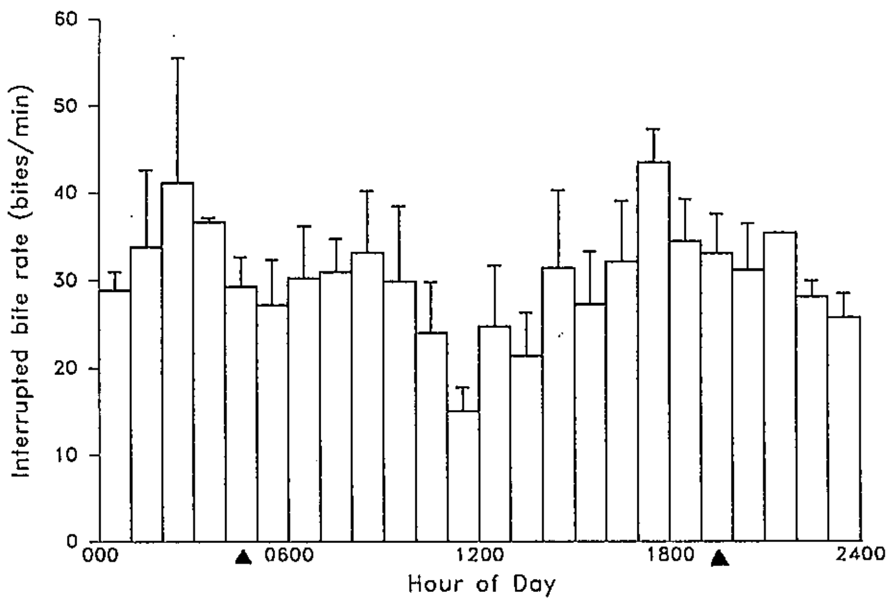
Both large and small males spent less time surveying in the bent posture at night than in the day (large male: T=21.0, $p<0.05$, n=6; small male: T=33.0, $p<0.05$, n=6) and with all males combined, males spent more time in a crouched posture at night (T=13.0, $p<0.05$, n=12) than in the day. Females did not show any tendency to use one posture more at night than in the day-time, either with all females combined or divided into females with young-at-foot and females with pouch-young.

3.4.4 Feeding rates and total bite number

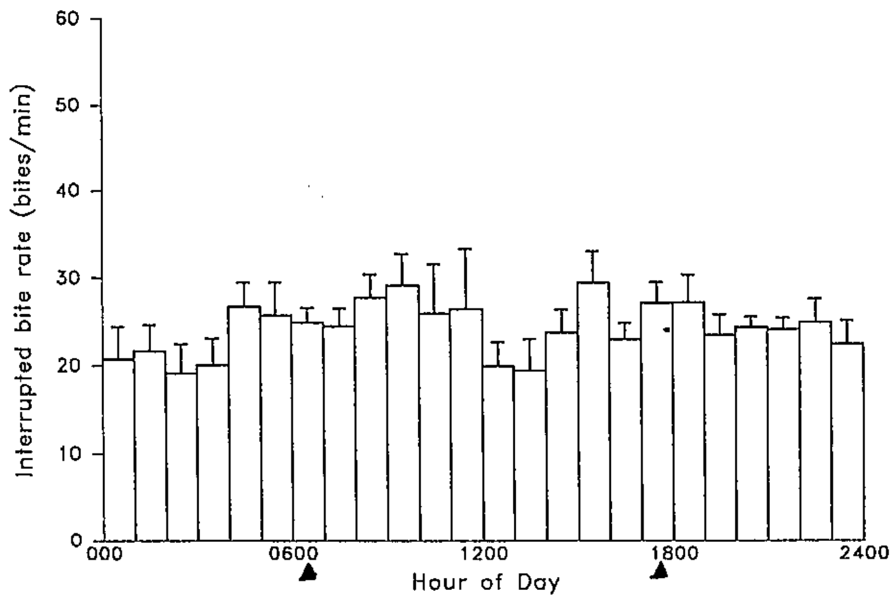
The changes in biting rates of kangaroos over 24 hours are compared between summer and winter in Figures 3.3a & b and 3.4a & b. Because I expected the use of different sward components to differ between day and night, only changes in biting rates of the intertussock swards were included. However, the distributions for biting rates on all sward components combined looked very similar to those for intertussock alone.

The pattern of interrupted biting rates (biting rates calculated from bites in 3-minutes), in summer followed the pattern of feeding activity such that foraging rates were lowest around midday and higher at other times (Figures 3.3a and b). However, in winter biting rates varied little over the 24-hour period and were generally lower than in summer. The uninterrupted biting rates (calculated from the time for ten uninterrupted bites) varied little over the 24-hour period in both summer and winter, suggesting that sward conditions may set a limit to an achievable biting rate (Figures 3.4a & b). Again, bite rates were higher in summer than in winter.

The ratio of the two biting rate measures followed a similar pattern to the uninterrupted biting rate (calculated from the time taken for 10 bites without interruption to chew) pattern such that in summer kangaroos were spending more of their feeding time chewing and surveying, when feeding in the middle of the day than at other times (Figures 3.5a & b). There was little diurnal variation in the Biting Ratio in winter.



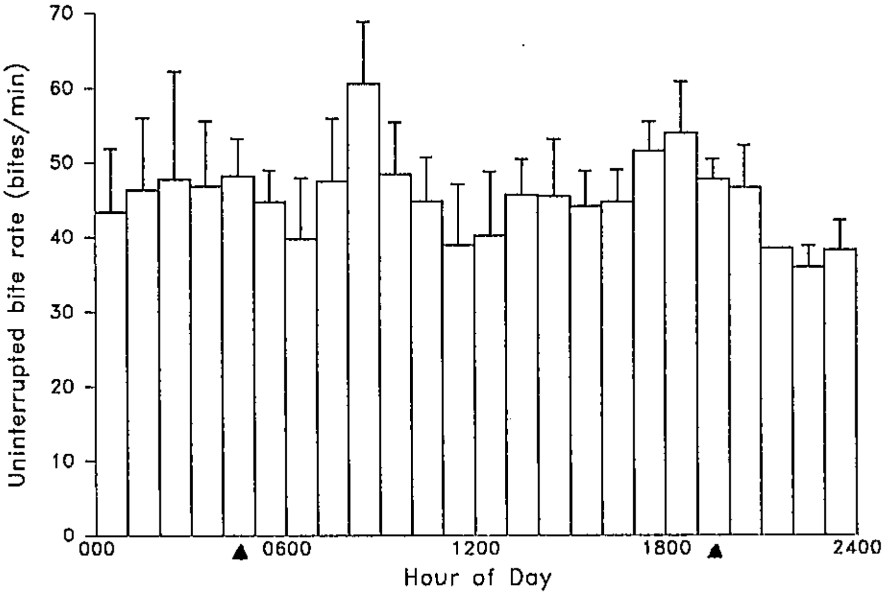
a) summer



b) winter

Figure 3.3 Mean interrupted biting rate in each hour, over 24 hours, for eastern grey kangaroos followed for 24-hour periods, in a) summer and b) winter. Data are based on 9 followings in summer (5 male and 4 female) and 10 in winter (5 male and 5 female). The times of dawn and dusk are indicated by pointers on the x axis.

a) summer



b) winter

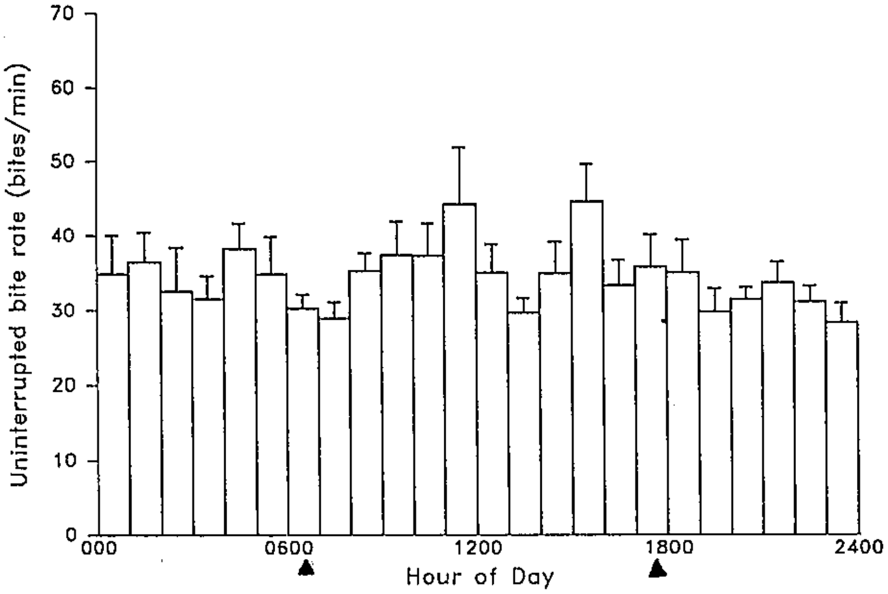
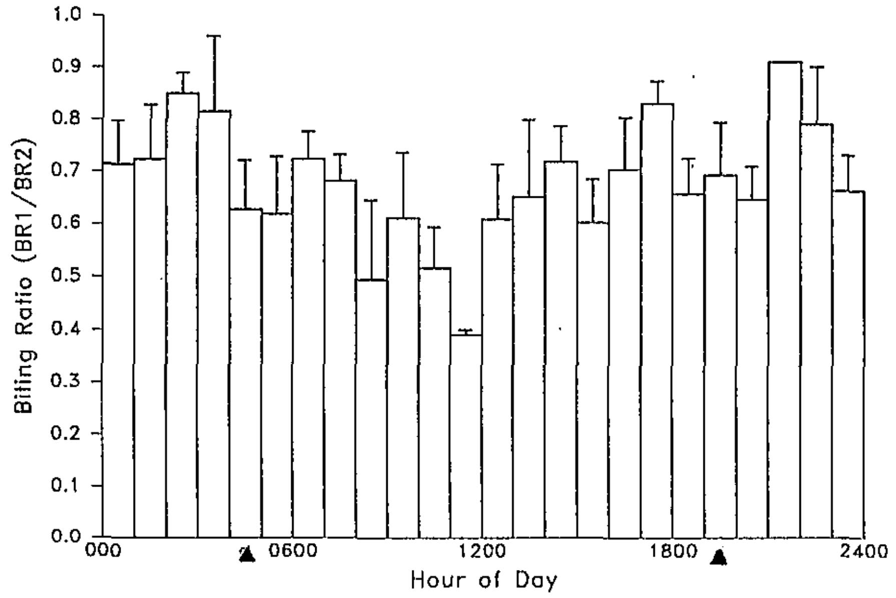


Figure 3.4 Mean uninterrupted biting rate in each hour, over 24 hours, for eastern grey kangaroos followed for 24-hour periods, in a) summer and b) winter. Data are based on 9 followings in summer (5 male and 4 female) and 10 in winter (5 male and 5 female). The times of dawn and dusk are indicated by pointers on the x axis.

a) summer



b) winter

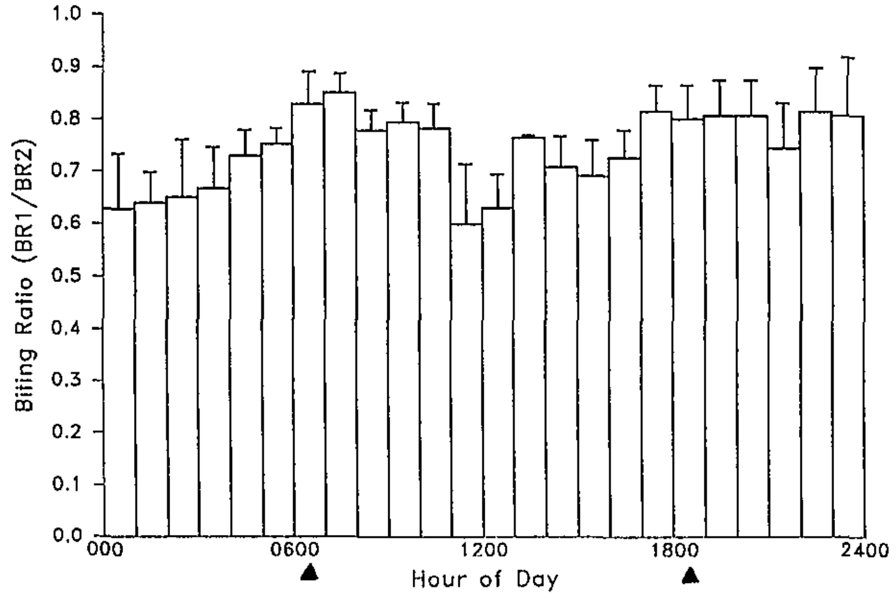


Figure 3.5 Mean biting ratio (+ s.e.m) each hour, over 24 hours, for eastern grey kangaroos followed for 24-hour periods, in a) summer and b) winter. Data are based on 9 followings in summer (5 male and 4 female) and 10 in winter (5 male and 5 female). The times of dawn and dusk are indicated by pointers on the x axis.

Table 3.3. Comparison of the mean feeding rates and total bite numbers of kangaroos followed for 24 hours. Significance levels based on two-tailed Student's t Test. (mean ± s.e.)

Measure	Summer Dec - Feb	Winter Jun - Aug	p
Interrupted biting rate (bites/min)	30.9 ± 1.7	21.1 ± 1.5	< 0.001
Uninterrupted biting rate (bites/min)	47.4 ± 3.3	28.6 ± 2.5	< 0.001
Biting ratio	0.69 ± 0.03	0.79 ± 0.03	< 0.05
Total bites in 24 hours	24200 ± 1700	19400 ± 1600	< 0.06
Total feed time (hours)	12.9 ± 0.5	15.0 ± 0.5	< 0.05
n	9	10	

There were no differences between males and females in their rates of biting or their total number of bites over 24 hours so data were combined for the sexes in Table 3.3. Both the interrupted and uninterrupted biting rates were higher in summer than in winter whereas the Biting Ratio was lower in summer. Low uninterrupted biting rates in winter suggest that in this season kangaroos were spending more time selecting or manipulating each bite. The poor availability of green grass in winter (see Chapter 2) probably made the selection of green leaf more time consuming, leading to low biting rates. The relationship between biting rates and sward conditions are investigated more fully in Chapter 5. Low biting rates combined with a poor quality diet led to a high feeding time being recorded in winter (mean 15.0 ± 0.5 hours per day compared to 12.9 ± 0.5 hours per day in summer) and little time spent surveying whilst feeding, as the kangaroos attempted to maintain intake.

3.4.5 Differences in foraging behaviour betweeen night and day

The biting observations made during the 24-hour watches were divided for each animal into those made during day-light and those in the dark. The feeding behaviour in the night and day were compared using the Wilcoxon signed-rank test on median values for each animal in that time period (Table 3.4). Animals were included only if at least 5 observations were available for both day and night. This gave a sample of 10 kangaroos.

Table 3.4 Medians of day-time and night-time foraging parameters of kangaroos followed for 24-hour periods. Comparisons made using Wilcoxon signed-rank test.

Variable	Night	Day	T	p
interrupted bite rate	26.6	30.8	70.0	0.02 *
uninterrupted bite rate	36.5	43.1	69.0	0.02 *
biting ratio	0.76	0.74	46.0	0.61
bites/mouthful	20.1	24.1	6.0	0.18
bites/patch	36.5	42.3	64.0	0.05 *
head-up/min	3.4	3.8	74.5	0.006 **
mean number of steps in a sequence	1.13	1.17	25.0	0.81
prop. of patches accept	0.91	0.92	20.0	0.48
prop. of steps that were *away* from a neighbour	0.88	0.91	24.0	0.45
number of steps in 3 min	2.41	2.47	25.0	0.29
number of hops in 3 min	0.23	0.00	5.0	0.42

Both interrupted and uninterrupted biting rates were faster in the day-time, but the biting ratio did not differ between night and day. Although kangaroos were biting faster in the day, the proportion of feeding time that they spent biting was the same in the day and night so their interrupted biting rate was decreased at night by the same proportion as the uninterrupted rate.

There was not a dramatic change in feeding behaviour after dark (section 3.4.3.) which would have been expected if the lack of light caused great problems to feeding animals. Faster feeding rates in the day-time may be the result of a greater intensity of feeding and/or a decrease in selection time per bite. There were no differences between day and night in the step-sequence length, the number of steps taken that were followed by an animal taking a bite in the patch (proportion of patches "accepted"), the number of steps or hops taken, or the number of steps taken away from the nearest neighbour (group size 1 excluded). It seems likely that if kangaroos were having problems selecting food items from the sward then there would be differences in their movement whilst feeding. Although the feeding variables presented in Table 3.3 are for animals feeding on intertussock swards alone there is considerable difference between feeding rates on different intertussock sward types (see Chapter 5). If kangaroos feed in different vegetation types at night compared to the day (see Chapter 4) it may be that differences in feeding rates between night and day are due to differences in the sward type on which the animals were feeding.

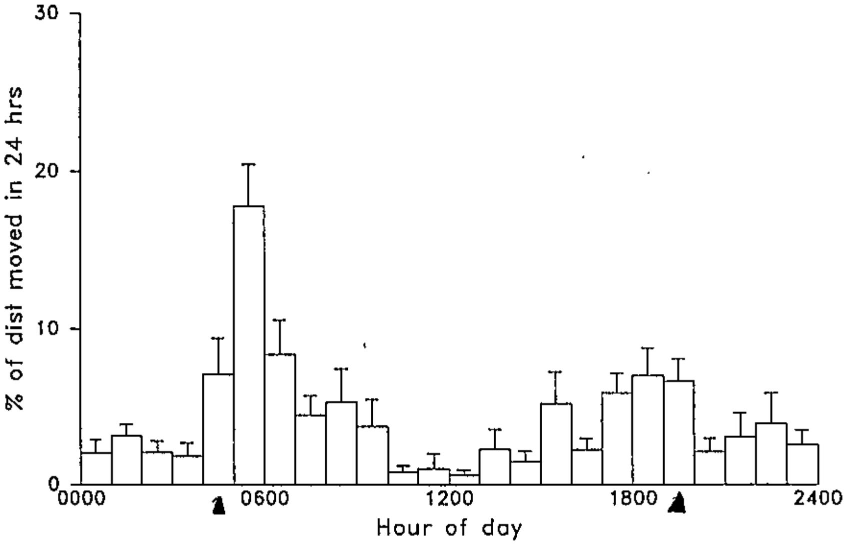
3.4.6 Scheduling of movement

Movement of kangaroos was not evenly distributed throughout the day and Figures 3.6a & b illustrate the mean percentage of the total distance moved in each of the 24 hours, in summer and winter. In both seasons most movement was executed in the three hours after dawn and least in the middle of the day and in the hours after midnight. Kangaroos began moving from their day-time resting place about three hours before dusk and continued to move through the afternoon feeding period until dusk when levels of movement declined.

To look more closely at the scheduling of movement, and to compare the timing of movement between seasons and sexes, the 24-hour period was divided into six time periods which matched the major periods of movement and inactivity. The time periods were: T1, from dawn to 3 hours after dawn; T2, from then until the start of T3; T3, from three hours before dusk to dusk; T4, from dusk until 3 hours after dusk; T5, from then until T6; T6, from three hours before dawn until dawn.

The percentage of the day's movement executed per hour, in each time period, are compared for males and females, in summer and winter in Table 3.5. A two-way analysis of variance with time as a repeated measure, and sex and season as grouping factors, showed a significant difference between time periods.

a) summer



b) winter

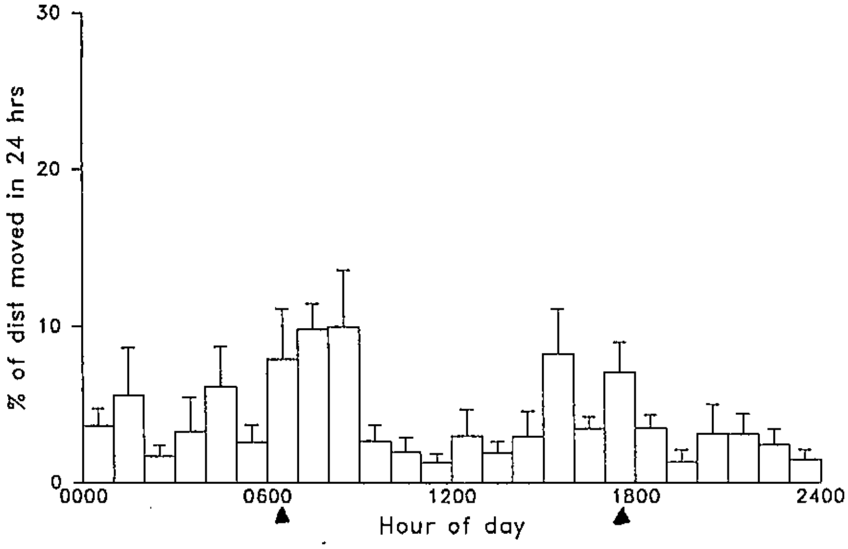


Figure 3.6 Mean percentages (+ s.e.m.) of the total distance moved in 24 hours, moved in each hour in a) summer and b) winter by 9 (5 male and 4 female) and 10 (5 male and 5 female) eastern grey kangaroos. The times of dawn and dusk are indicated by pointers on the x axis.

Table 3.5: The percentage of a day's total movement executed per hour by eastern grey kangaroos, in the six time periods defined in the text. Superscripts indicate significant differences between matched pairs (Student's t tests: $p<0.05$). Significant results of a two-way analysis of variance with sex and season as grouping factors, and time period as a repeated measure. The time periods are: T1, from 0-3 hrs after first light; T2, from then until 3 hrs before dusk; T3, from then until dusk; T4, from dusk until 3 hours after dusk; T5, from then until 3 hours before dawn; and T6 from then until dawn.

		Percent of days total movement executed per hour					
		Time Periods					
Records	(n)	T1	T2	T3	T4	T5	T6
All	24	9.49	2.40	4.96	4.37	2.96	3.96
All Males	12	8.66	1.94	5.03	4.16	3.45	5.44^{2}
All Females	12	10.31	2.86	4.89	4.57	2.47	2.47^{2}
Summer Dec-Feb	9	11.82	2.35	5.07	3.74	2.85	2.85
Winter Jun-Jly	10	9.23	2.27	5.67	3.43	2.94	4.40
Summer Males	5	11.13^{1}	1.98	4.40	3.73	4.06	3.80^{3}
Summer Females	4	12.67	2.82	5.91	3.75	1.33	1.67^{3}
Winter Males	5	6.93^{1}	1.76	6.80	3.53	2.79	6.73
Winter Females	5	11.53	2.78	4.53	3.33	3.09	2.07

Two-way analysis of variance

Source	df	F	p
sex	1	3.95	0.07
time	5	7.90	0.0001
time x sex	5	2.69	0.03

A greater percentage of the day's movement was executed in T1 (the 3 hours after dawn) than in other time periods, as seen in Figures 3.6a & b. The scheduling of movement was similar for males and females in all time periods except T6; more of the males' total movement was executed in T6 (the 3 hours before dawn) than the females. In winter, less of the males' total movement was executed in T1 than in summer and less than females in winter.

Although feeding movement and non-feeding movement were not distinguished in this study (because it was hard to estimate the distance moved in every movement), the majority of the distance covered by kangaroos in 24 hours seemed to be covered in a few short, fast bouts of hopping. This is illustrated by comparing Table 3.6, which looks at the percentage of 5-minute periods in which any movement was recorded (i.e. the frequency of movement), with Table 3.5.

Table 3.6: The percentage of 5-minute periods, in the six time periods defined in Table 3.5, during which a change in location was recorded for the eastern grey kangaroo being watched. Superscripts indicate significant differences between means (Student's t tests: $p<0.05$).

Percent of 5-minute periods in which a change of location was recorded

		Time Periods						
Records Used	(n)	T1 %	T2 %	T3 %	T4 %	T5 %	T6 %	All %
All	24	27.2	11.0	22.4	18.9	15.3	17.9	16.2
All Males	12	30.1	9.5	22.4	22.5	18.7	24.0^{1}	17.3
All Females	12	24.3	12.6	22.4	15.4	12.0	11.8^{1}	15.2
Summer	9	38.1^{2}	12.7	30.4^{3}	23.3	20.5^{4}	21.4	22.5^{5}
Winter	10	19.6^{2}	8.2	18.6^{3}	13.0	9.2^{4}	12.3	12.3^{5}
Male, Summer	5	42.4	12.0	33.2	29.4	27.2^{6}	29.6^{7}	25.0^{8}
Male, Winter	5	14.8	4.8	17.8	12.8	10.0^{6}	18.0	11.8^{8}
Female, Summer	4	32.7	13.5	27.0	15.7	12.2	11.2^{7}	17.2^{9}
Female, Winter	5	24.4	11.6	19.4	13.2	8.4	6.6	12.8^{9}

Two-way analysis of variance

Source	df	F	p
season	1	10.98	0.006
time $_t$	5	7.54	0.0004
time x sex$_t$	5	3.88	0.02

($_t$=log transformation and Greenhouse-Geisser correction used)

Kangaroos moved infrequently in the midday period (T2), but there was little difference between the frequencies of movement in T1 and the other time periods. Thus although kangaroos executed more of the day's movement in T1, they made almost as many movements at other times when they were active as they did in T1. This suggested that each movement in T1 was greater than in other time periods.

Males moved more frequently in T6 (the 3 hours before dawn) than did females; again this was the only time period in which there was a significant difference between the sexes. In all time periods, but only significantly so in T1, T3 and T5, kangaroos moved more frequently in summer than in winter.

3.4.7 Rates of movement

Mean rates of movement differed between time periods and were generally faster in the morning (T1) than in other time periods, as shown in Table 3.7. However, there was a significant difference between the sexes (males moved faster in most time periods), and a significant interaction between time period and sex. Females' rates of movement in both winter and summer were greatest in T1 and lowest for periods T5 and T6 (i.e. from 3h after dusk until dawn). Males moved very fast in T1 in summer, and slowest around midday (T2), but in winter their peak rate of movement was in T6 (before dawn).

Table 3.7: Average rates of movement, in metres per hour, for the whole of each time period, and for the full 24 hours, of male and female eastern grey kangaroo in summer (December to February) and winter (June and July). Significant results of a two-way analysis of variance, with sex and season as grouping factors and time period as a repeated measure.

Records	(n)	T1	T2	T3	T4	T5	T6	ALL
<u>Males</u>								
Summer	5	353.0^{1}	56.4	132.0	139.0	116.0^{2}	109.6^{3}	128.8^{4}
(s.e.)		(91)	(15)	(35)	(77)	(38)	(17)	(26)
Winter	5	74.0^{1}	35.2	50.8	42.8	31.2	103.0	50.0^{4}
(s.e.)		(21)	(28)	(20)	(16)	(10)	(6)	(18)
<u>Females</u>								
Summer	4	222.0	48.5	106.7	58.0	24.0^{2}	26.2^{3}	72.2
(s.e.)		(61) (11)	(28)	(15)	(8)	(7)	(10)	
Winter	5	127.6	28.6	48.8	37.4	28.6	22.6	43.6
(s.e.)		(30)	(5)	(15)	(11)	(10)	(8)	(4)

Two-way analysis of variance Source	df	F	p
sex	1	8.27	0.01
season	1	5.22	0.04
time	5	8.18	0.0001
time x sex	5	2.88	0.02

3.4.8 Changes in location of kangaroos

Given that kangaroos move further in the morning and in the late afternoon and early evening, what were they moving to or from? The movements to shade to rest, and from shade to begin feeding again, were the most obvious movements but there were other observable patterns. Using a pairwise comparison of easterly locations at the start and end of each time period (one-sample Wilcoxon signed-rank test), kangaroos showed a significant movement uphill in the three-hour period before dusk ($W=23.5$, $p<0.01$) and downhill in the three-hour period after dawn ($W=42.0$, $p<0.02$) in summer. This movement applied equally to males and females but it was not seen in winter. The difference between summer and winter may be explained by the difference in distribution of kangaroos prior to dusk. In winter, kangaroos spent the day further upslope than they did in summer (difference of means 240 m at 3 hours before dusk; two sample t test: $t=2.49$, $p<0.05$), so that they were as far upslope at dusk in winter as they were at dusk in summer.

Kangaroos from the northern end of the study area appeared to show a different pattern. Four out of the eight "northern" animals which were followed moved, not uphill but north into the open forest at night, and two of the remaining four northern animals stayed in the forest throughout the 24-hour period.

3.4.9 Total distance moved in 24 hours

Total distance moved in 24 hours varied widely, ranging from 400 to 5600m, both of these values being recorded from large males. The overall daily mean distance was 1873m ± 272m (s.e.); the male mean was 2280m ± 423m and the female mean 1467m ± 145m. Table 3.8 gives a summary of the distances moved by males and females in winter and summer. Males moved more than twice as far in summer as in winter but the difference for females was not as great. Males tended to move further than females in summer but a similar distance in winter. A two-way analysis of variance of mean distance, with sex and season as the grouping factors, showed that male and female means did not differ significantly ($F_{3,15}=3.16$, $p<0.1$) but summer and winter means did ($F_{3,15}=9.25$, $p<0.01$). The sex x season interaction was not significant.

Table 3.8. Comparison of mean daily distances moved by male and female kangaroos in summer and winter (mean ± s.e.). Probability levels based on two-tailed Student's t test. Significant results of a two-way analysis of variance with sex and season as grouping factors.

	Males	Females	p
Summer	3090 ± 630	1800 ± 330	0.13
(n)	(5)	(4)	
Winter	1200 ± 430	1050 ± 100	0.75
(n)	(5)	(5)	
p	0.04	0.16	

Two-way analysis of variance	df	F	p
Source			
sex	1	3.16	0.096
season	1	9.25	0.008
sex x season	1	2.02	0.176

There was great variation in the daily distance moved by males, some of which appeared to relate to the male's age or home-range size, or to the presence or absence of oestrous females. For example, a small adult male who was in the same group as his mother for all the 24 hours moved 970m, a typical daily distance for females. By contrast, an older male, closer to the age of dispersal, spent only 30 minutes in the same group as his mother, and moved a total of 3900m in the day.

3.5 Activities and movements of red-necked wallabies

3.5.1 General schedule of activity

Figure 3.7 illustrates the activities of wallabies over the 24-hour period. The schedule of activity of wallabies was more restricted than that of kangaroos, with wallabies feeding less during the midday period and around midnight than kangaroos. Thus, there was a bimodal pattern of activity, with wallabies resting for a period at night as well as during the day-time. Because of the unequal contribution of different watches to the hourly means and the combining of data from all seasons, the data were not suitable for statistical comparison with the kangaroo data.

Although wallabies were often out of sight during the midday resting period, wallabies which were in sight when resting were rarely lying down, especially if they were female. Like female kangaroos, female wallabies preferred a more upright posture for resting, perhaps to aid visibility. The "sitting" posture of resting wallabies was never seen to be assumed by adult kangaroos, except in brief bouts of grooming.

The four wallabies which were followed successfully fed for 56% of the 24 hours (13.4 ± 0.8 hours) and were biting or selecting bites for 87% of that time; these figures are well within the range of those for the kangaroos (Figure 3.8). However, wallabies spent 14% of their time alert which is more than twice the time that kangaroos spent alert. This fits in with our experience of wallabies being more nervous and flighty. Unfortunately it is not possible to tell whether the wallabies spent more time alert because of our presence or because they are naturally more attentive of their surroundings than are kangaroos.

3.5.2 Schedules of movement

Moving was a rare activity for wallabies, more so than for the kangaroos. Figure 3.9 shows the percentage of the total day's movement executed per hour for the four completed followings. Because the followings are all from different seasons, it is not possible to relate the pattern to the exact times of dawn and dusk. Given the large variation present in the data, wallabies do seem to schedule their movement in a similar manner to kangaroos, with a peak of movement around dawn and another peak in late afternoon. Like the kangaroos, wallabies moved little in the middle of the day or in the early hours of the morning. This is illustrated in Table 3.9 which compares the figures for all kangaroos and all wallabies by time period. There was a significant correlation between the EGK means and RNW means over time ($n=6$, $r=0.90$, $p<0.05$).

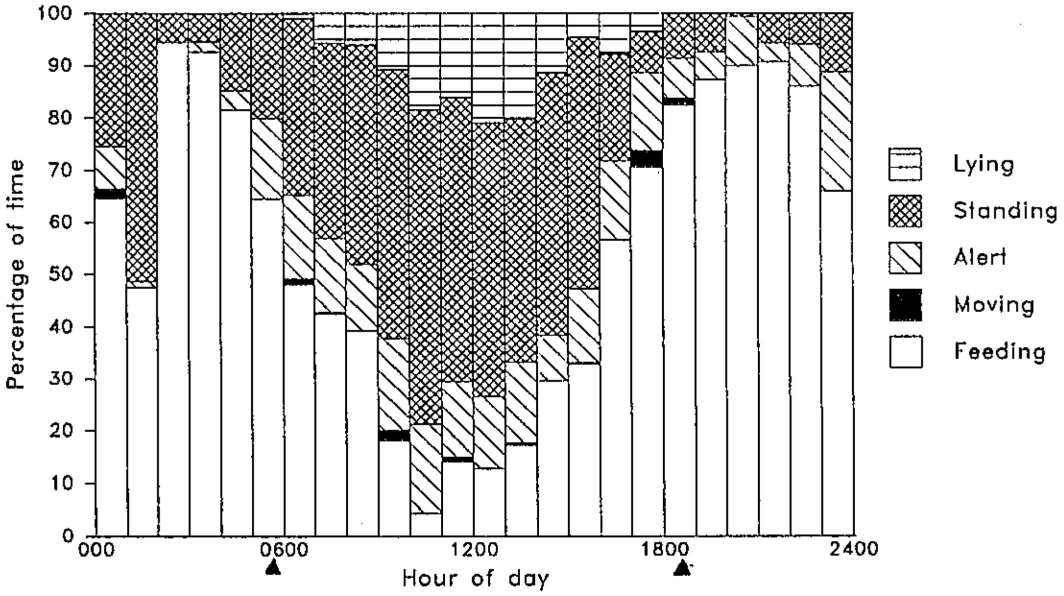


Figure 3.7 Mean percentages of each hour, in 24 hours, spent in different activities by 4 red-necked wallabies. Standing includes time spent resting out of sight in the midday period and time spent resting in the sitting posture. The times of dawn and dusk are indicated by pointers on the x axis.

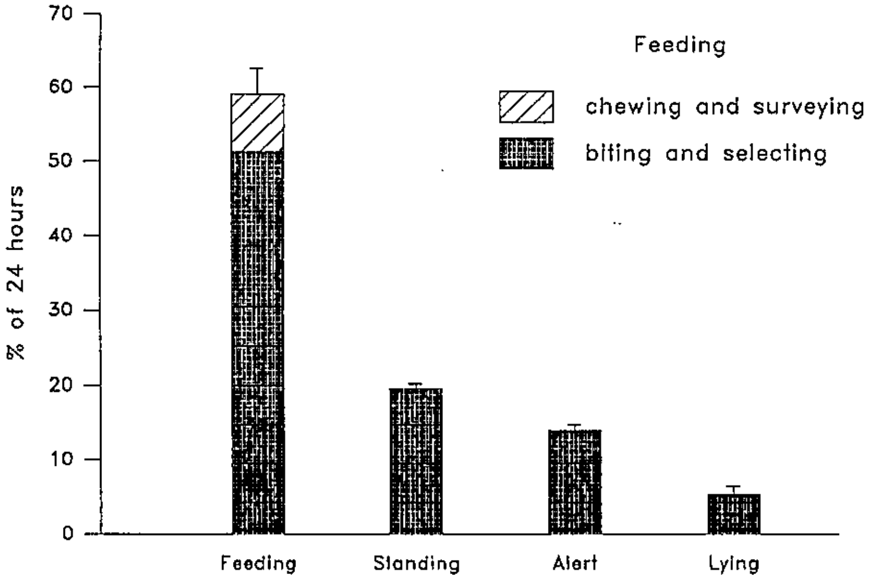


Figure 3.8 Mean percentage of 24 hours (+ s.e.m.) spent in each of four activities by 4 red-necked wallabies. Followings from different seasons are combined. Note that Feeding is further subdivided by the proportion of Feeding time spent biting or selecting bites and chewing whilst surveying.

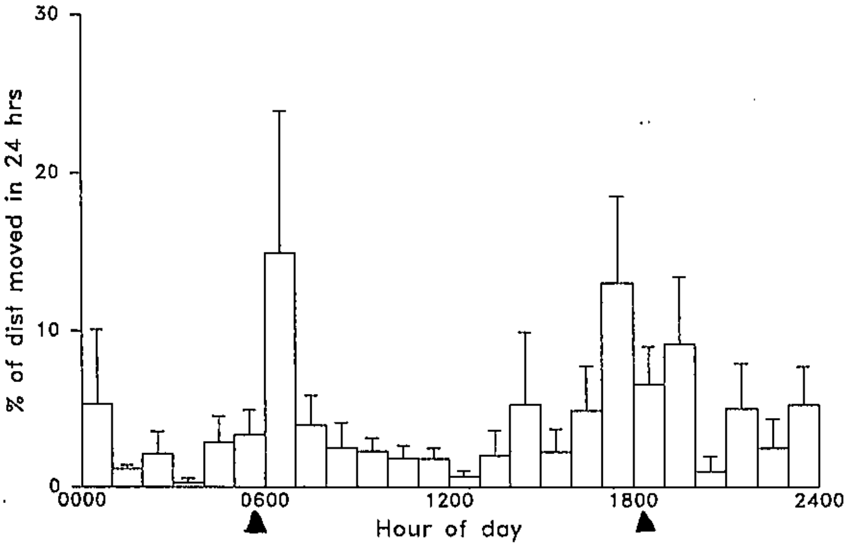


Figure 3.9 Mean percentages (+ s.e.m.) of the total distance moved in 24 hours, moved in each hour by four red-necked wallabies. The times of dawn and dusk are indicated by pointers on the x axis.

Table 3.9. The percentage of a day's total movement (± s.e. mean) per hour by eastern grey kangaroos (n=24) and red-necked wallabies (n=4), in the six time periods defined in the text.

Time Period	Eastern Grey Kangaroos mean ± s.e. metres	Red-necked Wallabies mean ± s.e. metres
T1	9.5 ± 0.9	8.2 ± 2.4
T2	2.4 ± 0.3	1.3 ± 0.4
T3	5.0 ± 0.8	5.1 ± 0.7
T4	4.4 ± 0.6	4.8 + 1.1
T5	3.0 ± 0.5	4.5 ± 0.6
T6	4.0 ± 0.7	3.1 ± 0.6

The varying scan intervals, used in different time periods when watching wallabies, did not allow me to calculate comparable frequencies of movement for the time periods. However, the rates of movement per hour in the different time periods are compared with the rates, for all the kangaroos, in Table 3.10. In both species rates of movement were lowest around midday; the peak rate of movement for kangaroos was in T1 but wallabies moved equally fast in T3 as in T1.

Table 3.10. Average rates of movement (± s.e. mean), in metres per hour, for all the eastern grey kangaroos and red-necked wallabies, in the six time periods.

Time Period	Eastern Grey Kangaroos mean ± s.e. m/hr	Red-necked Wallabies mean ± s.e. m/hr
T1	84.0 ± 31.0	68.2 ± 16.4
T2	46.2 ± 7.5	14.4 ± 0.9
T3	82.0 ± 12.6	70.5 ± 34.2
T4	86.5 ± 19.8	30.0 ± 9.5
T5	57.1 ± 12.3	54.7 ± 18.8
T6	74.6 ± 15.5	37.9 ± 15.6

3.5.3 Total distance moved

Although wallabies moved from resting places to feeding locations they did not show any overall movement uphill in the late afternoon (T3) or in the early evening (T4), or downhill before dawn (T6) or after dawn (T1). Their pattern of movement differed from kangaroos in their use of the western forest and gullies for resting and the westerly paddocks, along the valley floor, for feeding.

The mean total distance moved by wallabies was 1100 ± 255 m, which was similar to the distance moved by male and female kangaroos in winter. Five animals are included in the mean; the extra wallaby included was lost during the night in a patch of milkweed but was discovered in the same place a few hours later at dawn.

Total distance moved in 24 hours was proportionately greater for wallabies, given their much smaller body size. Considering the great problems we had keeping in contact with wallabies and the large number that were "lost", the figure for distance moved may be an underestimate. It is also possible that the more nervous wallabies moved further in response to our presence. However, if we suspected that a wallaby was moving in response to us on a following the watch was abandoned.

3.6 Discussion

3.6.1 The success of the 24-hour followings

Following kangaroos and wallabies on foot for a 24-hour period allowed us to collect unique information on all aspects of their daily activities and movements: the relation of their activity to their environment; their feeding patterns; and their interactions and associations with other individuals. The method proved very successful for the eastern grey kangaroo but proved very difficult in practice for the wallabies. The smaller size of wallabies, their tendency to hide in dense vegetation and their greater flightiness meant that most of the wallabies were "lost" before the completion of 24 hours of following. The wallabies that we did keep in contact with were the most tractable ones, whose movements were generally predictable.

The success of the technique relied on the habituation of the animals to our presence and our ability to recognize all or most of the individuals in the two study populations. It was also possible because of the comparatively small distances moved by the animals in a 24-hour period. Some animals were temporarily lost after a very sudden and lengthy movement (as a result of a dingo's approach, for example), but our knowledge of the animals' "haunts" often allowed us to predict where the animals had gone and to catch up with them.

3.6.2 24-hour schedules of activity for kangaroos and wallabies

The daily schedules of activity of kangaroos and wallabies at Wallaby Creek are similar to those reported for the same species in other studies. The cessation of feeding 2-3 hours after dawn and cessation of resting 2-3 hours before dusk has been reported for eastern grey kangaroos on the Northern Tablelands (Southwell, 1981), south-eastern N.S.W (Jaremovic, 1984) and red-necked wallabies (Southwell, 1976). Southwell (1981) reported three phases of activity for eastern greys: feeding, from late afternoon to morning; resting around midday; and an intermediate period between feeding and resting when kangaroos were more alert and moved often. Bell (1972) and Jaremovic (1984) reported similar patterns. The pattern differs from that reported by Priddel (1986) for red kangaroos and western greys in that eastern greys at Wallaby Creek and elsewhere feed, even at low levels, throughout the day; the red and western grey kangaroos in semi-arid shrublands in western New South Wales did not feed at all for a few hours around noon, but only rested in shady places.

The schedules of activities of wallabies at Wallaby Creek were very similar to the eastern grey kangaroos, except that wallabies were less likely to feed during the midday period and around midnight. Movement to the forest or vegetated gullies a few hours after dawn allowed wallabies to rest in the shade where they were also less visible to predators. However, the lack of high quality grasses in these resting places meant that wallabies were rarely seen to feed in the middle of the day, although they did occasionally browse the vegetation around them.

The bimodal pattern of activity shown by the red-necked wallabies, but not the eastern grey kangaroos, with a resting phase around noon and after midnight, has been reported by Priddel (1986) for red and western grey kangaroos and Osazuwa (1978) for wallaroos. Like Southwell (1981) we saw no synchronised night-time resting period for kangaroos, although individuals often rested for a period of time at varying times of the night.

3.6.3 Time-budgets and their relationship to the body sizes of kangaroos and wallabies.

In this study sample sizes were too small to compare the total foraging times of wallabies and kangaroos in each season, but it appeared that foraging times of the two species were very similar over 24-hours (around 60% of 24-hours). Few studies of the 24-hour time-budgets of wallabies have been carried out but Southwell (1976), in a comparative study of red-necked wallabies and eastern grey kangaroos, noted that kangaroos spent more time feeding and less time alert than wallabies. The greater time spent alert by wallabies, possibly at the expense of feeding time, may be a response to a greater risk of predation because of their small size, or because of the smaller groups they forage in. Aside from the constraints on foraging time imposed by other essential activities, such as vigilance for predators, foraging time is the result of a complex interaction between energy requirements, diet selection, foraging rates and food availability. A general pattern amongst ruminants of longer foraging times with increasing body size (Owen-Smith, cited in Clutton-Brock and Harvey, 1983) may hold for macropods, yet Short (1986) found that grey kangaroos fed for longer each day than red-kangaroos of the same size and feeding on the same pasture.

If minimizing the risk of predation conflicts with maximizing energy gains (e.g. foraging is more risky than resting) then animals may follow a 'satisficing model' rather than an 'optimizing' one, where instead of maximizing energy gains they seek only to stay alive (Herbers, 1981; Bunnell and Gillingham, 1985). Thus the balance between energy requirements and costs of foraging may bring about different solutions for animals of different body size. The proportion of time that kangaroos and wallabies devote to feeding in the morning and afternoon time periods will be examined in greater detail in Chapter 6.

3.6.4 Foraging time and pasture conditions

Grazing times of kangaroos did vary considerably between seasons, especially in the drought year of 1986; in that year winter feeding times reached a peak of 17.8 hours a day compared to only 12.3 hours for the spring that followed. The long feeding times were associated with very low biting rates such that total bite numbers in 24 hours were lower, despite the longer feeding times. Red and western grey kangaroos feeding on a sward of declining biomass also increased daily grazing time but whereas grey kangaroos at Wallaby Creek decreased their rate of biting, the biting rates (harvesting bites only) of red kangaroos increased and western greys fed at the same rate (Short 1986).

Sward heights and the percentages of live leaf in intertussock sward surface were at their lowest in winter (see Chapter 2) illustrating the low availability of green leaf in winter prior to burning. Kangaroos at Wallaby Creek responded to the low availability of green leaf by increasing their total grazing times and spending more time selecting each bite (see also Chapter 5) and thus fitted Novellie's pattern of selective feeders (Novellie, 1978). Red kangaroos in Short's study (Short, 1986) combined faster feeding rates with longer feeding times on low biomass swards in an attempt to maintain intake.

Total feeding times of kangaroos ranged from 10.1 hours to 17.5 hours per day and spanned the seasonal means reported by Southwell (1981) for the same species on the New England Tablelands, with values being higher in winter than summer in both studies. The times were considerably longer than those reported by Priddel (1986) for red kangaroos (7.1 - 10.5 h per day) or western grey kangaroos (5.9 - 9.8 h per day). It should be noted that Priddel included only the prehension and selection of bites as feeding (i.e. only when they had their heads down, biting). Using figures for the proportion of feeding time that kangaroos spent head down, biting (0.7 for summer and 0.8 for winter, Figure 2.2), the comparable figures for Wallaby Creek kangaroos are 7.4 h per day in summer and 14.0 h per day in winter, the latter still being appreciably higher than that for red and western grey kangaroos. Since the kangaroos in Priddel's study also rested for longer at night, the constraints of thermoregulation can not be the only reason for the shorter feeding times. It may be that food in that region was of a lower digestibility than at Wallaby Creek and that kangaroos needed to stop feeding to digest the food in their stomach. Stomach fill is known to be a factor determining the end of a grazing bout in ruminants but chemical factors are also responsible (Weston, 1982).

Herbivores show a wide range of foraging times over a 24-hour period: reindeer 16-20 h (Trudell and White, 1981); horses and cattle 14-15 h (Arnold and Dudzinski, 1978); red deer 10 - 13 h (Clutton-Brock *et al.*, 1982a). The feeding times recorded during the 1986 drought (up to 17.5 hours) were longer than those recorded for most ungulate species.

The low biting rate of kangaroos in comparison to most ruminants (c.f. Table 2, Short 1986), and smaller bite size would enable them to forage for longer because gut fill would take longer. Long feeding times were also recorded for semi-captive Bennett's wallabies feeding on poor pasture in Britain (Clarke and Loudon, 1985). The macropodine stomach, with its 'tubular flow' of digesta (Dellow and Hume, 1982) may also enable macropods to forage for longer because of their shorter mean retention time of both solid and liquid phases of digestion (Clarke and Loudon, 1985).

3.6.5 Activity budgets of males and females.

The total time that kangaroos at Wallaby Creek devoted to feeding did not vary between the sexes. Short (1986) found that captive males of the same species grazed for longer than females but free-ranging males grazed for a shorter period than females. This contrasts with Priddel's finding that male red and western grey kangaroos grazed for longer than females (Priddel, 1986). Thus, there appear to be no clear conclusions to be drawn as to whether differences in foraging time exist between the sexes. The interaction between diet quality, retention time and foraging times may explain the varying results. The diets of the sexes will be compared in the next chapter.

Given the degree of sexual dimorphism of eastern grey kangaroos (females are 50-60% of adult male weight) differences in foraging behaviour are expected, at least between large males and females without suckling young. Grazing herbivores have been shown to increase their grazing time at peak lactation to meet the high energetic demands of milk production (e.g. sheep: Arnold, 1975; red deer: Clutton-Brock et al., 1982b; Loudon et al., 1984; elk: Robbins et al., 1981). Some studies on ruminant species have suggested that limits to maximum grazing times, set by gut morphology and rates of passage, may not allow females to compensate totally for the increased demands leading to their loss in body condition during lactation (Allden and Whittaker, 1970; Milne et al., 1981; Doney et al., 1981).

For macropods, peak lactation corresponds with the time of the young's permanent emergence from the pouch (Green 1984) and therefore females with large pouch-young or young-at-foot are likely to be under greater energetic stress than other females. Females with large pouch-young also need to carry their young in the pouch for a large proportion of their time, adding to their energy load. The combined costs of energy use for milk production and locomotion have not yet been calculated, but it seems likely that the highest cost to the dam occurs just before the young's permanent emergence from the pouch. In this study female kangaroos with large pouch-young or young-at-foot fed for longer than females with small, or no pouch-young, as has been observed for Bennett's wallabies (Clarke and Loudon, 1985). Stuart-Dick compared the grazing times of four classes of eastern grey kangaroo females at Wallaby Creek and found that females with large young-at-foot grazed for less times than females with small pouch-young, and females with large pouch-young tended to have the highest grazing times (Stuart-Dick, 1987).

Females could also compensate for the increased costs of lactation by selecting a higher quality diet (see Chapter 4), or they may increase their rate of intake by biting faster (see Chapter 6). The fact that females with young-at-foot were in significantly poorer body condition than other classes of female (section 2.5.3) suggests that females were not able to compensate fully for the energy demands of lactation by changes in their foraging behaviour.

The sexes did differ in their preferred posture for resting, with females spending more time standing and less time lying than males. The difference in preferred posture may represent a thermoregulatory response or an anti-predator response. Russell (1971) showed that when ambient temperatures are high, red kangaroos spend more time standing up when resting, presumably because it easier for them to lose heat in this posture. Kangaroos at Wallaby Creek were often observed licking their forearms whilst resting in summer, particularly when they were standing. Standing would increase their evaporative heat loss because air currents further from the ground surface are faster. Standing would also decrease their heat load by reducing the surface area of their bodies exposed to the sun. Given their smaller body size compared to males, and thence their greater surface area to volume ratio, there seems little reason for females requiring a more efficient method of heat loss. Alternatively, females may prefer this resting posture because they are better able to survey their surroundings from a higher view point. Wallabies also used more upright postures for resting, generally adopting the sitting or bent postures.

3.6.6 Movements of kangaroos and wallabies

Other 24-hour studies of macropods have also revealed regular schedules of movement associated with movements to and from feeding, resting and drinking sites (Caughley, 1964a; Kaufmann, 1975; Southwell, 1976, 1981; Wyre, 1981; Osazuwa, 1978; Clarke and Loudon 1985). In this study, kangaroos and wallabies moved furthest and fastest in the first three hours after dawn (T1) and kangaroos also moved most frequently in this period. At Wallaby Creek, T1 encompassed the major movement downhill around dawn, the movement from the site of feeding to the resting site at the end of the morning feeding bout and normal movement during feeding.

Most of the significant differences between summer and winter movements of kangaroos were also seen in this time period; the morning movement downhill in summer contributed to this seasonal difference. In addition, kangaroos often had to move to find a shady resting spot in summer whereas in winter they would sometimes lie down where they had been feeding. In a study of red kangaroos in captivity, kangaroos moved to and from shade more often in summer than in winter (Russell 1971) and such movements may contibute to the greater and more frequent movement in summer. Differences in movement whilst feeding may also contribute to the seasonal difference; animals tend to move further during feeding bouts when food is sparse and highly dispersed (Jarman, 1974; Jarman and Jarman, 1978; Novellie, 1978). The relationship between feeding movement and vegetation will be investigated in Chapter 5.

Differences between the sexes in movement were seen at night rather than in the morning. Females showed their second highest rates and frequencies of movement in the afternoon (T3) but males showed them in T6. These differences were not due to a reduction in movement by males in T3 but instead to additional movements by males in T6 that were not seen for females. These extra movements were not made by all males and there was considerable variation amongst the ten males included in this analysis. For smaller males some of the variation could be explained by their age and proximity to the time of their weaning or dispersal. The response of large males to the presence of an oestrous female in the study area seemed to vary depending on the dominance status of the male; a dominant male escorting a female tended to move the typical distance moved by a female whereas subordinate males often left the oestrous group to contact other females.

If, as we believe, males are moving far and fast in order to contact as many females as possible they may not need to do this every day. On the contrary, it may be adaptive for them not to, since over-expenditure of energy may deplete a male to the point where he might lose hierachical status, and with it the probability of successful matings. Females approaching oestrus are detectable up to a week in advance and so a male need only check all the females every few days. I was not able to test for intra-male differences in movement but observations of males in the same group as the focal animal and which had already been followed as focal animals for long periods, suggest that such intra-male variation exists and deserves further investigation.

3.6.7 Day-time and night-time activities and the nocturnal habit of macropods.

Kangaroos showed slightly lower rates of biting at night compared to the daytime but there was little evidence that kangaroos were being more selective in the dark. The step and hop totals and the mean steps taken between feeding sites were the same at night and in the day, although kangaroos did take more bites in each patch at night compared to in the daytime. Nor was their reduced feeding rate due to their spending more time surveying in the dark; kangaroos raised their heads to survey less often at night.

Bennett's wallabies in a park in Britain showed higher biting rates at night compared to the daytime average (Clarke, 1984) although they too showed a bimodal pattern of biting rates with peaks in the early morning and late afternoon. In the study of Bennett's wallabies there was no opportunity for movement to different vegetation types at night. In this study kangaroos did show a movement uphill at night and downhill at dawn in summer such that changes in the type of feeding site between night and day may have contributed to the lower feeding rates (see Chapter 4).

The posture differences between night and day suggest that although predators may be more active at night and harder to see, kangaroos were not surveying for predators more in the dark than in daylight. Instead they remained crouched amongst vegetation and raised their heads little to survey. Unfortunately little is known of the visual capabilities of kangaroos in the dark, but if they use hearing and smell to detect predators at night then this strategy would seem logical. If they are attempting to remain hidden from predators at night then I would predict that they would be in smaller groups at night and that they would feed in denser cover vegetation at night than in the day.