

SECTION II

SOCIAL ORGANIZATION

CHAPTER 9ASPECTS OF SOCIAL ORGANIZATION

Recent studies (e.g. Jarman, 1974; Geist, 1974) have highlighted the interrelationship which exists between the ecology and social organization of a species. During the study of the ecology of the grey kangaroo and wallaroo the opportunity arose to collect data on aspects of the social organization of the two species. Data on group size and composition were collected during transect counts. Kangaroos individually recognizable by collars enabled data on home range and movements to be gathered on Lana.

## 9.1 MOVEMENTS

## 9.1.1 Introduction

Work on movement patterns in kangaroos has been concentrated in the arid and semi-arid regions of Australia. The distribution of red kangaroo is determined by the abundance of green feed (Frith, 1964; Newsome, 1965a,b). Extensive movements occur in response to the changing distribution of green herbage (Frith, 1964). Bailey (1971) has recorded red kangaroo moving up to 217 km. However sedentary individuals also occur. Thus Bailey (1971) sighted a female 10 times in 120 weeks always within a 0.8 km radius of the previous sighting. Red kangaroo in areas with a milder climate are more sedentary than are animals in more arid areas (Frith, 1964). Euros in the Pilbara region of Western Australia have been found to be sedentary (Ealey, 1967b). The longest distance between sightings for an individual was 1100 m. Emaciated euros have been found to stay around water holes that have dried even though water supplies were available less than 1.6 km away. Ealey (1967b) found that many animals dispersed after summer rains but most of these animals later returned to the same home range.

Kangaroos in the more mesic areas of Australia are generally believed to be sedentary. Thus Kirkpatrick (1967) considered that grey kangaroo rarely move more than a few kilometres in search of food, even during drought conditions. A suggestion by Denny (1975) that changes in numbers of eastern grey kangaroo west of the Darling River were caused by movements brought a quick rebuff from Caughley (1975) and Poole (1975). However Grant (1973) believed that transient animals occurred in a

population of eastern grey kangaroo that he studied.

In 1974 a kangaroo collaring program was begun on Lana by Dr. Peter Jarman to examine the claim by property owners surrounding Lana that kangaroos were breeding on Lana (a Wildlife Refuge) and then dispersing onto adjoining properties. In 1977, following a pattern tested and used on red kangaroo and euro by Dr. Martin Denny, I constructed a different type of collar to that previously used to mark the kangaroos. These new collars were put on the kangaroos so that data on loss of collars from the property (hence movement of kangaroos) over time could be studied.

Compared to arid and semi-arid areas, conditions in the present study areas favour the occurrence of sedentary behaviour. Rainfall is seasonally predictable and variation between years is not great. On Lana water is easily accessible year round. It is therefore likely that kangaroos on Lana would be able to confine their activities within a limited home range. A change in the pattern of occurrence of food resources over seasons would be limited to changes between habitats which are closely interspersed. Thus kangaroos would not need to undertake long distance movements as a result of changes in seasonal conditions. In contrast to arid and semi-arid areas, rainfall is fairly uniform over large areas and hence climatic factors will not lead to large differences in the food resources available between areas.

#### 9.1.2 Methods

In order to catch kangaroos on Lana 40 to 100 volunteers were spread in a line across the width of the study area along the road which ran through the area. They then walked west herding some kangaroos in front of them as they went. Kangaroos were captured in nets spread across a valley as they were herded through. Collars were placed on large sub-adult and adult animals only, to ensure that growth did not lead to the collar tightening around the neck. The collars used were lengths of machine belting to which were rivetted reflective tape of different colours glued onto hard plastic of two shapes (triangular and rectangular). The collars were adjusted to fit individual animals by using cattle tail-tags rivetted to the ends of the machine belting. The tail-tags had a limited life in the field as the plastic became brittle and eventually snapped. The new collars were placed on kangaroos on 30/7/77. At this time fifteen female and ten male grey kangaroo and eight female and nine male wallaroo were collared. On three occasions after that date the percentage of kangaroos with collars was estimated from the kangaroos seen while I was walking transects. Animals seen on

the transect around Mt. Lookout were not included in the sample as that area was not included in the catching area.

### 9.1.3 Results

The percentages of kangaroos seen with collars during the periods 17-20 days, 37-42 days and 128-133 days after the kangaroos were initially collared are shown in Table 9.1. The proportion of wallaroo with collars did not differ significantly between the first and second sample. The proportion of wallaroo with collars was close to being significantly different between the second and third samples ( $\chi^2 = 3.35$ ,  $df = 1$ ,  $p = 0.06$ ). For the grey kangaroo there was a significant drop in the proportion of individuals with collars during the first and second sample ( $\chi^2 = 5.87$ ,  $df = 1$ ,  $p < 0.05$ ). There was no difference in the proportion of grey kangaroo with collars between the second and third sample.

Table 9.1 Percentage of kangaroos seen with collars at different time intervals after being collared.

| Dates of Estimation | WALLAROO    |            | GREY KANGAROO |            |
|---------------------|-------------|------------|---------------|------------|
|                     | Number seen | % collared | Number seen   | % collared |
| 16-19/8/77          | 171         | 7.0        | 102           | 15.5       |
| 5-11/9/77           | 260         | 7.6        | 186           | 5.9        |
| 5-10/12/77          | 244         | 3.3        | 132           | 6.1        |

At all times I was on Lana after the catch in July 1977 up until early April 1978 searches for collars which might have fallen off kangaroos were made. Also during another kangaroo catch conducted on Lana on 9/4/78 the eighty people present were asked to look for collars as they herded the kangaroos. Only one grey kangaroo collar was found and this was on a dead animal which had been shot from the public road which bordered the northern section of the study area. Five collars were found which had been shed from wallaroo. Table 9.2 gives the sex ratio of wallaroo who were collared on 30/7/77 and the sex ratio for animals whose shed collars were found on Lana.

Table 9.2 Sex ratio of animals initially collared and animals whose collars were found shed on Lana for the wallaroo.

|                            | Female             | Male |
|----------------------------|--------------------|------|
| collared on 30/7/77        | 8                  | 9    |
| collars found up to 9/4/78 | 1 (on dead animal) | 4    |

There is direct evidence of movement of grey kangaroo off Lana. Three collars have been reported on kangaroos at distances greater than five kilometres from Lana (P. Jarman, pers. comm.). The furthest of these was seventeen kilometres from Lana. One of the kangaroos was seen eight kilometres from Lana less than a month after it was collared. The third of these collared kangaroos was seen thirteen kilometres from Lana. Mr. Dan Davis and neighbouring landholders (pers. comm.) have also reported seeing collared grey kangaroo on neighbouring properties. No collared wallaroo have been sighted off Lana. However one female wallaroo which was collared in March 1975 and seen near the western end of the study area in October 1976 was shot at the base of Mt. Lookout at the eastern end of the study area in February 1978.

Three grey kangaroo that were positively identified from collars found off Lana were all females. To investigate whether females may be more likely to disperse than males, the ratio of collared females to collared males seen on Lana after the catch was examined (Table 9.3). There was no drop in the proportion of collared animals seen that were females as the time since being collared increased. However sampling bias (i.e. different probabilities of sighting each sex over time) could easily be affecting the results.

Table 9.3 Sex ratio of collared grey kangaroo sighted on Lana after the catch in late July 1977.

| Month | Male | Female |
|-------|------|--------|
| 8/77  | 4    | 5      |
| 9/77  | 3    | 7      |
| 10/77 | 3    | 7      |
| 12/77 | 3    | 3      |

## 9.1.4 Discussion

There was no direct evidence of movement of wallaroo off Lana occurring. The percentage of wallaroo that were collared was the same in early spring as in winter. There was, however, a drop in the percentage of wallaroo collared between early spring and early summer. One wallaroo collar was found on a dead female and the rest, which would have come off live animals, were all from males. Two of these collars were found one metre apart in savanna woodland out from a rocky hill. Osazuwa (1978) found an increase in fighting between males in spring compared with winter in New England wallaroo studied in a large outdoor enclosure. Thus the drop in the percentage of wallaroo seen with collars after early spring may have been due to collar loss caused by fighting between males. The only movement from a home range recorded for a wallaroo was for a female that moved from one end of the study area to the other. However this movement is probably best considered as a change from residency in one home range to residency in an adjacent home range rather than as a tendency to disperse from the area.

There is direct evidence of movement of grey kangaroo off Lana occurring. Changes in the percentage of grey kangaroo collared can also be interpreted as evidence of movement of grey kangaroo off the study area. Thus there was an initial drop in the percentage of animals collared and then the percentage collared remained constant. No grey kangaroo collars shed from live animals were found on Lana. The pattern of collar sightings for the grey kangaroo may thus have been due to the movement off the property of animals which were transients. The collared population would then have consisted only of resident animals and the percentage of animals collared would remain constant. The transient animals may make up a large proportion of the collared animals due to their lack of experience with the area. Thus they are probably more likely to be able to be herded and caught than are resident animals who are familiar with the area and able to break back through the line of beaters. The transient animals may also be more prone to capture near the boundary fence where the net-line was sited. Whereas some grey kangaroo must disperse off Lana, other animals have been seen in the same area for a period of three years (see section 9.2). Bailey (1971) has shown that red kangaroo populations also consist of both sedentary and nomadic individuals.

It is possible that some grey kangaroo which disperse may return. A female that was collared in March 1975 was never seen until twice in the last two months during the time I actively searched for collared

animals on Lana (August 1976 to December 1977). Most of the kangaroos sighted with collars were seen within four months of my starting to search for collared animals or of when they were collared. Apart from the 14 months before the female just mentioned was sighted, the next longest period before a collared animal was sighted was 8 months. However the resighting of this female may have simply been due to its changing its home range from an area I did not actively search to an area I did actively search.

The movement of grey kangaroo and wallaroo off Lana has only been investigated for older animals as only adults and large sub-adults were collared. Dispersal of smaller sub-adults and juvenile animals off the study area was not studied but may occur. Kaufmann (1974), for example, presented evidence of some dispersal from the group home range occurring in sub-adult male whiptail wallaby *Macropus parryi*.

In both kangaroo species where dispersal from an area has been shown to take place (i.e. euro and red kangaroo) a search for food was thought to be the reason for these movements taking place (e.g. Ealey, 1967b; Newsome, 1965b; Bailey, 1971). I feel it is unlikely that a search for food per se was the reason for grey kangaroo moving off Lana. Rainfall and climatic conditions are fairly uniform over the surrounding areas and hence individuals are unlikely to find greater food resources available in other areas due to the effects of difference in rainfall or other climatic variables. However dispersal of some individuals will be adaptive if a dispersing individual is able to find an area where the level of the population in relation to the carrying capacity is below that on the area from which it dispersed. In the district in which the study took place there are large differences in the rate of culling of kangaroos between different properties which produces disparities in the density of the populations in relation to the carrying capacity. Before European settlement fire may have been the most important factor in creating new areas with abundant food resources where dispersing individuals could settle.

In the present study movement of animals born on the property and movement of animals which were caught as transients cannot be distinguished. Because of the large drop in the percentage collared, I think it is likely that the vast majority of animals were transients and not animals that had been resident in a home range on the study area. Lana is likely to be below the carrying capacity as culling of grey kangaroo is carried out regularly. Since areas around Lana are present where the grey kangaroo populations are not as heavily culled,

one would expect some settlement occurring on Lana. Some individuals may have in fact dispersed onto Lana and settled into a home range. However it is clear that many kangaroos moved across Lana and did not settle permanently.

The differences between the grey kangaroo and wallaroo in the occurrence of transient adults may be related to differences in the type of habitat they inhabit. Wallaroo only occur where suitable sheltering areas, in the form of rocky hills, are present. These areas will be more discontinuous and unevenly dispersed in comparison to grey kangaroo habitat. Thus wallaroo would have to disperse through large areas of unsuitable habitat and their chances of finding new areas of suitable habitat will be lower than for grey kangaroo. Grey kangaroo habitat may also be more of a disclimax when compared to wallaroo habitat. Suitable wallaroo habitat is probably always likely to be inhabited even if at low densities in areas of low food resources. Many areas now inhabited by grey kangaroo, if unmanaged, would become shrub dominated and hence unsuitable for use by grey kangaroo (Taylor, 1980). It may thus be possible for dispersing grey kangaroo to find newly-created areas (formed by disturbance to climax communities) which are far below the carrying capacity. Dispersing wallaroo may be unlikely to find suitable habitat which is not already colonized. Geist (1971) has also explained differences in the dispersal rates of moose (*Alces alces*) and bighorn sheep (*Ovis canadensis*) on the basis of differences in the stability of their habitats.

## 9.2 HOME RANGE

### 9.2.1 Introduction

Most studies of social organization in macropods have suffered from a lack of recognizable individuals. Thus many of these studies have not been able to comment on home range use (e.g. Kirkpatrick, 1966; Croft, 1981a,b; Caughley, 1964b; Southwell, 1976). However all studies of macropods in which individuals were recognized have shown that at least some individuals of all species studied remain within limited home ranges. Thus, although some red kangaroo do move considerable distances, Bailey (1971) and Frith (1964) have commented on the presence of individuals in the same area for a number of years. Ealey (1967b) found a pattern of limited home range use with overlap occurring between some individuals for the euro in a semi-arid region of Western

Australia. The most detailed study of home range use of a macropod species was carried out by Kaufmann (1974a) on the whiptail wallaby. He found that individuals occurred in discrete "mobs" which broke up into subgroups of varying size and composition. The ranges of adjacent mobs overlapped slightly. Kaufmann (1975) also claimed that two discrete mobs of eastern grey kangaroo occurred in his study area. However these two mobs were on ridges separated by open pasture which kangaroos rarely crossed. His interpretation of the social significance of these mobs was probably influenced by his findings for whiptail wallaby. Thus it is yet to be shown that discrete mobs of grey kangaroo occur in continuous habitat.

The present study was undertaken to investigate the claim by Kaufmann (1975) that mobs occur in the eastern grey kangaroo and to examine home range use in the wallaroo. For the purposes of this study the home range of an individual is taken to be "the area over which an animal normally travels in pursuit of its routine activities" (Jewell, 1966).

Mobs were considered as occurring if a group of individuals had broadly or completely overlapping home ranges with the ranges of at least some individuals ending at a common boundary. No individual which shared part of the mob home range should have a range which broadly overlapped the common boundary. To be interpreted as having social significance the common boundary should be independent of any boundary between favourable and unfavourable habitat. Mobs were considered as not occurring if the boundaries of home ranges of individuals in the same area were totally independent of each other.

#### 9.2.2 Methods

Whenever a recognizable individual kangaroo was seen on Lana its position was plotted on a map of the study area. Most kangaroos were recognized from their collar pattern but a few adult male wallaroo were recognized from tears in their ears. Less than 10% of the kangaroos on the study area were collared. Active searching for collar sightings was carried out from September 1976 until December 1977. Most recognizable individuals were seen while I was walking transects. Spotlighting for collared animals was also carried out at night. Sightings were thus spread over a period from dawn till midnight. From December 1977 until August 1979 no active search for collared animals took place but recognizable individuals were seen in the course of field work. These sightings were also included. Most of the field work was concentrated

around the rocky hills. Hence savanna woodland out from rocky hills was not intensively searched for recognizable kangaroos.

### 9.2.3 Results

The distribution of sightings of recognizable individuals is given in Fig. 9.1 for the grey kangaroo and Fig. 9.2 for wallaroo males and Fig. 9.3 for wallaroo females. Wallaroo males and females were plotted in different figures for the sake of clarity. All recognizable males were adults and only a few of the females were sub-adults. For some individuals only a few sightings were obtained and the results for most individuals cannot be taken as representing the whole of an area an individual could normally be found in. The results are, however, interpretable in terms of the relationship of home range use among individuals.

This study of home range use by grey kangaroo and wallaroo was limited by the small proportion of animals that could be recognized. In interpreting the pattern of home range use for each species it is assumed that unmarked animals behaved in the same manner as did marked animals. Transient animals also occur in the grey kangaroo population (section 9.1) and their use of the area will differ to that of resident animals.

The grey kangaroo population on the area which was surveyed for recognizable individuals appears to be divided into five "mobs" of kangaroos which occupy common home range areas. The reality of mobs E and D would have to be confirmed by more sightings. The members of a mob had broadly overlapping ranges with some individuals sharing a common boundary to their home range. The home range boundaries of mobs mostly occurred within habitats which were extensively utilized by the grey kangaroo and thus did not coincide with the occurrence of unfavourable habitat. No individual present within the mob home range had a range which broadly overlapped the mob home range boundary. The only overlap of mobs which was found was the occurrence of individual  $\Delta$  from mob B on the edge of the home range of mob C. Individuals within a mob occupied the mob home range to different extents. For example, P (adult female) of mob C was seen only in a small part of the mob home range whereas D (adult female) of mob C was seen over most of the mob home range. Large adult males did not appear to occupy a greater area of the mob home range than did adult females. For example in mob B the female  $\Delta$  ranged more widely than either of the recognizable males ( $\blacktriangle$  and  $\bullet$ ) in this mob. It is, however, possible that this was

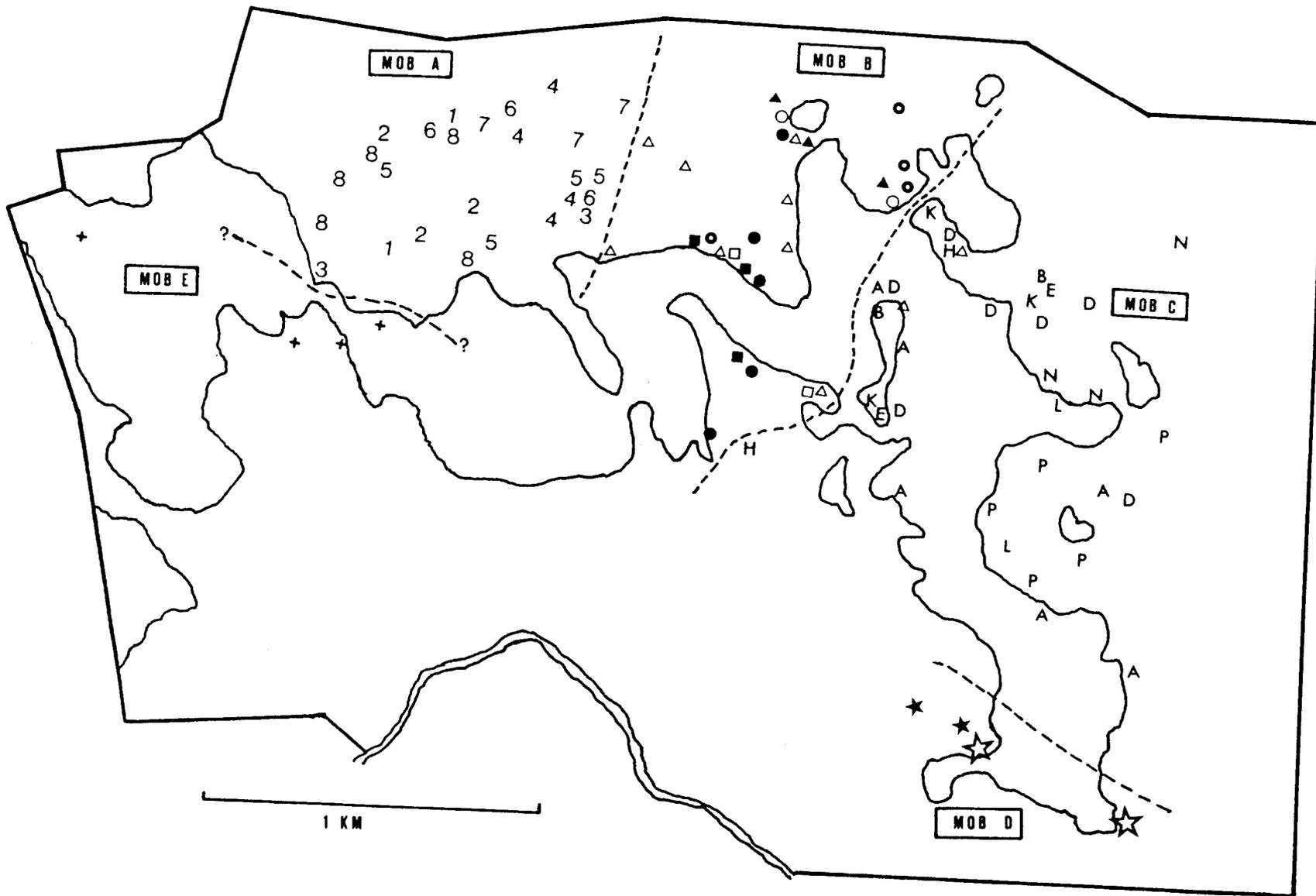


Fig. 9.1. Distribution of sightings of recognizable grey kangaroo on Lana. ---- represents the boundaries between mob home ranges.





related to the larger number of sightings for this female compared to the males. In mob C individuals D and A were sighted a similar number of times and both were found over most of the mob home range. A was a large adult male and D was an adult female. The approximate areas occupied by the three mobs for which it was possible to estimate home range size were 92 ha (mob A), 85 ha (mob B) and 95 ha (mob C).

For the wallaroo there was no indication that groups of individuals shared a common home range as in the grey kangaroo. Instead, home ranges were centred on areas of rocky hill with extensive overlap between individual home ranges occurring. However the boundaries of individual home ranges were completely independent of each other. Some females restricted their movements to very small areas. For example, the home range for B was only 400 metres across. This individual was sighted the greatest number of times so that its small home range was not due to a lack of sightings in comparison to others. Although some females did restrict their movement large adult males did not appear to roam more widely than all females. For example, if a large adult male and a female who both had large home ranges for their sex (e.g. female W and male A) are compared, the home ranges are similar.

#### 9.2.4 Discussion

The present study has confirmed the contention of Kaufmann (1975) that eastern grey kangaroo occur in mobs. The size of the mob range quoted by Kaufmann (1975) (i.e. 525 ha or 1.5 km by 3.5 km) is much greater than found in the present study. This may have been due to the improved pastures present on my study areas. However, the sizes of the mob home ranges in the present study may be somewhat underestimated due to sightings of individuals being based around the rocky hills. The mob home ranges may have extended further out into the woodland to the south of the study area. It is interesting to note however that my estimates of the home range size for mobs are similar to that found for the whiptail wallaby (Kaufmann, 1974a). It was not possible to compare the economic home range size (*sensu* Kaufmann, 1974a), for grey kangaroo in my study to that found by Kaufmann (1975) as the number of kangaroos present in a mob was not known.

As found by Kaufmann (1975), mobs were broken up into subgroups of various sizes whose composition did not remain constant (see sections 9.3 and 9.4). Mobs are probably only rarely, if ever, all present together at the one place. Both Kaufmann (1974a) and I found variation between individuals in the area of the mob home range which was occupied. Very little overlap occurred between mobs. Kaufmann (1975) found no

overlap between grey kangaroo mobs but this was probably due to the presence of unfavourable habitat between the two mobs. Whiptail wallaby mobs also appear to overlap very little (Kaufmann, 1974a). Neither I nor Kaufmann (1975, 1974a) saw any behaviour which could be classed as aggressive behaviour between individuals of different mobs in order to maintain the mob home range as a monopolized zone. However Grant (1973) reported seeing an unfamiliar male being chased away by a male from the resident population (= mob?) on his study area. Undefended monopolized group home ranges have been shown to occur in many other mammals (e.g. Grubb and Jewell, 1966; Riney and Caughley, 1959; De Vore and Hall, 1965).

Wallaroo were found to occur in overlapping home ranges. This is the same pattern as that found by Ealey (1967b) for the euro in an arid area of Western Australia.

Kaufmann (1974a) found that large adult male whiptail wallaby ranged over a greater area than did adult females. In the present study there was no evidence of any difference between large adult males and adult females in the size of their home range for either the grey kangaroo or wallaroo. This lack of a difference between the sexes is surprising since one would expect males to wander more widely in order to increase their chances of finding oestrous females to mate with. Large male and female home range size may have been found to be similar due to the small number of sightings for individuals or due to the fact that sightings were recorded over a long period of time. It is possible that large males range over larger areas than females only on a smaller time scale. Thus over the period of a week, for example, large adult males may cover a large area but over the period of a year large males and females may have similar sized home ranges. Some radio telemetry work done on grey kangaroo tends to support this (P. Jarman, pers. comm.). Two adult males and two females were tracked for a period of two months and the males ranged over a larger area than the females.

The question arises as to why wallaroo do not occur in mobs as do grey kangaroo. Grey kangaroo occur in fairly continuous habitat and feed upon grasses that are abundant and relatively evenly dispersed (Chapter 4). In contrast wallaroo occur in much less continuous habitat. They depend on the presence of rocky hills for shelter. Sections of these rocky hills differ in the degree to which they are preferred as sheltering habitat. Thus best sheltering habitat in the study areas occurs as small isolated patches scattered over the rocky hills (Chapter

5). Wallaroo also feed extensively on the abundant, high quality short grasses which occur in sheep camps whereas the grey kangaroo is less dependent on these areas (Chapters 4 and 5). These sheep camps occur as small areas scattered over the hills and the base of hills. Thus resources for the wallaroo occur as scattered patches within their habitat whereas the resources for the grey kangaroo population are more evenly distributed through their habitat. Clumped, widely distributed resources do not favour the formation of monopolized areas (e.g. Brown, 1964; Clutton-Brock and Harvey, 1977; Geist, 1974). Thus there is probably selection against formation of mobs in the wallaroo but not in the grey kangaroo.

### 9.3 GROUP SIZE

#### 9.3.1 Introduction

In one of the first studies on group size in kangaroos, Caughley (1964b) suggested that the size of groups for eastern grey kangaroo and red kangaroo was determined by an essentially random process of animals joining and leaving. However, although many authors have since presented data on group sizes for various kangaroo species (e.g. Red kangaroo: Caughly, 1964b; Frith, 1964; Russell, 1979; Croft, 1981a. Eastern grey kangaroo: Caughley, 1964b; Kirkpatrick, 1966; Bell, 1972; Grant, 1973; Kaufmann, 1975; Taylor, 1975; Southwell, 1976. *M. robustus*: Russell and Richardson, 1971; Kaufmann, 1974b; Croft, 1981b. *M. antilopinus*: Russell and Richardson, 1971), few have quantitatively examined the factors responsible for determining group sizes.

Newsome (1965a) found that the largest sized groups of red kangaroo occurred in areas of the highest density. Kaufmann (1975) found a larger mean group size for eastern grey kangaroo on areas with better pasture. Kaufmann (1974a) found group size in the whiptail wallaby to vary seasonally being greatest during late winter and early spring when individuals were concentrating on the areas of best forage. These observations, plus a comparison of the results from different studies of the same species, suggest that mean group size of a species is not fixed but will vary depending on a variety of factors. The present study was undertaken to try to examine quantitatively some of the factors which might influence group size in the eastern grey kangaroo and wallaroo.

### 9.3.2 Methods

While walking transects, I recorded the group sizes of kangaroos seen. The criterion used to assess a group was the ability of individuals to maintain visual contact with one another and their common response to an alert behaviour or fleeing of a group member. Groups were loosely defined as those individuals seen within 50 metres of each other. However, based on the criterion of what constituted a group, exceptions to this were recognized. For example, individuals in habitat with dense shrub which were obviously not in visual contact were not included in the same group even though within 50 metres of each other. Group sizes were recorded for wallaroo and grey kangaroo on both study areas for three different periods of the day (early morning, day, late afternoon) and the twelve months of the year at the same time as the habitat use data were collected. The statistical analysis of group size frequencies was based on a non-parametric test because group sizes were not normally distributed.

### 9.3.3 Results

#### (a) Comparison of group size between months and time of day

No differences were found in group size frequencies between months for the grey kangaroo and wallaroo on either Lana or Newholme. There were no differences between group size frequencies among times of day for the wallaroo on Newholme or Lana, or for the grey kangaroo on Newholme. The frequency of occurrence of group sizes was not uniform over the three periods of the day for the grey kangaroo on Lana ( $\chi^2 = 25.1$ ,  $df = 14$ ,  $p < 0.05$ , Table 9.4). Group size frequencies during the day and during the late afternoon were not significantly different. Group size frequencies during early morning were significantly different from those found during the day ( $\chi^2 = 17.8$ ,  $df = 7$ ,  $p < 0.05$ ) and during the late afternoon ( $\chi^2 = 16.2$ ,  $df = 7$ ,  $p < 0.05$ ). Mean group sizes are shown in Table 9.5. Group sizes were, on average, smaller for the grey kangaroo on Lana during early morning than during the day or late afternoon. Although group size frequencies were not significantly different over times of the day for the grey kangaroo on Newholme the mean group sizes show a trend similar to that found on Lana.

Table 9.4 Percentage occurrence of group sizes at different times of the day for the grey kangaroo on Lana.

| Group Size    | TIME OF DAY     |       |                  |
|---------------|-----------------|-------|------------------|
|               | Early Morning % | Day % | Late Afternoon % |
| 1             | 18.6            | 17.7  | 12.9             |
| 2             | 29.3            | 17.7  | 21.6             |
| 3             | 19.8            | 18.7  | 14.9             |
| 4             | 12.0            | 8.4   | 13.4             |
| 5             | 6.6             | 9.4   | 7.7              |
| 6             | 4.2             | 5.9   | 6.2              |
| 7             | 3.0             | 3.9   | 5.7              |
| >7            | 6.5             | 18.3  | 17.6             |
| No. of groups | 167             | 203   | 194              |

Table 9.5 Mean group size for the grey kangaroo and wallaroo on Lana and Newholme at different times of day.

| SPECIES       | PROPERTY | TIME OF DAY   |      |                |
|---------------|----------|---------------|------|----------------|
|               |          | Early Morning | Day  | Late Afternoon |
| Grey kangaroo | Lana     | 3.38          | 5.04 | 4.87           |
| Grey kangaroo | Newholme | 2.57          | 3.34 | 2.93           |
| Wallaroo      | Lana     | 2.04          | 2.12 | 2.30           |
| Wallaroo      | Newholme | 1.72          | 2.04 | 1.63           |

(b) Comparison of group sizes on Lana and Newholme

Group size frequencies for the grey kangaroo and wallaroo on Lana and Newholme for all times of day are shown in Table 9.6. Group size frequencies are significantly different between Lana and Newholme for both the grey kangaroo ( $\chi^2 = 22.4$ ,  $df = 6$ ,  $p < 0.001$ ) and wallaroo ( $\chi^2 = 12.8$ ,  $df = 4$ ,  $p < 0.01$ ). For the grey kangaroo the major difference between properties is the greater proportion of animals seen in larger group sizes on Lana. For the wallaroo the major differences between properties are the greater proportion of individuals seen alone and the lower proportion of individuals in larger groups on Newholme. When Lana is

compared to Newholme for group size frequencies for grey kangaroo and wallaroo for each time of day, only during late afternoon is there a significant difference between the two properties (grey kangaroo,  $\chi^2 = 13.4$ ,  $df = 4$ ,  $p < 0.01$ ; wallaroo,  $\chi^2 = 13.7$ ,  $df = 3$ ,  $p < 0.01$ ).

Table 9.6 Percentage occurrence of group sizes for the grey kangaroo and wallaroo on Lana and Newholme.

| GROUP SIZE         | GREY KANGAROO |               | WALLAROO  |               |
|--------------------|---------------|---------------|-----------|---------------|
|                    | Lana<br>%     | Newholme<br>% | Lana<br>% | Newholme<br>% |
| 1                  | 16.3          | 22.2          | 43.2      | 54.5          |
| 2                  | 22.5          | 34.0          | 32.1      | 28.8          |
| 3                  | 17.7          | 14.2          | 11.9      | 9.0           |
| 4                  | 11.2          | 12.3          | 5.3       | 3.9           |
| 5                  | 7.9           | 6.8           | 2.5       | 0.4           |
| 6                  | 5.5           | 3.7           | 1.6       | 2.1           |
| 7                  | 4.2           | 2.5           | 1.2       | 1.3           |
| 8                  | 3.0           | 1.9           | 0.9       |               |
| 9                  | 1.6           | 1.2           | 0.4       |               |
| 10                 | 1.9           | 0             | 0.4       |               |
| 11                 | 2.1           | 0.6           | 0.1       |               |
| 12                 | 1.0           | 0.6           | 0.1       |               |
| >12                | 5.1           |               | 0.3       |               |
| No. of groups seen | 564           | 162           | 1610      | 233           |
| Mean group size    | 4.49          | 2.96          | 2.17      | 1.79          |

(c) Comparison of group size in the grey kangaroo and wallaroo

The grey kangaroo has a significantly different group size frequency distribution to the wallaroo on both Lana ( $\chi^2 = 332$ ,  $df = 10$ ,  $p < 0.001$ ) and Newholme ( $\chi^2 = 55$ ,  $df = 4$ ,  $p < 0.001$ ). The major difference between the species on both Lana and Newholme is the greater proportion of wallaroo found alone in comparison with the grey kangaroo.

(d) Randomness of group size occurrence

In order to test whether the frequency of occurrence of group sizes was random, the group size frequency distribution was compared to an expected frequency distribution based on a truncated Poisson distribution (Cohen, 1960). A truncated Poisson distribution was used and not a Poisson

distribution as the first term of the series in a Poisson distribution (i.e. a group size of zero) is meaningless. The results are given in Fig. 9.4. For both species on both study areas group sizes of one and/or two and the largest group size category are found more than expected. The group sizes between the upper and lower limits are found less than would be expected if group size occurrence were random.

(e) Relationship between mean group size and density

Mean group size was plotted against the density of kangaroos in each habitat present on the two study areas for each time period (i.e. early morning, day, late afternoon) averaged over the year. Any habitat-time combination in which only one group was sighted was not included. The results are shown in Fig. 9.5 for the grey kangaroo and Fig. 9.6 for the wallaroo. Although there is a significant correlation between mean group size and density for both species the amount of variation in mean group size explained by differences in density is not great (grey kangaroo = 41%; wallaroo = 38%). When only times of day when kangaroos were actively feeding (i.e. early morning, late afternoon) on Lana are included, the amount of variation explained increased greatly (grey kangaroo = 72%; wallaroo = 64%).

#### 7.3.4 Discussion

Group size frequencies for the grey kangaroo and wallaroo have been shown not to be constant. Group sizes are not determined at random but rather are probably influenced by many factors, a few of which have been examined in the present study.

Grey kangaroo group sizes were found to vary depending on the time of day. The mean group size for grey kangaroo was smallest during early morning. The low mean group size found during early morning is probably due to splitting of groups during the night. Group coordination may be more difficult during the night than during the day. Groups probably coalesce again during the day whilst the animals are at increased densities in sheltering habitat. Most authors who have presented data on group sizes in macropods have not investigated changes over time of day. Kaufmann (1974a) comments on an apparent increase in group size during the day for whiptail wallaby but presents no data to support this. He suggests that groups probably split up more during the night. Southwell (1976) found no differences in mean group size between times of day for the population of eastern grey kangaroo which he studied.

No significant changes in group size were found to occur over the seasons for either species. However seasonal changes in group size have

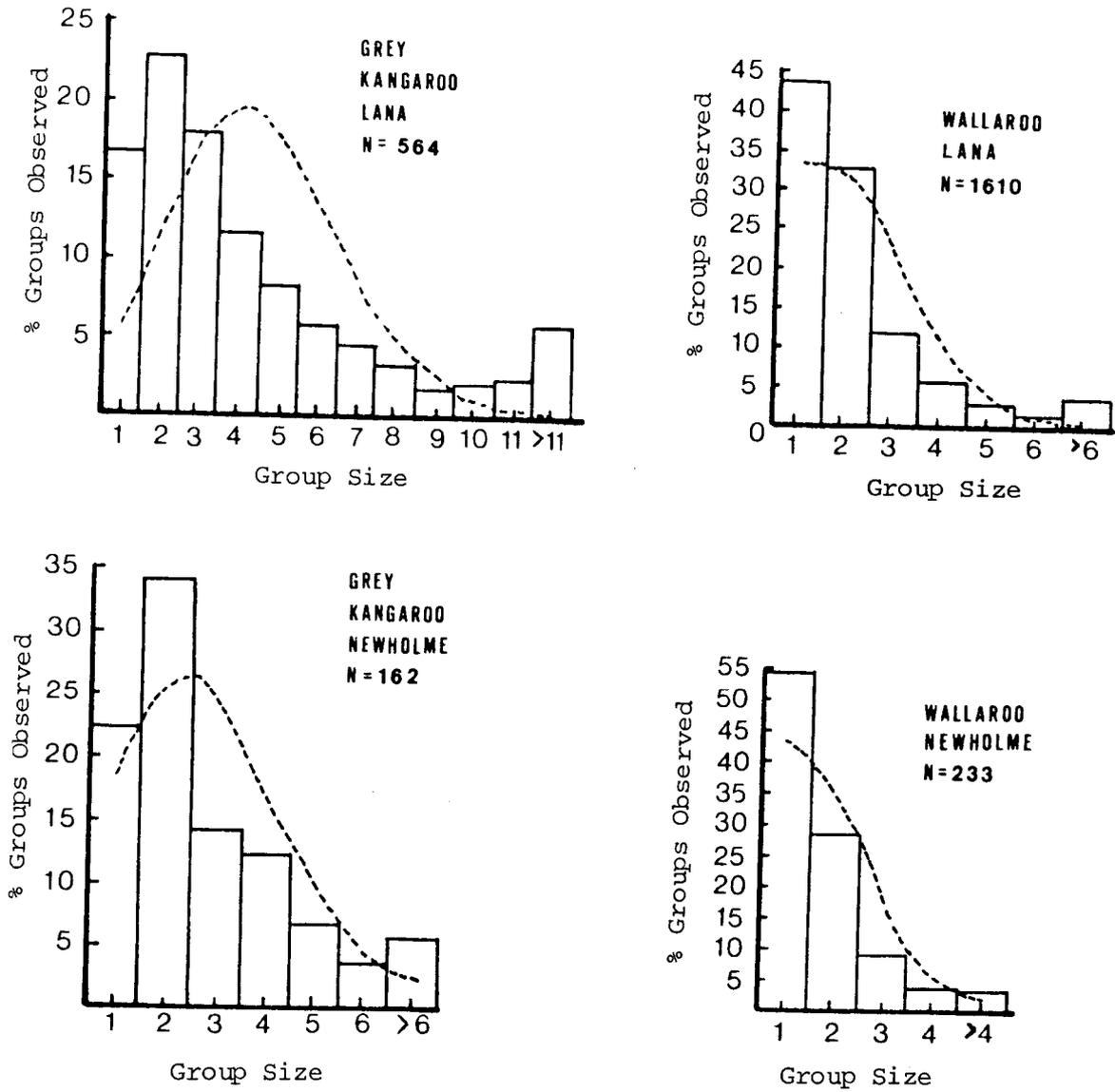


Fig. 9.4. Group size frequencies observed compared to those expected if group sizes are distributed randomly. ---- = distribution of group sizes expected from a truncated Poisson distribution.

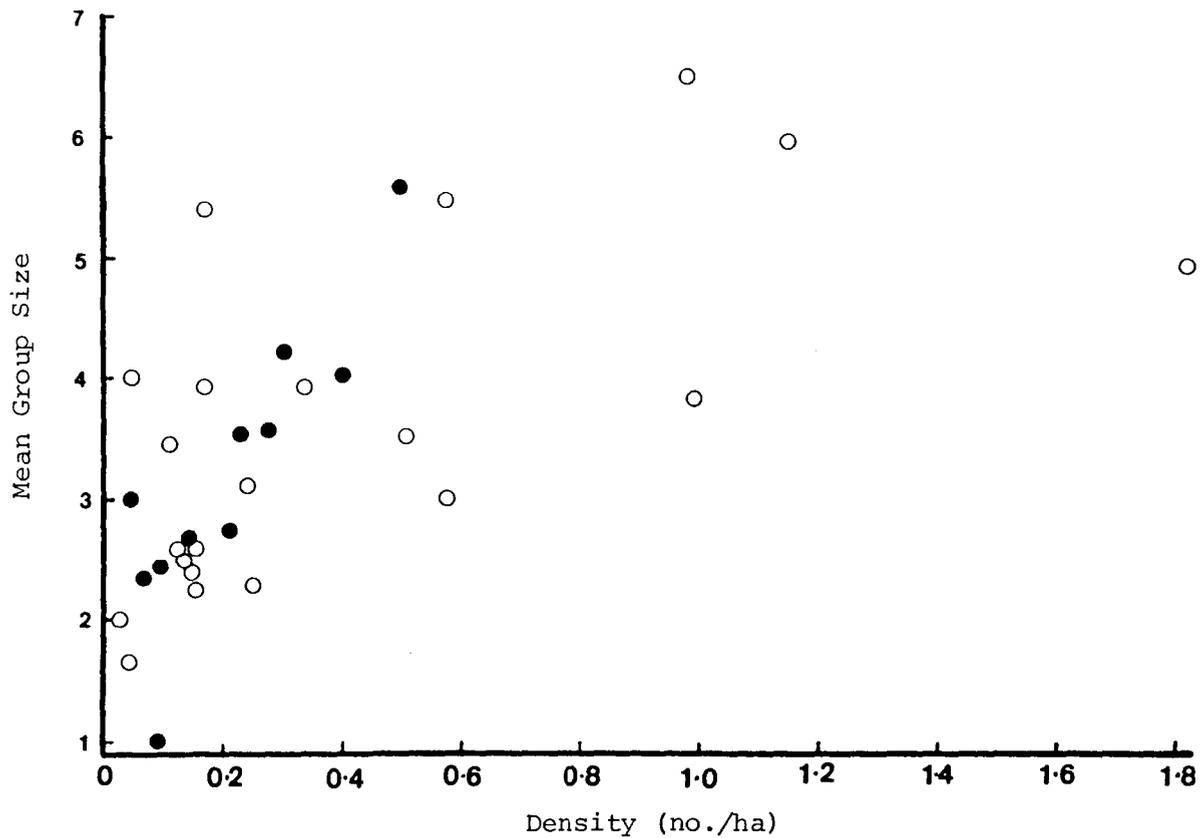


Fig. 9.5. Relationship between mean group size and density for the grey kangaroo.  $r = 0.64$  for all points;  $r = 0.85$  for feeding times on Lana.

● = Lana feeding times;

○ = All other time and property combinations.

For all points:  $Y = 2.05X + 2.76$

For Lana feeding periods:  $Y = 7.13X + 1.72$

where  $Y$  = mean group size  
and  $X$  = density

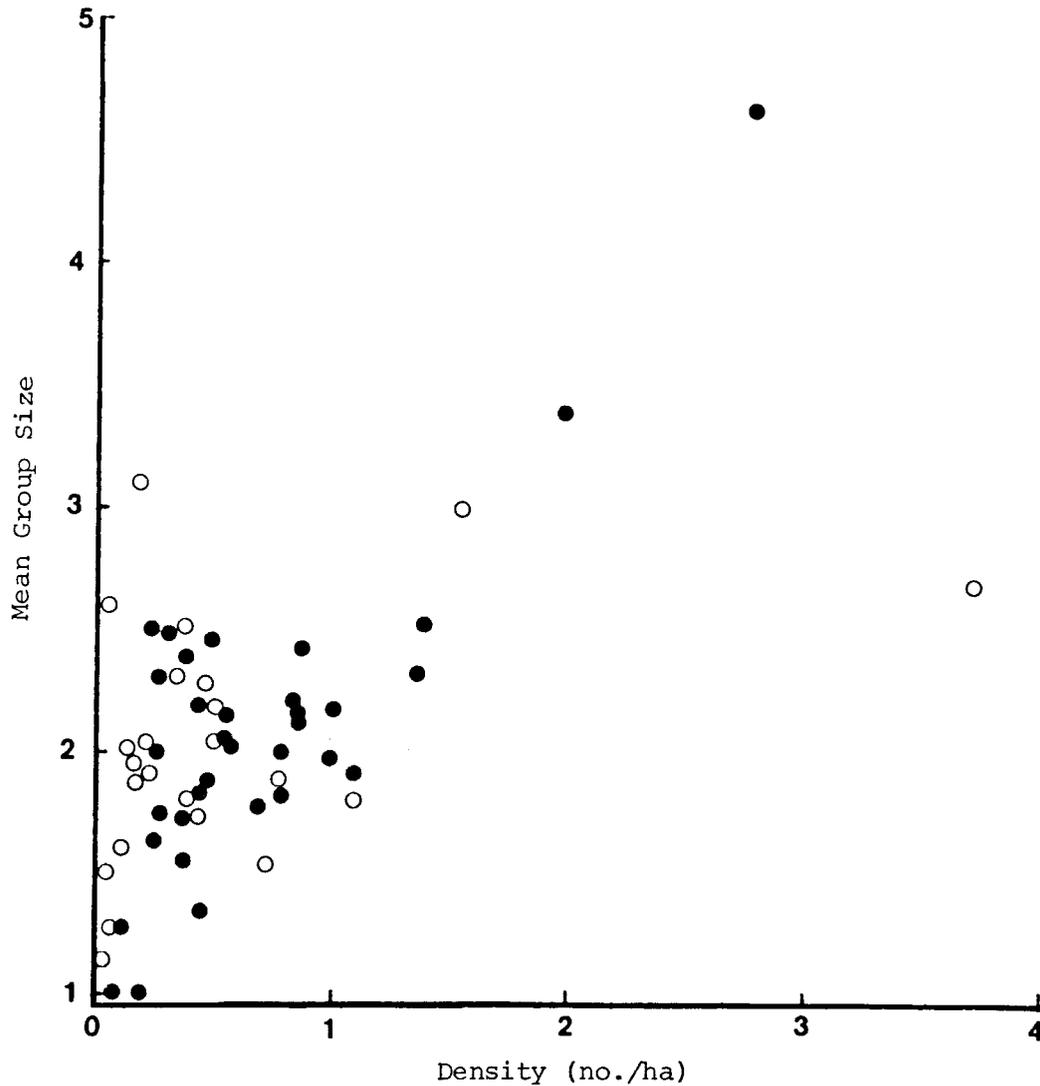


Fig. 9.6. Relationship between mean group size and density for wallaroo.  $r = 0.64$  for all points;  $r = 0.80$  for feeding times on Lana.

● = Lana feeding times;

○ = All other times and property combinations.

For all points:  $Y = 0.56X + 1.74$

For Lana feeding times:  $Y = 0.91X + 1.52$

where  $X$  = mean group size  
and  $Y$  = density

been shown to occur in whiptail wallaby (Kaufmann, 1974a) and western grey kangaroo (Johnson, 1979). Kaufmann considered changes in group size to result from individuals concentrating on areas of best forage during late winter and early spring. Pasture conditions remained fairly constant over Johnson's (1979) study and he considered that reproductive activity was influencing group size i.e. group sizes were largest when reproductive activity was least. Although it is possible that major changes in the distribution of forage for the two species in the present study did not occur, both species have seasonal peaks in their breeding (section 6.3). Thus changes in reproductive activity did not have any significant effect on the mean group size for either the grey kangaroo or wallaroo in the present study.

Although there were no seasonal trends in group size which could be related to changes in the distribution forage, it was obvious, at least for the wallaroo, that differences between areas in the distribution and abundance of food were influencing group size. Thus the largest wallaroo groups occurred in the small scattered sheep camps where wallaroo congregated to feed on the abundant high quality grasses present. Structural habitat features also influenced group size in wallaroo. Large wallaroo groups were sometimes found where small patches of favoured sheltering or resting habitat were found.

Mean group size was significantly correlated with density for both the grey kangaroo and wallaroo. Other workers have also found correlations between mean group size and density for some macropod species (e.g. Southwell (pers. comm.) for eastern grey kangaroo; Johnson (1979) for red kangaroo). However Johnson (1979) found no correlation between group size and density for the western grey kangaroo. Several factors would have been responsible for lowering the correlation between mean group size and density in the present study.

- (1) Too few groups were seen in some habitats at certain times to enable the calculation of an accurate mean group size. Thus several of the values for mean group size were based on the sighting of only two to five groups.
- (2) Differences in density existed within habitats. For the wallaroo on Lana, because of good sample sizes, most subhabitats could be separated and separate mean group sizes calculated. For the grey kangaroo too few sightings in most subhabitats meant that habitats had to be used as a basis of the density and mean group size estimates.
- (3) Changes in habitat use, and thus density within habitats, occurred over the course of a year (Chapter 5). Small sample sizes for most habitats necessitated grouping all seasons even

though densities may have differed between seasons. (4) Delineation of habitats was based on factors likely to affect abundance. These habitats were sometimes not suitable as units for the determination of the relationship between mean group size and density. This is seen most clearly for some of the very small sheep camp areas on Newholme. Here one animal could be present and thus a high density would be recorded (due to the small area of sheep camps) yet its chances of meeting other individuals and forming groups were probably the same as an individual occurring in other habitats with a lower density.

Mean group size was found to be lower on Newholme compared to Lana for both the wallaroo and grey kangaroo. Since the density of both grey kangaroo and wallaroo is lower on Newholme and it has been shown that mean group size is correlated with density, a lower mean group size for grey kangaroo and wallaroo on Newholme is to be expected. The higher density of animals on Lana may lead to the formation of larger groups due to the coalescence of smaller groups when they meet. Individuals should have a greater chance of meeting other animals when the density is greater. Food abundance and dispersion may also play a role in the formation of larger groups on Lana. Thus group size frequencies were only significantly different between Lana and Newholme during late afternoon, a time when kangaroos are most actively feeding. Although early morning is also a period of active feeding it is probably the case that most individuals spend a lower proportion of time feeding then compared with late afternoon (e.g. Osazuwa, 1978; Coulson, 1978; pers. obs.). Greater food abundance occurring in patches (i.e. sheep camp areas) on Lana may lead to formation of large groups due to the presence of many individuals on these small areas of abundant food. Visibility may also play a role in the formation of larger groups on Lana as the majority of feeding habitat on Lana (i.e. savanna woodland) is more open than the majority of areas used for feeding on Newholme. Higher visibility may lead to a greater rate of fusion of groups and enable better group co-ordination.

The mean group sizes that have been reported for the eastern grey kangaroo are 3.2 (Caughley, 1964b), 6.4 and 3.7 (Kaufmann, 1975), 3.9 (Bell, 1972), 2.5 (Southwell, 1976), 2.1 (Taylor, 1975) and 4.5 and 3.0 (present study). Mean group sizes found for *M. robustus* are 2.1 (Kaufmann, 1974b), 2.1 (Croft, 1981b), 1.4 (Russell and Richardson, 1971) and 2.2 and 1.8 (present study). It should be obvious from the above discussion that many factors influence the mean group size and hence differences in mean group size between studies should be expected.

On both Lana and Newholme the mean group size for grey kangaroo was greater than for wallaroo. More wallaroo are seen alone than for the grey kangaroo. Group composition is not fixed in either the grey kangaroo or wallaroo. However the two species differ in the short term cohesiveness of groups. The larger mean group size for grey kangaroo is probably related to the more open habitat which they inhabit. If groups of grey kangaroo are disturbed, in the vast majority of cases, all animals move off together in a co-ordinated manner. If a wallaroo group is disturbed, more often than not, individuals in the group will scatter in many directions and head independently, or in ones and twos, towards sheltering habitat. Co-ordination of group movement will not be possible in rocky habitat especially under conditions where animals are fleeing from a disturbance. Large wallaroo groups are mainly formed because of mutual attraction of animals to areas of favourable resources. Thus large wallaroo groups can be found in sheep camp areas where there is abundant high quality grass, or in favoured sheltering areas such as small dense rock slope at the top of hills. Although some large groups of wallaroo are found in favoured sheltering areas, the majority of the sites utilized for resting will accommodate fewer individuals than will the majority of sheltering sites used by grey kangaroo. Thus grey kangaroo utilize extensive woodland areas for shelter whereas wallaroo prefer certain sites among rock clumps or at the base of large rocks.

Both grey kangaroo and wallaroo have an alarm signal (a thump with their hind feet) which is reacted to by other individuals. Members of a group can thus benefit from increased predator detection in groups. Southwell (1976) has found that members of large groups of grey kangaroo spent considerably less time alert than members of smaller groups. Although few natural predators are present on the study areas, on Lana considerable human predation of grey kangaroo occurs and predation from dingoes will have been important in the past. Grey kangaroo which occur in open habitats are able to maintain group co-ordination when moving and can hence benefit from occurring in large groups by increased predator surveillance and possibly by being able to decrease the amount of time required by each individual to remain alert. Group formation as an anti-predator adaptation is also thought to occur in other mammalian herbivore species inhabiting open areas (e.g. Jarman, 1974; Estes, 1974). Wallaroo, although they can benefit from detection of predators by other individuals whilst in a group, are unable to maintain cohesion of large groups in most of their habitats. The predator avoidance behaviour of wallaroo is simply to reach suitable sheltering habitat as quickly as possible where, presumably, they are able to

outrun or escape predators because of the rugged terrain and their agility.

#### 9.4 WALLAROO GROUP COMPOSITION

##### 9.4.1 Introduction

Social classes of many mammalian species have been shown to associate together non-randomly. This non-random association may result from a preference of one social class to associate with members of its own social class or another social class. In the soay sheep, for example, in the non-breeding season rams occur in all-male groups and ewes and lambs occur in groups together (Grubb and Jewell, 1966). Non-random association of social classes may also result from individuals of one social class being forced from the company of another social class. Territorial male impala, for example, prevent bachelor males from associating with breeding females present in their territory (Jarman, 1979).

Since the suggestion by Caughley (1964b) that group formation in kangaroos was essentially a random process, many authors (e.g. Russell, 1979; Kaufmann, 1974a, 1975; Kirkpatrick, 1966) have commented on the association of adult females and young-at-foot and the brief association between adult males and oestrous females. However the association between other social classes of kangaroo has not been investigated to any great extent.

Data were gathered on the occurrence of social classes in groups in order to investigate the association between these classes. Only data on wallaroo were collected as grey kangaroo proved too difficult to classify as to social class while I was walking transects, where the first priority was to gather data on habitat use.

##### 9.4.2 Methods

Six wallaroo social classes were recognized. Classes within the same sex were differentiated by visual assessment of size and, in females, by the presence of pouch young or young-at-foot. Sex was readily determined by coat colour, males having much darker coats than females. The social classes recognized are:

- (1) Large adult males. These males were differentiated from other adult males by their muscular development of the

chest and forearms. Body weight was probably 40 kg or greater.

- (2) Medium adult males. These were sexually mature males obviously larger than adult females who had not attained the muscular development of forearms and chest to the same extent as a large adult male.
- (3) Sub-adult males. These were individuals usually less than the size of an adult female. This class would not have been sexually mature. Sub-adult males would probably have been from 1 to 2.5 years old.
- (4) Adult females. Sexually mature females who were not accompanied by a young-at-foot made up this category. The presence of a pouch young and/or size was used to distinguish adult females.
- (5) Adult females with young-at-foot were sexually mature females who were accompanied by young-at-foot.
- (6) Sub-adult females were sexually immature females obviously smaller than adult females. Sub-adult females were probably from one to two years old.

Young-at-foot made up a seventh social class. However, since they always occurred with their mother, their association with other individuals is based on the mother's preference for or avoidance of other social classes and hence they can be included with their mother. Some adult males were unable to be classified as either large or medium because of poor visibility. This was frequently the case with solitary individuals who fled before I could get a good look at them. Unless stated in the analysis these animals have been included with the medium adult male category. This will tend to lessen any differences which exist between large adult males and medium adult males so that if a difference is found between these two classes the probability of the difference being a real one is increased.

The analysis of group composition was carried out on only those groups for which all individuals were classified according to social class. Sixteen percent of groups on both Lana and Newholme contained unclassified individuals. A lot of the analysis comparing social classes was done on data from Lana only as Newholme sample sizes were usually too small for statistical analysis. Whenever group size is quoted in this section it refers to the group size when young-at-foot are excluded from the count of the number of individuals. This was

done because young-at-foot were always accompanied by an adult female and thus the adult female with a young-at-foot can be thought of as one unit.

#### 9.4.3 Results

##### (a) Association of social classes on Lana

The percentage of each social class seen alone on Lana is given in Table 9.7. Sub-adult males and sub-adult females were found alone least of all social classes. Adult females were found alone least of the adult classes. The percentage of large adult males seen alone was slightly higher than the percentage of medium adult males found alone but the difference is not statistically significant. Adult females with young-at-foot had the greatest percentage of individuals of any social class seen alone (i.e. with the adult female accompanied only by a young-at-foot).

Table 9.7 The percentage of each social class of wallaroo seen alone on Lana. The total number of sightings of individuals of each social class were for individuals seen in groups which were included in the analysis.

|                   | SOCIAL CLASS     |                   |                |              |                                 |                  |
|-------------------|------------------|-------------------|----------------|--------------|---------------------------------|------------------|
|                   | Large adult male | Medium adult male | Sub-adult male | Adult female | Adult female with young-at-foot | Sub-adult female |
| % Solitary        | 39.7             | 37.1              | 24.1           | 27.9         | 57.1                            | 17.7             |
| Total number seen | 247              | 483               | 352            | 792          | 343                             | 147              |

In order to investigate the association of social classes, the frequency of occurrence of dyads of each combination of social classes was examined. All groups were scored for the number of dyads of each combination of social classes present. For example, suppose we had a group containing two large adult males and three adult females. This would be scored as containing the following: one large adult male - large adult male dyad; six large adult male - adult female dyads; and three adult female - adult female dyads. The frequency of occurrence of each combination of social classes in dyads was compared to that expected if the composition of groups were a random selection from the population at large. Thus if social classes associate at random then, for example, the probability of sighting a large adult male and an

adult female in the same group is twice the probability that an individual sighted in a group is a large adult male multiplied by the probability that an individual sighted in a group is an adult female. The probability of sighting two large adult males in the same group is the probability than an individual sighted in a group is a large adult male multiplied by itself (i.e.  $p(\text{large adult male})^2$ ). The number of dyads of each combination of social classes expected, if association between the social classes is random, was obtained by multiplying the probability of occurrence of each dyad by the total number of dyads seen in all groups.

Since the percentage of individuals in each social class in groups of different size was not constant (Table 9.8), the association of social classes was examined in groups of different size. Association of social classes in groups of two and three was similar, as was the association of social classes in groups of 4 and >4, and so the similar group sizes were grouped.

Table 9.8 Percentage of individuals in each wallaroo social class for groups of different size on Lana.

| SOCIAL CLASS                    | GROUP SIZE |        |        |        |         |
|---------------------------------|------------|--------|--------|--------|---------|
|                                 | 1<br>%     | 2<br>% | 3<br>% | 4<br>% | >4<br>% |
| Large adult male                | 12.2       | 9.0    | 9.0    | 6.1    | 12.3    |
| Medium adult male               | 22.2       | 17.5   | 20.0   | 18.9   | 22.6    |
| Sub-adult male                  | 10.6       | 15.6   | 15.1   | 22.3   | 19.6    |
| Adult female                    | 27.5       | 38.9   | 36.2   | 38.5   | 32.4    |
| Adult female with young-at-foot | 24.3       | 11.8   | 9.9    | 5.4    | 6.5     |
| Sub-adult female                | 3.2        | 7.2    | 9.8    | 8.8    | 6.6     |
| Number of individuals           | 805        | 668    | 345    | 148    | 398     |

The significance of the difference between the number of dyads obtained to that expected for each combination of social classes is shown in Table 9.9 for small groups (i.e. 2 and 3) and in Table 9.10 for the larger groups (i.e.  $\geq 4$ ).

In small groups large adult males and medium adult males were found together significantly less than expected whereas in large groups they were found together significantly more than expected.

Table 9.9 Comparison of the frequency of occurrence of each combination of wallaroo social classes in dyads seen in group sizes of 2 and 3 on Lana to the frequency of each dyad expected (shown in brackets) if association between social classes is random. Total number of dyads seen in these groups was 679.

|                                 | SOCIAL CLASS     |                   |                |                 |                                 |                  |
|---------------------------------|------------------|-------------------|----------------|-----------------|---------------------------------|------------------|
|                                 | Large adult male | Medium adult male | Sub-adult male | Adult female    | Adult female with young-at-foot | Sub-adult female |
| Large adult male                | 7<br>(6.2)       | 15 *<br>(25.3)    | 12 *<br>(22.2) | 54<br>(47.6)    | 21 *<br>(12.2)                  | 6<br>(10.1)      |
| Medium adult male               |                  | 51 ***<br>(25.8)  | 29 *<br>(45.3) | 76 *<br>(97.0)  | 21<br>(25.0)                    | 12<br>(20.5)     |
| Sub-adult male                  |                  |                   | 24<br>(19.9)   | 62 *<br>(85.2)  | 36 **<br>(21.9)                 | 21<br>(18)       |
| Adult female                    |                  |                   |                | 110 *<br>(91.1) | 43<br>(46.9)                    | 55 **<br>(38.6)  |
| Adult female with young-at-foot |                  |                   |                |                 | 8<br>( 6.0)                     | 10<br>( 9.9)     |
| Sub-adult female                |                  |                   |                |                 |                                 | 6<br>( 4.1)      |

\*  $p < 0.05$

\*\*  $p < 0.01$

\*\*\*  $p < 0.001$

Table 9.10 Comparison of the frequency of occurrence of each dyad combination of wallaroo social classes seen in group sizes of four or greater on Lana to the frequency of each dyad expected (shown in brackets) if association between population classes is random. Total number of dyads seen in these groups was 1431.

|                                 | SOCIAL CLASS     |                   |                   |                  |                                 |                  |
|---------------------------------|------------------|-------------------|-------------------|------------------|---------------------------------|------------------|
|                                 | Large adult male | Medium adult male | Sub-adult male    | Adult female     | Adult female with young-at-foot | Sub-adult female |
| Large adult male                | 20<br>(13.1)     | 75 **<br>(53.4)   | 57<br>(46.8)      | 125 *<br>(100.2) | 18<br>(25.8)                    | 22<br>(21.2)     |
| Medium adult male               |                  | 78 **<br>(54.4)   | 134 ***<br>(95.5) | 197<br>(204.4)   | 39<br>(52.6)                    | 33<br>(43.3)     |
| Sub-adult male                  |                  |                   | 51<br>(41.9)      | 192<br>(179.5)   | 36<br>(46.2)                    | 41<br>(38.0)     |
| Adult female                    |                  |                   |                   | 175<br>(192.0)   | 53 ***<br>(98.9)                | 64<br>(81.4)     |
| Adult female with young-at-foot |                  |                   |                   |                  | 2 **<br>(12.7)                  | 15<br>(20.9)     |
| Sub-adult female                |                  |                   |                   |                  |                                 | 4<br>(8.6)       |

Large adult males and sub-adult males were found together significantly less than expected in small groups. In small groups large adult males were found with adult females with young-at-foot significantly more than expected. Medium adult males were found together significantly more than expected in both small and large groups. Medium adult males and sub-adult males were found together significantly more than expected in large groups and significantly less than expected in small groups. Medium adult males and adult females were found together significantly less than expected in small groups. Sub-adult females were found with adult females significantly more than expected in small groups whereas sub-adult males were found with adult females significantly less than expected in small groups. Sub-adult males were found with adult females with young-at-foot significantly more than expected in small groups. Adult females occurred together significantly more than expected in small groups. Adult females with young-at-foot were found with both adult females and other adult females with young-at-foot significantly less than expected in large groups.

(b) Association of social classes on Newholme

On Newholme 54.5% of all individuals seen were alone compared with 43.2% on Lana. The percentage of each social class seen alone on Newholme is given in Table 9.11. As on Lana adult females with young-at-foot were found alone to the greatest extent, adult females were found alone least of the adult classes, sub-adult males and females were found alone least often although the percentage of sub-adult males found alone is nearly the same as that for adult females. Of the two adult male classes medium adult males were found alone more often than large adult males.

Table 9.11 The percentage of each social class of wallaroo seen alone on Newholme. The total number of sightings of individuals of each social class were for individuals seen in groups which were included in the analysis.

|                   | SOCIAL CLASS     |                   |                |              |                                 |                  |
|-------------------|------------------|-------------------|----------------|--------------|---------------------------------|------------------|
|                   | Large adult male | Medium adult male | Sub-adult male | Adult female | Adult female with young-at-foot | Sub-adult female |
| % Solitary        | 48.9             | 57.6              | 32.0           | 32.8         | 77.8                            | 18.2             |
| Total number seen | 45               | 59                | 25             | 137          | 18                              | 22               |

This is the opposite of that found on Lana. However these figures are probably not strictly comparable because the percentage of unclassified adult males found alone was greater on Newholme (77.3%) than on Lana (49.2%). Although more animals were seen alone on Newholme, the increase in the percentage of each social class seen alone is not uniform. The increase in the percentage of each social class seen alone on Newholme compared to Lana is as follows: all adult males, 15.9%; sub-adult males, 7.9%; adult females, 4.9%; adult females with young-at-foot, 20.7%; and sub-adult females, 0.5%. Only adult males (both classes included) were found significantly more often alone on Newholme ( $\chi^2 = 9.6$ ,  $df = 1$ ,  $p < 0.01$ ). The increase in the percentage of adult females with young-at-foot seen alone on Newholme was close to being significant ( $p = 0.08$ ).

On Newholme most of the frequencies of occurrence of social classes in dyads were too small to test statistically for a difference from those expected if association was random. However the few which were able to be tested for statistical significance showed a similar pattern to that found for the association of social classes on Lana.

(c) Frequency of occurrence of social classes in different sized groups

The percentage of each social class found in each group size on Lana is given in Table 9.12. The only social classes which did not differ significantly in the pattern of their occurrence in groups were large adult males and medium adult males, and sub-adult males and sub-adult females. Both large adult males and medium adult males show a decrease in the percentage of individuals found in a group as one goes from the smallest to the largest group size. If uncategorized adult males are not included in the medium adult male category large adult males and medium adult males are still not significantly different. In contrast to other social classes, both sub-adult males and sub-adult females were found in groups of two more frequently than they were found alone.

Table 9.12 The percentage of each social class of wallaroo seen in each group size on Lana. Adult females and their young-at-foot were classified as one "individual" when determining group size.

| GROUP SIZE      | SOCIAL CLASS     |                   |                |              |                                 |                  |
|-----------------|------------------|-------------------|----------------|--------------|---------------------------------|------------------|
|                 | Large adult male | Medium adult male | Sub-adult male | Adult female | Adult female with young-at-foot | Sub-adult female |
|                 | %                | %                 | %              | %            | %                               | %                |
| 1               | 43.9             | 46.3              | 29.4           | 37.6         | 58.9                            | 19.0             |
| 2               | 25.7             | 23.8              | 32.2           | 34.4         | 22.5                            | 32.1             |
| 3               | 12.1             | 12.4              | 13.8           | 14.0         | 9.0                             | 23.3             |
| 4               | 3.6              | 5.2               | 7.3            | 4.9          | 2.1                             | 8.8              |
| 5               | 3.1              | 4.1               | 5.9            | 3.2          | 2.7                             | 6.6              |
| 6               | 4.5              | 3.9               | 4.9            | 2.2          | 2.7                             | 4.4              |
| 7               | 0.9              | 0.8               | 1.7            | 0.9          | 0.3                             | 1.5              |
| 8               | 3.1              | 1.3               | 2.4            | 1.2          | 0.6                             | 2.2              |
| 9               | 2.2              | 1.8               | 1.7            | 1.2          | 0.9                             | 1.4              |
| 12              | 0.5              | 0.2               | 0.4            | 0.2          | 0.3                             | 0                |
| 15              | 0.4              | 0.2               | 0.3            | 0.2          |                                 | 0.7              |
| No. of groups   | 223              | 387               | 289            | 587          | 333                             | 137              |
| Mean group size | 2.52             | 2.35              | 2.79           | 2.28         | 1.88                            | 2.99             |

(d) Habitat use by social classes

In order to investigate whether differences in habitat use between social classes could be influencing their association pattern, the proportion of individuals found in different habitats was compared for each pair of social classes. There were no significant differences between any social classes in the proportions seen in different habitats during feeding periods on Lana. The proportion of each social class in each habitat for sheltering periods on Lana is given in Table 9.13. Dense woodland and low-sight-distance slope were grouped for the analysis when the number of sightings for a social class was below five in either of these habitats. The only social classes which differed significantly in their distribution among habitats were large adult males and medium adult males ( $\chi^2 = 11.4$ ,  $df = 5$ ,  $p < 0.05$ ), and large adult males and adult females with young-at-foot ( $\chi^2 = 19.6$ ,  $df = 5$ ,  $p < 0.01$ ). The greatest contribution to the difference in habitat preferences for both these social class comparisons was the greater proportion of large adult males occurring in dense rock slope habitat.

Table 9.13 Percentage of each social class of wallaroo found in different habitat types on Lana during sheltering periods. Figures in brackets are the number of each social class seen in each habitat type.

| SOCIAL CLASS                    | HABITAT          |                |                     |              |                  |                          |              |
|---------------------------------|------------------|----------------|---------------------|--------------|------------------|--------------------------|--------------|
|                                 | Savanna woodland | Dense woodland | Large boulder slope | Rocky slope  | Dense rock slope | Low-sight-distance slope | Gentle slope |
| Large adult male                | 10.7<br>( 8)     | 5.3<br>( 4)    | 8.0<br>( 6)         | 24.0<br>(18) | 30.7<br>(23)     | 4.0<br>( 3)              | 17.3<br>(13) |
| Medium adult male               | 19.2<br>(20)     | 2.9<br>( 3)    | 17.3<br>(18)        | 28.8<br>(30) | 15.4<br>(16)     | 5.8<br>( 6)              | 10.6<br>(11) |
| Sub-adult male                  | 12.6<br>(12)     | 5.3<br>( 5)    | 12.6<br>(12)        | 33.7<br>(32) | 15.8<br>(15)     | 8.4<br>( 8)              | 11.6<br>(11) |
| Adult female                    | 17.2<br>(38)     | 5.4<br>(12)    | 12.2<br>(27)        | 24.5<br>(54) | 15.8<br>(35)     | 7.2<br>(16)              | 17.7<br>(39) |
| Adult female with young-at-foot | 19.4<br>(18)     | 11.8<br>(11)   | 12.9<br>(12)        | 21.5<br>(20) | 6.5<br>( 6)      | 6.4<br>( 6)              | 21.5<br>(20) |
| Sub-adult female                | 20.8<br>(10)     | 2.1<br>( 1)    | 12.5<br>( 6)        | 16.7<br>( 8) | 18.8<br>( 9)     | 12.5<br>( 6)             | 16.6<br>( 8) |

In order to examine habitat preferences of social classes on Newholme it was necessary to group habitats to increase sample sizes. Medium adult males and sub-adult males, and adult females and adult females with young-at-foot were also grouped for the statistical analysis. An overall  $\chi^2$  was used because of low frequencies. For feeding periods there were no significant differences in habitat preferences among social classes. The results for sheltering periods are shown in Table 9.14. The overall  $\chi^2$  for sheltering periods was significant ( $\chi^2 = 20.8$ ,  $df = 6$ ,  $p < 0.01$ ). The frequencies are too small to test for differences between pairs of social classes. However, it appears that medium adult males were found in dense rock areas less frequently than large adult males. Sub-adults may also be found in these areas less than large adult males although sample sizes are small. Adult females with young-at-foot were seen too few times to be able to comment on.

Table 9.14 Percentage of each social class of wallaroo found in different habitat types on Newholme during sheltering periods. Figures in brackets are the number of each social class seen in each habitat type.

| SOCIAL CLASS                    | HABITAT                                               |                                         |              |
|---------------------------------|-------------------------------------------------------|-----------------------------------------|--------------|
|                                 | <i>Poa costiniana</i> and <i>labillardieri</i> slopes | Dense rock and <i>Cymbopogon</i> slopes | Others       |
| Large adult male                | 28.6<br>(4)                                           | 50.0<br>(7)                             | 21.4<br>(3)  |
| Medium adult male               | 6.7<br>(1)                                            | 13.3<br>(2)                             | 80.0<br>(12) |
| Sub-adult male                  | 14.3<br>(1)                                           | 0<br>(0)                                | 85.7<br>(6)  |
| Adult female                    | 20.6<br>(13)                                          | 31.8<br>(20)                            | 47.6<br>(30) |
| Adult female with young-at-foot | 33.3<br>(1)                                           | 33.3<br>(1)                             | 33.4<br>(1)  |
| Sub-adult female                | 54.5<br>(6)                                           | 0<br>(0)                                | 45.5<br>(5)  |

#### 9.4.4 Discussion

It has been shown that wallaroo social classes do not associate at random. No permanent association of individuals (apart from the occurrence of young-at-foot with their mother), such as male-female pair bonding, or grouping of social classes, such as the presence of bachelor herds, was found. However, some social classes associated at frequencies different to that expected on the basis of random association. It therefore appears that social forces are present which influence the occurrence of animals in groups.

Large adult males were not found to occur alone to a greater extent than medium adult males. However this was probably due to unidentified adult males being included in the medium adult male category. Thus most of the unidentified males were seen alone and a proportion of these would have been large adult males. When unidentified adult males are excluded from the medium adult male category, 8.2% more large adult males on Lana and 3% more large adult males on Newholme were found alone compared to medium adult males on these areas. Croft (1981a,b) found in both the red kangaroo and euro that large adult males occurred alone more often than medium adult males. The high percentage of large adult males seen alone may result from a high rate of joining and leaving

groups in order to maximise their chances of encountering an oestrous female with which to mate. There was a significant increase in the percentage of adult males seen alone on Newholme compared with Lana. Because the density of wallaroo is lower on Newholme, adult males may have to spend more time moving between groups in their search for females and hence will be seen alone more often on Newholme.

Large adult males were found significantly more than expected with adult females with young-at-foot in small groups. A higher proportion of adult females with young-at-foot were found in small groups (31.5%) than in large groups (9.6%). Large adult males may associate with these adult females with young-at-foot more than expected due to their high probability of being in oestrus. Oestrus follows a day or two after the pouch young permanently leaves the pouch (Sharman and Calaby, 1964; Kirkpatrick, 1968). Adult females with young-at-foot in small groups may have younger young-at-foot than those in large groups (see below). Thus, unless there is a significant pouch young mortality, adult females with young-at-foot in small groups may be more likely to be in oestrus than other adult females. Croft (1981a) has found that in the red kangaroo males acted sexually towards females with young-at-foot more than would be expected from the time males were in dyads with adult females with young-at-foot as compared with adult females. Johnson (1979) also found that large male red kangaroo were seen with females with young-at-foot more than expected.

Large adult males were not seen with adult females with young-at-foot more than expected in large groups. Only 30% of adult females with young-at-foot seen in groups were in large groups (i.e. groups of four or more) on Lana. Adult females with young-at-foot may avoid occurring in large groups in order to minimise the possibility of separation from their young-at-foot (see below). Hence it is possible that adult females with young-at-foot in large groups will be those females with advanced young-at-foot. Older young-at-foot would be less likely to become separated from their mother and if they were to become separated they would have a greater chance of surviving than would younger animals. If adult females with young-at-foot in large groups were accompanied by older young-at-foot they would be unlikely to be close to oestrus and thus would not attract the attention of large adult males.

Large adult males were found significantly more often than expected with adult females in large groups but not in small groups. This strategy may maximise the number of adult females encountered by large adult males. Thus in large groups there are likely to be more adult females

present in the one group which large adult males can thus check for oestrus at the same time. It is also possible that there is a difference between adult females in small and large groups. For example, more adult females with large pouch young could be found in larger groups. These females would be more likely to be close to oestrus than would females with small pouch young. Johnson (1979) found for red kangaroo that females with large pouch young showed a greater preference for the greenest pasture than did females without large pouch young. Although no differences in habitat use were found for social classes during feeding periods in the present study, differences between females with different sized pouch young were not examined. If adult females with large pouch young did favour the greenest pasture this would mean a preference for sheep camps. The largest groups were found in sheep camps and hence (if in fact adult females with large pouch young do show a greater preference for the greenest pasture) adult females with large pouch young could be more likely to occur in larger groups than adult females with small pouch young.

Medium adult males were found together significantly more than expected in both small and large groups. In the euro Croft (1981b) found that medium adult males were sighted more often in single sex groups than other male classes. Croft (1981b) showed that medium adult males had the highest probability of acting agonistically towards another individual and that 89% of these interactions were with other medium adult males. Croft concluded that medium adult male association resulted from their engagement in ritualized fighting. This is probably the case but there may also be another factor influencing medium adult males to occur together in groups. If a medium adult male is found with another medium adult male when an oestrous female is encountered they may increase their chances of stopping the attendant large adult male from completing a successful copulation with the oestrous female. Medium adult males have never been observed to copulate with an oestrous female in the wild (e.g. Kaufmann, 1974a; Croft, 1981a,b). If a medium adult male were to discover a female approaching oestrus it is likely that he would be supplanted by a large adult male before oestrus occurred. Males appear to be able to tell when a female is approaching oestrus. Once a female nearing oestrus is discovered by a male he will form a consort relationship with her unless a larger male is present or until he is supplanted by another male. Croft (pers. comm.) has observed a succession of displacements by larger males of other males from the presence of a female red kangaroo approaching oestrus. Thus it is unlikely that a medium adult male would ever copulate with an oestrous female when large adult

males were present in the population. In order to maximise their chance of copulating with a female, the best strategy for a medium adult male would be to try to prevent a successful copulation by a large adult male. The female would then enter oestrus again later on when the medium adult male's chances of forming a consort relationship with her may be increased. Kaufmann (1974), Croft (1981a,b) and Osazuwa (1978) have all observed large adult males being harrassed by other males whilst in a consort relationship with a female approaching oestrus. Osazuwa (1978) has observed a consort male unable to complete a successful copulation due to the constant harrassment of other males around the oestrous female. He considered the male was so exhausted as to be unable to mount the female properly.

Medium adult males and sub-adult males, and large adult males and medium adult males, and large adult males and sub-adult males were all found together significantly less than expected in small groups. Thus in small groups males of different social classes appear to avoid occurring together. It is possible that larger males may be intolerant of smaller males. Croft (1981b) found in euros that large adult males directed agonistic behaviour towards medium adult males more frequently than expected on the basis of the proportion of time this dyad was observed. Medium adult males have been observed to flee from an approaching large adult male. Large adult males have been observed to purposely head towards any medium adult males involved in ritualized fighting. The medium adult males involved immediately broke off and ran from the approaching large adult male. The occurrence of medium adult males with adult females significantly less than expected in small groups may also be due to harrassment by large adult males. Thus a large adult male may purposely split up any groups of medium adult male and adult female which it encounters. In large groups large adult males and medium adult males, and medium adult males and sub-adult males were found together significantly more than expected. Large adult males and sub-adult males were also found together more than expected although not significantly so. In larger groups the presence of more individuals (especially adult females) may "distract" the larger male's attention away from the smaller males. Male social classes may be found together more than expected in large groups due to their attraction to the presence of females in a group rather than being an attraction to males of another class. On Lana 92% of large groups contained either an adult female or an adult female with young-at-foot and on Newholme all large groups contained an adult female or an adult female with young-at-foot.

Adult females were found together significantly more than expected in small groups. Geist (1971) has interpreted female grouping in bighorn sheep as an attempt by the females to minimise energy wastage by reducing interactions with males. Adult females were not found together more than expected in large groups. It may be that adult females rarely associate in groups of more than three. Large groups may be formed by other social classes joining these female groups. Large groups with more than three females may be formed when a number of these smaller groups of females are found together with other social classes because of the presence of favourable resources.

Adult females with young-at-foot were found to be the most solitary of all the social classes. Croft (1981a,b) also found that adult females with young-at-foot were the most solitary social class in the red kangaroo and euro. On Newholme adult females with young-at-foot had the greatest increase in the percentage of individuals found alone when compared to Lana. On Newholme where the density of wallaroo was lower, adult females with young-at-foot may have been better able to remain solitary. Croft (1981a) suggested that adult females with young-at-foot may prefer to remain alone so that the young-at-foot will not become separated from the mother during times of sudden alarm and flight. Data from the present study suggest that adult females with young-at-foot may avoid groups with other adult females (either with or without young-at-foot). Thus in large groups adult females with young-at-foot were found significantly less than expected with adult females and other adult females with young-at-foot. When present in groups adult females with young-at-foot were found significantly more often in groups with no other females than were adult females ( $\chi^2 = 6.9$ ,  $df = 1$ ,  $p < 0.01$ ). Adult females with young-at-foot may thus be avoiding groups so that their young-at-foot will not follow another female by mistake during times of flight. Since the sexes differ markedly in coat colour young-at-foot are probably able to distinguish females from males easily.

Sub-adult males and sub-adult females were found alone least of all social classes. Sub-adults may be more vulnerable to predation than other classes and it may be beneficial for them to occur with other animals to increase their chances of detecting predators. They may also benefit from association with adults because of the experience these animals have of the area. Adults may be better able to locate resources (i.e. food and shelter) and may be better able to react to temporal and spatial changes in resource levels. Sub-adult females are probably found alone less often than sub-adult males due to their association

with their mother. Thus sub-adult females were found significantly more than expected with adult females in small groups. Sub-adult males, however, were found significantly less than expected with adult females and significantly more than expected with adult females with young-at-foot in small groups. This difference in the pattern of association for male and female sub-adults may be related to males having been classified as sub-adults over a greater age range than were females. Thus, since sub-adult males were, on average, older than sub-adult females, they may be less likely to associate with their mother. It may also be advantageous for sub-adult males to associate with other social classes in order to gain as much social experience as possible. This may help the sub-adult male to attain a high social status when an adult. Whether the sub-adult males' association with adult females with young-at-foot is related to this gaining of social experience is not known.

The pattern of association of social classes was probably responsible for the differences in the frequency of different sized groups in which social classes were found. Large adult male and medium adult male were not significantly different in the frequency of different sized groups in which they were found. This is probably a result of both these classes leaving and joining groups to search for females in oestrus. Sub-adult females and sub-adult males were also not significantly different in the frequency of different sized groups in which they were found. Both these classes probably share a strong preference for the company of other animals and are thus found in groups far more often than they are found alone.

No differences in habitat preferences of social classes were found during feeding periods. However during sheltering periods medium adult males and adult females with young-at-foot were found less often in dense rock areas than were large adult males. This may be related to a preference for non-dense rock areas by medium adult males and adult females with young-at-foot in comparison to large adult males. It is also possible that medium adult males and adult females with young-at-foot are harrassed by large adult males and choose to leave (or not to enter) these dense rock areas because of the presence of large adult males. I think the latter is more likely. Dense rock areas, especially on Lana, occur as small patches at the top of rocky hills. These areas have been shown (Chapter 5) to be favoured sheltering habitat for the wallaroo population. Since these areas are small it would be relatively easy for large adult males to harrass any other individual which occurred

there. Evidence has already been presented to show that large adult males are intolerant of medium adult males. Adult females with young-at-foot may avoid or leave dense rock areas to escape constant sexual checking by large adult males.

Group composition in the wallaroo appears to be a result of a complex of interacting association preferences and intolerances between social classes. These association tendencies also influence the group sizes in which each social class is found. The level of intolerance shown by larger males towards smaller males may also be influenced by the size of the group and the presence or absence of adult females. Habitat also appears to play a role in determining the extent to which these intolerances influence the occurrence of social classes together.

#### 9.5 WALLAROO POPULATION COMPOSITION

The proportions of each social class seen during feeding periods was used as an index of the percentage of these classes found in the population. Animals seen when sheltering were not included as it was shown that some social classes exhibited differences in habitat preferences during these periods (see section 9.4.3(d)). During feeding periods animals were most likely to be active and in more open areas and thus more visible than when sheltering. The number of animals seen in each social class on Lana and Newholme is shown in Table 9.15.

Table 9.15 The number of individuals of different social classes seen on Lana and Newholme during feeding periods.

| AREA     | SOCIAL CLASS |                |              |                  |
|----------|--------------|----------------|--------------|------------------|
|          | Adult male   | Sub-adult male | Adult female | Sub-adult female |
| Lana     | 551          | 257            | 819          | 99               |
| Newholme | 75           | 18             | 89           | 11               |

Both adult male classes were grouped because of some adult males being unclassified as to size. Also the adult female and adult female with young-at-foot categories were grouped as it has already been shown (Chapter 6) that a greater proportion of adult females were accompanied by young-at-foot on Lana. The ratio of sub-adults to adults for females was not significantly different on the two areas but the male sub-adult

to adult ratio was ( $\chi^2 = 6.1, df = 1, p < 0.05$ ). There were more adult males in relation to sub-adult males occurring on Newholme than on Lana. There are two possible ways this could result. Sub-adult male survival rates may be lower on Newholme or adult male survival rates may be higher on Newholme. Sub-adult males are unlikely to have higher survival rates than sub-adult females. The sub-adult female to adult female ratio is similar on the two areas so that it is more likely that the adult male survival rate is higher on Newholme. There are more sub-adult males than sub-adult females on both areas. This is probably due to my having classified males as sub-adults over a greater age range than females were classified as sub-adults.

Geist (1971) examined survival rates of male bighorn sheep in what he termed "high quality" and "low quality" populations. High quality populations were vigorous, expanding populations with abundant food resources. Geist (1971) found that, although lamb mortality was higher in low quality populations, adult male survival was greater in low quality populations than in high quality populations. Adult males from high quality populations had vigorous growth and reached their ultimate proportions early. They fought extensively during the breeding season and often returned exhausted from the rut. Adult males from low quality populations grew and matured slowly. They interacted with other males far less than males in high quality populations.

Both Newsome (1977), for the red kangaroo, and Johnson (1979), for the red and western grey kangaroo, have found the adult sex ratio to be biased in favour of females. Newsome's (1977) study was conducted on a population which had been harvested and thus shooting pressure on large males could have led to the differences in mortality rates between males and females. However, the populations in Johnson's (1979) study had been protected from shooting for the previous ten years. A bias in the adult sex ratio in favour of females was also found on both areas in the present study but especially so on Lana. Neither wallaroo population had been subjected to harvesting. Thus, as in bighorn sheep, it may be the case that males have higher mortality rates than females because of the stress brought about by competition between males for females. A higher density of males on Lana, may lead to higher levels of competition between males. Higher levels of competition may lead to higher mortality rates among large adult males who must defend oestrous females from many other males. Ritualized fighting between medium adult male and courting of oestrous females by large adult males with many attendant males present was observed many times on Lana but

never observed on Newholme. However, the average age of males above 2.5 years of age in a shot sample obtained on Lana and Newholme was similar (Lana, 6.8 years, N = 8; Newholme, 7.5 years, N = 7), thus showing little evidence of a higher mortality of adult males on Lana. However a larger sample size may be needed to accurately assess the mean age of adult males on the two properties. Quantitative data are also needed on the level of competition between males in order to investigate the hypothesis, of higher adult male mortality on Lana, further.

## CHAPTER 10

RELATIONSHIP BETWEEN THE BEHAVIOURAL ECOLOGY OF  
THE GREY KANGAROO AND WALLAROO AND THEIR  
STATUS AS AGRICULTURAL PESTS

Because of the wallaroo's need for rocky hills as shelter and their reluctance to feed far from these sheltering areas, the area of woodland and/or grassland available to the wallaroo as feeding habitat is dependant on the amount of interface between these feeding areas and the sheltering areas. Grey kangaroo, on the other hand, are not dependant on rocky hills and will be present on all areas used for stock grazing as long as the tree density has not been reduced below a critical minimum required to satisfy their shelting requirements. Because of these differences in habitat requirements, grey kangaroo are present on far more properties in the New England area than are wallaroo. As a result far more permits are issued to landholders to enable culling of grey kangaroo than are issued for the culling of wallaroo in the New England region.

However, although these differences in habitat requirements are responsible for some of the differences in the perceived pest status of the two kangaroo species, differences in the behaviour of the two species also appears to influence landholders' awareness of the degree of competition between the two species and their domestic stock. Grey kangaroo are much more visible to landholders than are wallaroo. Thus large groups of grey kangaroo can be seen on Lana if one wanders around through the paddocks during the day. However few wallaroo are seen because of their sheltering in rocky hills. Landholders are usually unaware of the size of wallaroo populations on their properties because of this tendency of wallaroo to occur in rocky hills during times when landholders are most likely to be moving around their properties. Also, during late afternoon when wallaroo are feeding they are also less conspicuous than grey kangaroo because of their occurrence in smaller groups and their presence only around the base of rocky hills. Moreover, damage done by wallaroo is often mistakenly blamed on grey kangaroo. An example of this occurred with the landholder on Lana. I was showing the owner of Lana some figures for the number of grey kangaroo and wallaroo seen on each of my transects. On one of the transects the number of wallaroo seen was large in comparison to the number of grey kangaroo. The owner commented that he was surprised I had seen so few grey kangaroo in that transect as he had recently examined some areas

around the base of hills on part of the transect and had noticed the grass was heavily grazed and that many kangaroo pellets were present. Thus he appeared to be blaming the grey kangaroo for the damage, yet my observations had shown that wallaroo were found frequently in the areas he had mentioned and that grey kangaroo were there only rarely.

The owner of Lana was also frequently commenting on the large number of grey kangaroo on his property and the need to have them culled. He never mentioned that wallaroo numbers were high or that there was a need to reduce wallaroo numbers also. In fact grey kangaroo were culled regularly yet wallaroo were never requested to be included in the kangaroo harvesting on Lana. However when I placed new collars on the kangaroos I was able to use the percentage of animals in the population that were collared to estimate the total numbers of grey kangaroo and wallaroo on part of my study area. At that time I estimated 161 grey kangaroo and 243 wallaroo to be present. These estimates were made less than one week after the animals were collared and so movement of grey kangaroo off Lana will not have affected the results greatly (see section 9.1). Because of the low percentage of the population that was collared (15.5% of grey kangaroo and 7.0% of wallaroo), these estimates will not be extremely accurate (see Robson and Regier 1964). However, it is highly probable that there were, at the least, as many wallaroo present as there were grey kangaroo.

The kangaroo harvesting technique used in the New England area (and over most of Australia) is to shoot kangaroos at night from a vehicle with the aid of a spotlight. This technique will also probably be responsible for lowering the number of wallaroo harvested compared to grey kangaroo. It is usual for professional shooters to harvest kangaroos for the property owner. The shooters will thus be interested in gaining the most kangaroos they can in the quickest possible time and in the easiest way. During the summer, when I obtained the services of a professional shooter to collect a sample of wallaroo, it took us from 8 p.m. until about 2 a.m. to obtain five wallaroo. This was not because wallaroo were not abundant but simply because, as it was summer and good quality grass was abundant, the wallaroo had finished feeding early in the night and had returned to the rocky hills where they were inaccessible to the vehicle and to being spotlighted. In winter it was much easier to obtain the wallaroo as they fed in woodland areas out from rocky hills a lot longer during the night. Grey kangaroo were easily collected during all seasons because of their presence in accessible and open habitats. Hence if a professional shooter is working on a property

where there are many wallaroo and the owner has a permit to cull them then it is still likely that the shooter will collect grey kangaroo preferentially and only harvest wallaroo on an opportunistic basis as this is the easiest and quickest way for them to operate. Shooters are likely to avoid driving around close to the bases of rocky hills, where their chances of encountering wallaroo are increased, because of the difficult terrain here (e.g., presence of rocks, uneven surface).

Thus three factors are probably primarily responsible for the grey kangaroo being harvested as a pest species to a greater extent than wallaroo. These are:

- (1) Different habitat requirements lead to grey kangaroo being present on larger areas of stock grazing country than are wallaroo;
- (2) Differences in group size and visibility in pasture areas lead to differences in the perceived pest status of the two species by the grazier; and
- (3) Grey kangaroo are more easily commercially harvested than are wallaroo.

## CHAPTER 11

COMPARISON OF THE ECOLOGY OF  
THE EASTERN GREY KANGAROO AND WALLAROO

Many of the previous studies on the ecology of macropodids have been detailed examinations of a single species (e.g. Ealey, 1962; Frith, 1964; Newsome, 1965a,b; Holsworth, 1967; Inns, 1980). Studies which have compared species occurring sympatrically have concentrated on one aspect of their ecology and have not considered overall community structure and organization (e.g. Caughley, 1964a; Ellis *et al.*, 1977; Griffiths and Barker, 1966; Kaufmann, 1974b). There are some cases where ecological separation in macropod communities is obviously based on differences in diet. For example, grey kangaroos and swamp wallabies (*Wallabia bicolor*) coexist in many areas in eastern Australia; grey kangaroos are grazers and swamp wallabies are browsers (Taylor, 1975). The distribution of the eastern grey kangaroo and wallaroo overlaps over much of eastern Australia. These two species are similar in size and morphology and are both grazers (Kirkpatrick, 1965a, 1968). The present study was undertaken to examine in detail the ecological relationship between the grey kangaroo and wallaroo in an area of sympatry.

The study was conducted on two areas in the New England Tablelands which differed in the quality of food present and where eastern grey kangaroos and wallaroos occurred sympatrically. An intensive study of diet, habitat use, condition and nutritional status of kangaroos was carried out over the course of a complete seasonal cycle of pasture growth. Limited data on reproduction and social organization were also collected.

Ecological separation of broadly sympatric herbivore species can be based on the use of different habitats, or parts of a habitat, for feeding (e.g. Batcheler, 1960) or the use of different plant species or plant parts within the same area (e.g. Gwynne and Bell, 1968) or a combination of these. The design of the present study allowed an examination of the role of differences in dietary and habitat preferences in determining ecological separation of the grey kangaroo and wallaroo over the full range of seasonal changes in food abundance and in areas differing markedly in the quality of food present. A comparison of the ecology of the two species also allowed an examination of the role of ecological factors in determining social

organization and reproductive strategies.

The feeding strategy of the two species was very similar. Thus the diet of both species contained a large proportion of grass in all seasons (page 90). Grass species differed in their protein and fibre content. Low-fibre grasses contained higher levels of protein than did tussock grasses or high-fibre grasses (Table 3.9). Both species selected for low-fibre grasses and selected leaf in preference to other plant parts (Figs. 4.3 and 4.4). Both species responded to a drop in the availability of good quality grass by increasing the proportion of the lower quality tussock grasses in the diet (Fig. 4.2). Thus there was a higher proportion of tussock grasses in the diet of both species in autumn and winter than in summer and spring and for kangaroos on the unimproved property compared with those on the improved property. Thus the species responded similarly when faced with changes in food quality and abundance with different seasons or properties. The majority of the populations of both species remained within limited home ranges (Sect. 9.2). An increase in long distance movement did not occur in response to a deterioration in food quality (Sect. 9.1). Instead, both species changed their pattern of habitat use with season in response to changing patterns of relative occurrence of preferred food items (pages 116-122). For both species the greatest availability of good quality food occurred in summer (Table 3.3 and page 48). For both species protein content of food in the stomachs was highest in summer and lowest in autumn (Table 7.1) and body condition was, in general, highest in summer and lowest in winter (Sect. 7.3.2). The majority of young of both species emerged from the pouch during spring and summer (Sect. 6.3). Although the distribution of births per month differed for the two species (Figs. 6.5 and 6.6), differences in the length of pouch life (Kirkpatrick, 1965b) ensure that pouch young of both species emerge around the time of maximum availability of good quality food.

Differences in the dietary and habitat preferences of the grey kangaroo and wallaroo are listed in Table 11.1. Two factors are primarily responsible for determining these differences: (1) the differential response of the two species to high quality plants and *Microlaena* in particular; and (2) differences in the preferences of the two species for rocky hills. It was hypothesized in the introduction (page 4) that, all else being equal, the greatest use should be made of the highest quality pasture. This appears to be the case for the wallaroo but not the grey kangaroo. *Microlaena*, shown by chemical

Table 11.1 Summary of the differences in the dietary and habitat preferences of the grey kangaroo and wallaroo.

|                                                                                   | Wallaroo                                                                                                                                                                                                                                                                                                                                         | Grey kangaroo                                                                                                                                                                                                                                                                                                                                                                                                         |
|-----------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| DIET                                                                              | <i>Microlaena</i> important component                                                                                                                                                                                                                                                                                                            | <i>Microlaena</i> less important; <i>Sporobolus</i> and <i>Eragrostis</i> have equivalent importance of <i>Microlaena</i> to wallaroo                                                                                                                                                                                                                                                                                 |
|                                                                                   | Legumes increase in importance in spring compared with winter                                                                                                                                                                                                                                                                                    | No increase in importance of legumes in spring compared with winter                                                                                                                                                                                                                                                                                                                                                   |
| HABITAT USE                                                                       |                                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                                                                                                                                                                                                                                                                                       |
| (A) Shelter preferences                                                           | Areas with dense rock at top of hills preferred                                                                                                                                                                                                                                                                                                  | Avoid steep rocky hills; in other areas prefer dense woodland or areas with low visibility                                                                                                                                                                                                                                                                                                                            |
| (B) Factors governing distribution during feeding periods, in order of importance | <ol style="list-style-type: none"> <li>1. Areas over 200 m from rocky hills not used</li> <li>2. Feeding areas on or adjacent to favoured sheltering sites preferred</li> <li>3. Higher use of areas with higher quality plants especially if <i>Microlaena</i></li> <li>4. Use increases with increase in biomass of low-fibre grass</li> </ol> | <ol style="list-style-type: none"> <li>1. Steep rocky slope avoided</li> <li>2. Treeless areas over 200 m from woodland not used</li> <li>3. Use increases with increase in biomass of low-fibre grass</li> <li>4. Quality and species of grass: Some areas of high quality grass (i.e. sown pasture) used preferentially. Areas with <i>Microlaena</i>, although of high quality, not used preferentially</li> </ol> |

analysis to be one of the highest quality grasses (Table 3.4), occurred in dense clumps in sheep camp areas. The diet of wallaroos contained more *Microlaena* than did the diet of grey kangaroos (Table 4.1). Wallaroos also utilized *Microlaena* pasture to a greater extent than predicted on the basis of the biomass of low-fibre grass present whereas grey kangaroos did not (Figs. 5.15 and 5.18). Also, the density of wallaroos in areas of high quality pasture in sown pasture areas was four times greater than in areas of normal pasture whereas the density of grey kangaroos in sown pasture was only twice that in normal pasture (Tables 5.4 and 5.8). There was no significant difference between the density of kangaroos per unit biomass of low-fibre grass for the two species on the unimproved property (page 145). However wallaroos did achieve a significantly higher density for a given biomass of low-fibre grass on the improved property (page 145). However, in order to confirm this finding, the densities of the two species per unit of biomass of low-fibre grass need to be remeasured on an improved pasture area where culling does not occur as it does for grey kangaroos on Lana. Note that the prediction is not for a greater density of wallaroos than grey kangaroos on areas of improved pasture but that the density of wallaroos per unit of biomass of low-fibre grass during feeding periods will be greater than for grey kangaroos. If the area used by grey kangaroos has a higher average biomass of low-fibre grass than the area used by wallaroos a higher density of grey kangaroos could result.

Differences in the importance of high-quality plants in the diet of the two kangaroo species also influenced the timing of changes in habitat use with changes in seasonal pasture conditions (Figs. 5.7 and 5.8, pages 118-120). Thus grey kangaroos increased their use of *Microlaena* pasture in winter (July, August), when there was a shortage of good quality food, compared with summer but wallaroos maintained a high use of these areas in both seasons. Wallaroos increased their use of savanna woodland in spring compared with winter to a much greater extent than did grey kangaroos. This was thought to be due to wallaroos seeking the high quality legumes present in this habitat in spring. The diet of wallaroos contained a higher proportion of legumes in spring than did the diet of grey kangaroos (Fig. 4.2).

However differences in the use by the two species of rocky hills appear to be more important than dietary preferences in influencing differences in the way the two species are distributed over the study areas and minimizing the areas shared during feeding

periods. Grey kangaroos avoided steep rocky slopes and open pasture areas more than approximately 200 metres from woodland (Sect.5.3.1(a) and 5.3.2.(a)). Wallaroos, on the other hand, were rarely seen more than 200 metres from the rocky hills (page 114). Wallaroos therefore tended to have exclusive use of the steeper slopes and grey kangaroos tended to have exclusive use of woodland areas more than 200 metres from rocky hills. The main overlap in the distribution of the two species occurred in woodland areas around the bases of the rocky hills. Even within these areas where overlap occurred the two species differed in their distribution pattern. Thus in woodland the density of wallaroos was greatest in areas of frequent rock whereas the opposite was true for grey kangaroos (Tables 5.4 and 5.8). The density of wallaroos was also greatest on areas of gentle slope which had steeper slope above whereas grey kangaroos showed no such preference (Tables 5.4 and 5.8).

Ecological factors have been shown to be important determinants of social organization (e.g. Jarman, 1974; Clutton-Brock and Harvey, 1977). Although only a small amount of data was gathered on the social organization of the grey kangaroo and wallaroo it appears that differences in the ecology of the two species have been accompanied by the evolution of differences in their social organization. It was hypothesized (page 241) that both species would be sedentary because of the predictability of rainfall. This proved to be true for the majority of individuals of both species (Sect. 9.2). However a small percentage of the grey kangaroo population were found to undertake long distance dispersal (Sect. 9.1). These differences were thought to be due to differences in selection for individuals to disperse because of differences in the type of areas utilized by the two species (page 246). Areas suitable for wallaroos (i.e. rocky hills) are more discontinuously and unevenly distributed in comparison with woodland areas required by grey kangaroos. Much of the woodland utilized by grey kangaroos consists of disclimax communities which become unsuitable for use if not managed (Taylor, 1981). For the grey kangaroo the chances of an individual which disperses finding suitable habitat which is below the carrying capacity is probably greater than for the wallaroo.

The grey kangaroo and wallaroo were found to differ in the spatial organization of individuals' home ranges. Wallaroos occurred in independent overlapping home ranges whereas groups of grey kangaroos appeared to share a "mob" home range (Sect. 9.2). Differential

patterns of dispersion of resources was thought to have lead to the evolution of these differences between the two species (Sect. 9.2.4). Highly favoured sheltering and feeding sites for the wallaroo are widely dispersed and densely distributed whereas resources for the grey kangaroo are more evenly distributed throughout their range. Clumped, widely distributed resources do not favour the formation of monopolized areas (e.g. Brown, 1964; Geist, 1974). There is probably selection against formation of mobs in the wallaroo but not in the grey kangaroo. A smaller average group size for wallaroos compared with grey kangaroos was thought to result from differences in the areas utilized by the two species (Sect. 9.3). The more open habitat of the grey kangaroo allows group co-ordination and better predator surveillance. The rocky hills which wallaroos inhabit do not allow sustained cohesion of groups. Predator avoidance by the wallaroos depends on maintaining easy access to the rocky hills where the rugged terrain and an individual's agility can be used to escape predators.

From this comparison of the grey kangaroo and wallaroo it appears that differences in the habitat preferences of the two species have been the major evolutionary factor influencing the differences in their ecology and social organization. The home ranges of wallaroos are based around rocky hills. Feeding is limited to areas with access to the hills but preference is shown for small areas of high quality pasture scattered over and around these hills. Large groups of wallaroos can be found in areas with abundant food but when disturbed these groups scatter and disperse into rocky habitat. Grey kangaroos inhabit areas that are more open than those preferred by wallaroos. They avoid the rocky hills and do not occur in areas more than 200 metres from woodland. Although grey kangaroos prefer grasses with a low-fibre content, they are less selective for quality than are wallaroos and depend on the more abundant species to a greater extent. The open habitat of the grey kangaroo allows co-ordination between individuals and grey kangaroos form larger, more stable groups than do wallaroos.