

CHAPTER ONE

Introduction

1.1 General

Although Darwin was deeply interested in ecology and the social behaviour of animals, it has only been during the last two decades that a general theory of the evolutionary ecology of social behaviour has begun to take shape. The grounds for this theory were laid with the acceptance by most biologists of the view that evolution within species is mediated primarily by natural selection acting at the level of the individual, rather than at the higher levels of the group or the population. According to this view, changes in gene frequencies within populations are driven by heritable variations in the reproductive fortunes of individuals, or of groups of genetically related individuals. This Darwinian first principle has been advocated, and the consequences of it explored, by Hamilton (e.g. 1964, 1975), Williams (1966), Maynard Smith (e.g. 1964, 1982), Trivers (1972), Dawkins (1982a, b) and others. Because the adaptive values of social behaviours have often been explained in terms of their presumed benefits to groups or populations (see Wynne-Edwards 1962), this shift in focus from groups to individuals has had a profound influence on the development of thinking on the evolution of social behaviour.

The theory has grown as workers in the field have tried to understand the part ecological circumstances play in the evolution of social organisations, and it is now thought that two fundamental relationships lie within the entanglement of ecology and social behaviour. Firstly, the distribution, abundance and nature of a species' resources and the threats of predation determine, in large measure, the dispersion and grouping of species members, and, secondly, the dispersion and grouping of species-mates controls the formation and importance of the competitive or cooperative strategies

that individuals adopt in order to enhance their reproductive success (see Jarman 1974, Wilson 1975, Emlen and Oring 1977, Clutton-Brock and Harvey 1978, Wrangham 1982).

Although the simplicity of this distinction is marred by the observation in some species, and possibility in many others, that the reproductive strategies of individuals may influence the dispersion and grouping typical of their species, the conceptual framework it provides has been particularly helpful to our growing understanding of the origins of the various mating systems found in animals. Emlen and Oring (1977) have presented a coherent theoretical account of how ecological constraints set the ways in which some members of the available sex (usually males) are able to control the access of others to members of the limiting sex (usually females): generally speaking, males compete for access to females by means appropriate to the dispersions and grouping of females, which in turn are largely set by the females' resource ecologies and their responses to the risks of predation. In African antelope, for example, the females of small species which feed on widely-spaced and rare food items (such as new leaves of perennial shrubs) and hide from predators are usually evenly dispersed and solitary; males of these species are, in consequence, able to monopolise only one mate at a time, and they set up lifetime territories, each of which encompasses the range of a single female. In larger species, the females of which feed on abundant food items (grasses which grow in large swards) and form groups to evade predation, some males can, by excluding other males from patches of habitat used heavily by females, monopolise many mates and thereby beget a disproportionately large share of the next generation (Jarman 1974). A wide range of variations on this theme is analysed by Emlen and Oring (1977) so that, although the effects of some factors, such as mate choice by females, on the distribution of reproductive success among males, are as yet dimly understood (see Bateson 1983), we have a clear view of the ecology of male reproductive strategies and inter-male variation in reproductive success in animals.

The effects of social behaviour on reproductive success have been given less attention for females than for males. This may be because males compete directly for mates more often than females do, and such

competition may take flamboyant forms, while females' strategies for rearing young may require prolonged observation to distinguish. In addition to this, variations in reproductive success amongst females can often be easily seen to have an ecological basis, and the possibility that some ecological determinants of reproductive success might be socially mediated has tended to be overlooked. However, reproductive competition between females is certainly strong in some species (see Wasser 1983) and females may sometimes compete more intensely than males. African wild dogs *Lycaon pictus*, for example, live in packs of a dominant breeding pair, several subordinate males, and a lesser number of subordinate females. Both members of the dominant pair try, although they do not always succeed, to suppress mating by subordinates of their own sex; in addition to this, however, if a subordinate female does manage to breed, the dominant female will usually prevent the provisioning of her pups by other pack members (Frame *et al.* 1979).

Because the reproductive strategies, competitive or cooperative, of females have often been neglected, we still have no general set of hypotheses to predict how ecological circumstances will determine their occurrence, their form, and their effect in producing variations between individual females in reproductive success. The righting of this imbalance in our knowledge of males and females must begin with field studies which give equal attention to inter-individual variation in reproduction and its causes in both sexes.

I have tried to do this for red-necked wallabies *Macropus rufogriseus banksianus* (Desmarest 1817), and in this thesis I analyse some aspects of their ecology, describe their social organisation, and show how the participation by individual males and females in reproduction varies according to their social behaviour. The remainder of this opening chapter introduces the macropodoids in general, and the red-necked wallaby in particular. Chapter two describes my study area at Wallaby Creek, and the methods of study used. Chapter three describes the distributions and home ranges of red-necked wallabies at Wallaby Creek at different seasons, shows how classes of the population differ in their use of habitat, and documents some effects of habitat on the reproductive performance of

females. Chapter four analyses variability in the sizes of groups of wallabies and suggests how this variability may be related to changes in the quality and dispersion of their food. Chapter five analyses seasonality of breeding and its causes. Chapters six and seven follow the relationships between mothers and young from birth to the dispersal of sons and the reproductive maturity of daughters; they compare the relationships between mothers and infants with those observed in ungulates, and show how the continued association between mothers and adult daughters results in the formation of extended matrilineal social groups among females. Chapters eight and nine, describing reproductive competition between males, and courtship behaviour, show how interactions between males lead to differences between them in reproductive success and indicate the role of female behaviour in influencing the extent of this variation and the kinds of strategies that males may adopt. Chapter ten analyses variations in the reproductive success of females in relation to their social organisation, and makes a specific examination of the costs to adult females of sharing their home ranges with close relatives. Chapter eleven, the final discussion, draws some general conclusions from the details of the preceding chapters, and compares them with the results of studies of other species of mammals. Two appendices describe survivorship and mortality, especially of infants, and analyse sex ratios of pouch young.

The Macropodoidea

The super-family Macropodoidea - the kangaroos, wallabies and rat-kangaroos ('macropods' for convenience) - is the most diverse and widely spread of the major marsupial groups. Fifty-eight species of macropods are known from recent times (Kirsch and Calaby 1977, Seebeck and Johnston 1980, Maynes 1982). They vary in size from the tiny musky rat-kangaroo *Hypsiprymnodon moschatus*, weighing only half a kilogram, to the red kangaroo *Macropus rufus*, whose males may approach 100 kilograms; and live in all of the major habitat types of Australia and New Guinea, from sub-alpine woodland to arid grassland.

The earliest known fossil macropods are from the Miocene, and they suggest a possum, or possum-like, ancestor (Archer 1981). These early

macropods were small browsers, but with the general drying of the Australian continent over the following epochs and the replacement of the moist forests which had covered much of the land by dry forests, savannas and grasslands (Galloway and Kemp 1981), the macropods increased in size and number, and adaptations for grazing appeared (Archer 1981, Bartholomai 1978, Sanson 1978). The modern species of Australian macropods fall into three groups, loosely defined on the basis of size and geographical distribution. Most of the species weigh less than 10 kilograms, and macropods of this size class occur in nearly all Australian environments. This group is represented in wetter areas by some of the rat kangaroos (*Bettongia*, *Fotorous*, *Aepyprymnus*, *Hypsiprymnodon*), pademelons (*Thylogale*), some rock wallabies (*Peradorcas*, *Petrogale*), the quokka (*Setonix brachyurus*) and tree kangaroos (*Dendrolagus*), while in arid and semi-arid regions are found other rat kangaroos (*Bettongia*, *Caloprymnus*), hare wallabies (*Lagorchestes*, *Lagostrophus*) and nail-tailed wallabies (*Onychogalea*) and some other rock wallabies (*Petrogale*). Medium-sized species, of 10 to 20 kilograms adult weight - the 'typical' wallabies (*Wallabia*, and the smaller members of the genus *Macropus*) - are restricted to the forested periphery of the continent, while species of greater than 20 kg (the remaining *Macropus*, the kangaroos) are found almost everywhere in Australia.

Among the small species of macropods are some very specialized feeders. The musky rat-kangaroo, for example, feeds on fruits and invertebrates (Johnson and Strahan 1982) and the brush-tailed bettong *Bettongia penicillata* mostly eats underground fungi (Christensen 1980). Most of the other rat-kangaroos and small wallabies also prefer foods high in nutritive quality and low in fibre content (see Storr 1964, Redenbach 1982). The large kangaroos feed on a broad range of grasses and forbs, but most are predominantly grazers (Taylor 1983, Ellis *et al.* 1977), eating foods relatively high in fibre and low in nutritive quality. The intermediate forest wallabies are probably more selective feeders than the larger kangaroos, but all are browsers and/or grazers (swamp wallabies *Wallabia bicolor* for example are browsers (Harrington 1976), while black striped wallabies *Macropus dorsalis* feed mainly on grasses (P. Tierney, *pers. comm.*)).

The tendency for larger species of macropods to feed less selectively on foods of lower quality is paralleled by exaggerations of sexual dimorphism and gregariousness with increasing body size : most small macropods are monomorphic, but among the kangaroos some males may be more than twice as heavy as females; and, as Table 1.1 illustrates, average group sizes tend to be greater in the larger species (data on group sizes are not available for many of the very small species within which groups may be difficult to define or recognise, but, with the possible exceptions of a few species such as burrowing bettongs *B. lasueur* (Wood Jones 1924, Stoddart 1966) and banded hare wallabies *Lagostrophus fasciatus* (Prince 1983) and the fact that rock wallabies often occur in loose colonies, the very small macropods appear to be generally asocial.

The red-necked wallaby is one of the middle-sized forest wallabies, and stands mid-way along many of the continua that characterise the adaptive radiation of the macropods.

1.3 The red-necked wallaby

Like other forest wallabies, red-necks are lightly built and agile, although they are rather more dumpy than whiptail and agile wallabies. Males are more heavily built than females, grow larger and develop thickly muscled forearms and shoulders - females have remarkably fine arms and shoulders, and usually have delicate faces. These wallabies vary in colour, from a dusky, almost chocolate grey in some individuals to a rich nankeen in others. Most have rufous patches on their necks, shoulders and rumps, grizzled grey backs, white bellies and chests, rufous forearms, and black paws and feet. Face colouring varies widely between individuals, but many have reddish muzzles and greyish foreheads, and all have a white stripe along each cheek (see Plate 3).

Like most other macropods, they have been only patchily studied : the following sections bring together knowledge of relevance to this thesis.

1.3.1 Taxonomy, distribution and habitat preferences. Red-necked wallabies are found in a belt of forest that spans 20° of latitude in



Fig. 1.1 Distribution in Australia of the red-necked wallaby, with the location of my study area.

eastern Australia (see Fig. 1.1); in the north of this range the wallabies experience an equatorial climate, influenced by the monsoonal weather patterns of further north, and in the southern extreme of their range they face cold, often freezing winters. The taxonomic status of the species has recently been reviewed by Johnston and Sharman (1979), who recommend dividing it into two sub-species: *M.r. rufogriseus* in Tasmania and the Bass Strait islands, and *M.r. banksianus* on the mainland. There is little electrophoretic, chromosomal or morphometric variation between these two sub-species, but they differ in pelage (*M. r. rufogriseus* has a longer, darker grey coat) and breeding biology, (see below). *M.r. rufogriseus* is usually referred to as Bennett's wallaby, while the name red-necked wallaby refers to the mainland sub-species, or to the species group as a whole.

Red-necked wallabies live in various types of wooded country, but avoid wet forests and very dense thickets (Calaby 1966, Green 1974); they are generally found in greatest numbers near openings in forest where herbs and grasses are abundant. In Tasmania, Bennett's wallabies are replaced in dense closed forests by red-bellied pademelons *Thylogale billardierii* (Hocking and Guiler 1983), and on the mainland by swamp wallabies and black-striped wallabies, while in open vegetation types they are replaced by eastern grey kangaroos, whiptail wallabies and (while they survived) toolache wallabies *M. greyi*. In the north of Australia, the habitat type used by red-necked wallabies is occupied by agile wallabies.

Bennett's wallabies have been introduced into New Zealand, and a population now occupies a large tract of land in the South Island, in and around the Hunter's Hills (Gilmore 1977, Catt 1977). Small populations of Bennett's wallabies, probably founded by escapees from menageries, have become established in two parts of England (Gilmore 1977, Yalden and Hosey 1971).

1.3.2 Ecology and behaviour. Unfortunately, no systematic study of the diet of Australian *M. rufogriseus* has been published, but the plants eaten by the feral Bennett's wallabies in the Peak District of England have been determined by faecal pellet analysis (Yalden and

Hosey 1971). The bulk of the food eaten by these wallabies was made up of heather *Calluna vulgaris*, and a grass *Molinia caerulea* was the next most important component of the diet. Heather was most important in winter, and *Molinia* increased in importance in summer. Other plants eaten, in descending order of their proportional contribution to the total volume of the diet, were pine *Pinus sylvestris*, bilberry *Vaccinium myrtillus*, bracken *Pteridium aquilinum*, a grass *Festuca ovina* and birch *Betula verrucosa*. Wodzicki (1950, cited in Gilmore 1977) reported that Bennet's wallabies in New Zealand eat various grasses and sedges, bracken *Pteridium esculentum* and the leaves of some trees, as well as crops and market vegetables. Red-necked wallabies at Wallaby Creek fed most often on grasses and forbs that had been kept short and growing by the grazing pressure of macropods and cattle. They ate native species (e.g. narrow-leaved carpet grass *Axonopus affinis*) as well as introduced pasture plants (e.g. clovers *Trifolium* spp.), and were attracted to cultivated paddocks planted with fodder crops, such as lucerne *Medicago* spp., particularly during winter when the uncultivated pastures had usually ceased growing. They avoided long, rank grasses, but would eat the inflorescences and seeds of grasses in late summer, and occasionally took the leaves of some woody shrubs. All of these observations suggest the red-necked wallaby to be a mixed feeder, taking browse as well as grass, but preferring plant parts low in fibre and high in nitrogen. In diet choice and feeding style, they are probably intermediate between browsers like the swamp wallaby and grazers such as the black-striped wallaby and eastern grey kangaroo.

M. rufogriseus feeds most actively during the late afternoon, night and early morning. Clarke (1984) showed that at Whipsnade Park near London feeding activity was maintained through the entire night. In the Grampians in western Victoria, Coulson (1978) reported the red-necked wallaby to be more diurnally active than either the eastern or western grey kangaroo. Coulson's results suggest that the wallabies are crepuscular and that activity wanes during the night, but his results are open to several interpretations because he inferred activity cycles from frequencies of sightings of animals, rather than from direct observations of behaviour.

The social behaviour of captive Bennett's wallabies has been recorded by LaFollette (1971) and Morboeck (1979). LaFollette documented consistent dominance relationships between individuals in both sexes, and showed that dominance reversals could be induced among males by removing a dominant male for a time, then placing him back with the other wallabies.

1.3.3 Breeding biology. The major difference between the breeding biologies of the two sub-species of the red-necked wallaby is in the seasonality of breeding. Most Bennett's wallabies are born in late summer and autumn, and none are born during spring and summer (Merchant and Calaby 1981, J.C. Merchant pers. comm., Catt 1977, Fleming et al. 1983), while on the mainland the wallabies may give birth at any time of the year, although birth frequencies may vary significantly from month to month : at Bonalbo in northern New South Wales more females give birth in late spring and summer than in winter (J.C. Merchant pers. comm.). This difference persists even if animals of the two sub-species are maintained in captivity under identical conditions (Merchant and Calaby 1981).

Breeding cycles of the two sub-species are in other ways similar (Merchant and Calaby 1981). A single young is born after a 30 day gestation; the oestrous cycle lasts 33 days. Birth is closely followed by mating and the embryo thus conceived enters quiescence until after the permanent emergence, or loss, of the young from the pouch. In most macropods with this type of breeding pattern, birth follows permanent emergence of the pouch young by only a day or two, but in red-necked wallabies, 16 to 29 days may elapse between vacation of the pouch by one young and the birth and entry to the pouch of another. In Bennett's wallabies, blastocysts remain quiescent throughout the non-breeding season regardless of the presence or absence of a pouch young. Pouch life normally lasts nine or nine and a half months, so that on the mainland females may give birth once every ten months but the seasonal pattern of breeding in Bennett's wallabies allows females only one young every twelve months.

Females may reach sexual maturity at 14 months of age, males at 19 months (Catt 1977, Merchant and Calaby 1981).

1.3.4 Growth and sexual dimorphism. Growth curves have been constructed for the New Zealand population (Catt 1981) and for a population in the Warwick district of south-east Queensland (see Fig. 1.2; the data were recorded by T.H. Kirkpatrick in the late 1950's and early 1960's, and lodged in the Queensland Museum, from where they were collected by P.J. Jarman, pers. comm.). Females grow to asymptotic weights of 10-12 kg, at three or four years of age, and vary little about this asymptote. Males, however, continue to grow until at least seven years of age, and do not approach any concise asymptotic weight; the body weights of mature males vary widely, some are not much larger than females, while others may be twice the asymptotic female weight. There is no evidence of a latitudinal trend in body size or sexual dimorphism.

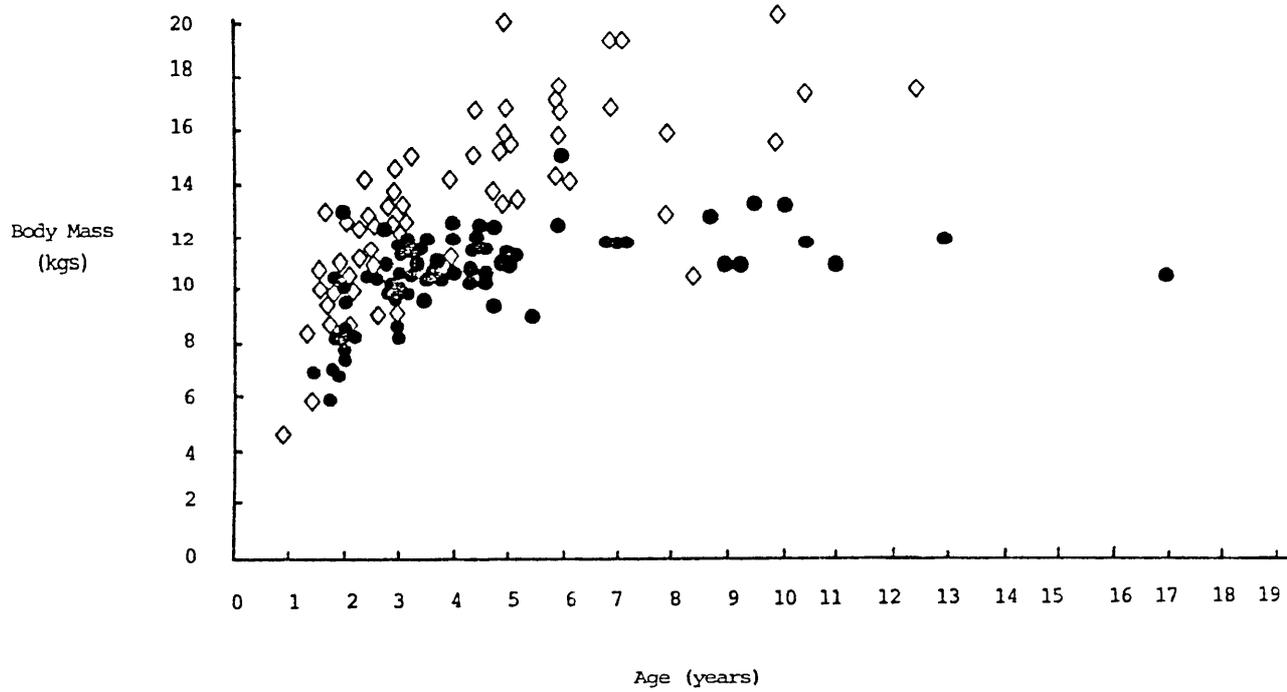


Fig 1.2 Body growth of male(◇) and female(●) red-necked wallabies.

TABLE 1.1: Mean group sizes in various species of macropods. Body weights are approximate averages of adult male and female weights, taken from Strahan (1983)

Species	Body mass (kg)	Mean group size	Source
Rufous bettong, <i>Aepyprymnus rufescens</i>	3.0	1.27	Southgate (1980)
Parma wallaby, <i>Macropus parma</i>	4.5	1.34	Maynes (1977)
Red-legged pademelon, <i>Thylogale stigmatica</i>	4.7	1.46	Personal observation
Black-striped wallaby, <i>M. dorsalis</i>	12.0	4.30	Personal observation
Whiptail wallaby, <i>M. parryi</i>	13.0	6.00	Kaufmann (1974a)
Swamp wallaby, <i>Wallabia bicolor</i>	15.0	1.10	Kaufmann (1974b)
Agile wallaby, <i>M. agilis</i>	15.0	1.51	P.M. Johnson (1980)
Red-necked wallaby, <i>M. rufogriseus</i>	15.0	1.24 - 1.82	This study, Chapter 4
Antilopine wallaroo, <i>M. antilopinus</i>	25.0	4.50 2.50	Croft (1982) Russell and Richardson (1971)
Eastern wallaroo, <i>M. r. robustus</i>	30.0	1.79 - 2.17	Taylor (1982a)
Euro, <i>M. r. erubescens</i>	30.0	2.10	Croft (1981b)
Eastern grey kangaroo, <i>M. giganteus</i>	35.0	3.70 1.75-10.45	Kaufmann (1974b) Southwell (1984a)
Western grey kangaroo, <i>M. fuliginosus</i>	35.0	2.00 - 3.10	Johnson (1983)
Red kangaroo, <i>M. rufus</i>	40.0	2.20 2.60 2.40	Croft (1981a) Johnson (1983) Caughley (1964)



Plate 1. Dry sclerophyll forest to the west of Wallaby Creek.



Plate 2. Pasture and woodland to the east of Wallaby Creek.

CHAPTER TWO

Materials and Methods

2.1 The study area

2.1.1 Locality, topography and soils. The small narrow valley of Wallaby Creek ($28^{\circ} 29'S$, $152^{\circ} 27'E$; 460 m. a.s.l.) lies in the northern headwaters of the Clarence River, on the eastern fall of the Great Dividing Range. My study area includes 216 ha. of the alluvial flats and lower slopes of this valley (see Fig. 2.1). This area is dissected by a number of intermittently flowing gullies which join Wallaby Creek, and is bordered to the north by Wild Cattle Creek, a semi-perennial stream. Wallaby Creek is a perennial stream, but because of the small area of its catchment and the steepness of the higher slopes of the valley, the volume of water it carries varies widely, and it may flood abruptly after heavy storms. The area is underlain mainly by Mesozoic sedimentary rocks, which have given rise to yellow podzolic soils of fair to poor quality on the valley slopes; rich alluvial flats up to 200 m wide lie on either side of the creek.

2.1.2 Climate and weather. Wallaby Creek is in a climatic zone classified as 'equatorial' by Walther and Leith (1967) because its winters are mild and some rain falls in every month of the year. Rainfall is unevenly distributed throughout the year, however : more rain falls in summer than in winter. The line depicting mean monthly rainfall over the past 37 years in Fig. 2.2 shows this variation to be approximately four-fold. The mean annual rainfall over this period has been 1006 mm. Monthly volumes of rainfall over the three years of data collecting for this study and the preceeding year deviated from the average pattern in a number of ways : 1980 was an unusually dry year, except for one very wet month; the winters of 1981 and 1982 were

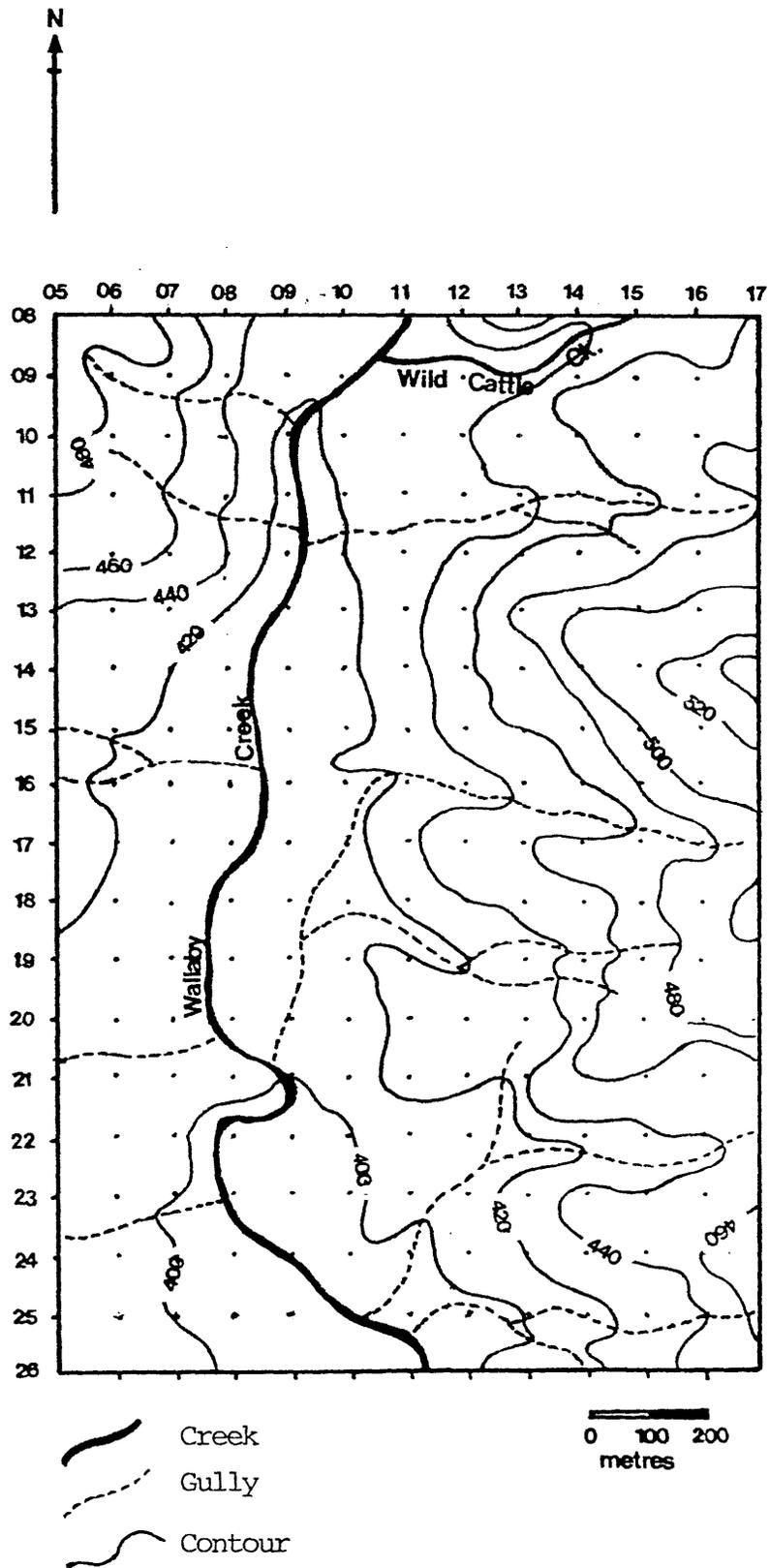


Fig. 2.1 Topographic map of the study area; elevations in metres. Each point represents an intersection of grid lines.

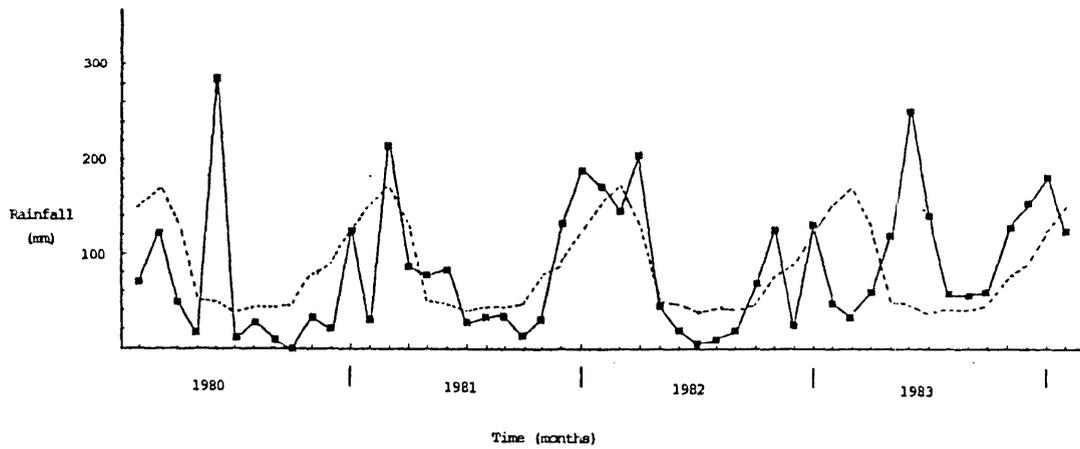


Fig. 2.2 Monthly rainfall at Wallaby Creek (solid line shows rainfall over the study period, dashed line is the long-term average trend).

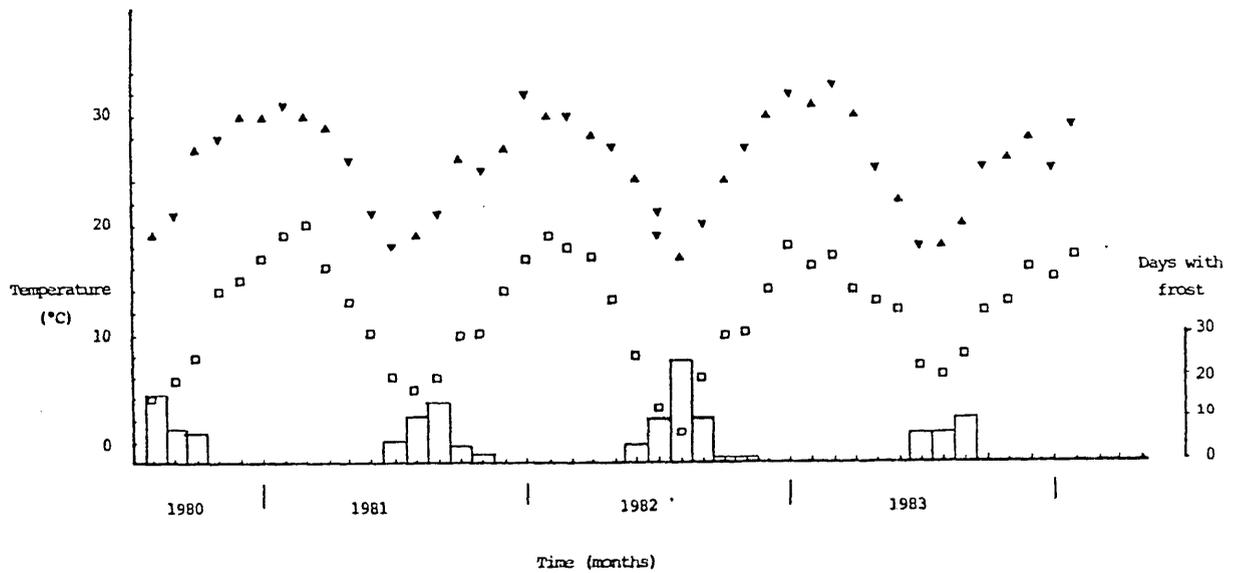


Fig.2.3 Mean daily maximum(\blacktriangle) and minimum(\square) temperatures for each month of the study period, with monthly frost-fall(bars).

also dry, as was the summer of 1982/83, but heavy rains fell through the remainder of 1983.

Mean monthly maximum temperatures may reach 33°C in late summer, and mean monthly minima may drop as low as 1°C in winter (Fig. 2.3). The summers of 1981/82 and 1982/83 were both more than usually warm, the winter of 1982 was relatively cold and the following winter was unusually mild. The first frosts usually fall in May or June, the last frosts in September or October. More frosts fell in the cold winter of 1982 (24 in that July) than in any of the other years.

Apart from the contrasts between winter and summer conditions, seasons at Wallaby Creek are rather ill-defined. There is no distinct autumn, and spring is characterised by a steady easing of winter temperatures and increase in rainfall, rather than an abrupt transformation of the weather. In making seasonal comparisons, therefore, I have either divided the year into two six-month periods, the 'summer months' (November to April) and the 'winter months' (May to October), or compared peak summer and winter conditions by looking only at shorter three or four month periods within those two halves of the year.

Day-length varies from approximately 10.5 hours in June to 14.5 hours in January (I recorded times of dawn and dusk in the field each month, and defined the timing of light changes by my ability to see and recognise wallabies).

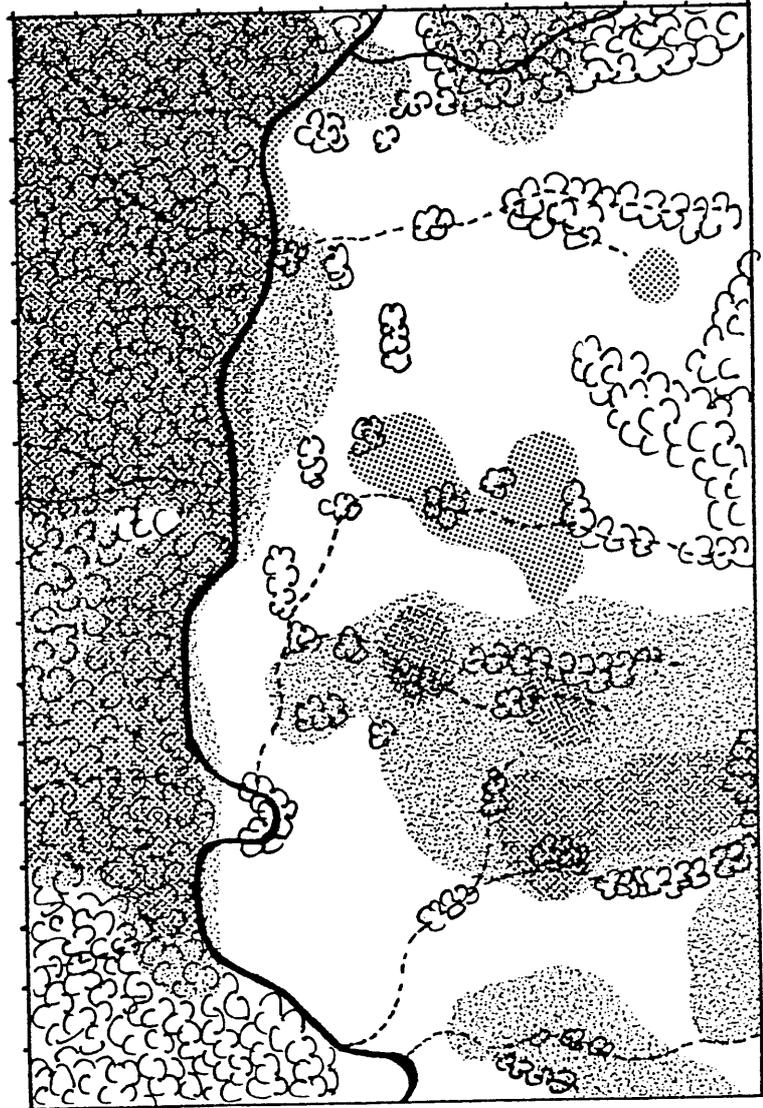
2.1.3 Vegetation. The valley was originally completely covered by forest, but patchy clearing of trees by European settlers has left a mosaic of native and introduced pastures, small and large stands of trees, and large tracts of relatively undisturbed forest. The valley contains three major forest types : rainforest, wet sclerophyll forest and dry sclerophyll forest. Most of the forest in my study area is of the dry sclerophyll type, although wet sclerophyll and rainforest elements occur in some places, particularly in gullies and along Wallaby Creek. Dominant tree species are forest red gum *Eucalyptus tereticornis*, rough-barked apple *Angophora floribunda* and forest oak *Casuarina torulosa*, with grey ironbark *E. decrepta*, narrow-leaved mahogany *E. acmenioides*, grey gum *E. propinqua*, Dunn's white gum *E.*

dunni and silky oak *Grevilia robusta* also being important. The most common rainforest tree in this part of the valley is Brush box *Tristania conferta* which grows in many of the gullies to the east of the creek. Ground vegetation in the forest includes thick swards of bladey grass *Imperata cylindrica* and kangaroo grass *Themeda australis* on flat or gently sloping areas; swamp foxtail *Pennisetum alopecaroides* and *Lomandra* sp. close to the creek; and tangled growths of *Lomandra* sp., various shrubs, creepers and ferns on steeper slopes and in the gullies. Some of the gullies are choked with lantana *Lantana camara*.

The pastures on the cleared parts of the study area are composed of both native and introduced species; natives tend to predominate on the slopes, introduced species on the flats, which have been cultivated from time to time. The most widespread palatable native grasses are narrow-leaved carpet grass and kangaroo grass, with which grow a variety of short forbs and other grasses. *Poa* tussocks and bladey grass also grow in many places, especially on steep slopes and in gullies, and may form dense beds: both of these grasses grow to a metre or more in height, and, when mature are unpalatable to wallabies. Beds of swamp foxtail, mingled with bladey grass and *Poa*, grow on deep, moist uncultivated soils near Wallaby Creek. Pastures on the lower slopes and flats contain high proportions of paspalum and clovers. Narrow belts of kikuyu grass *P. clandestinum* and Rhodes grass *Chloris gayana* surround the dams. The flats to the east of the creek in the southern half of the study area have been cultivated and are dominated by introduced pasture species.

The vegetation map of Fig. 2.4 shows the distribution of trees, beds of bladey grass, beds of tussocks, and open pastures (cleared areas with relatively low biomasses of tussocks and bladey grass) in the study area (see also Plates 1 and 2). The map was compiled from aerial photos, and from vegetation surveys conducted by P.J. Jarman and C.J. Southwell.

2.1.4 Land use. The land in the study area is put to two major uses : timber production in the forest to the west of Wallaby Creek and north of Wild Cattle Creek (the Beaury State Forest), and beef cattle



-  High biomass of bladey grass.
-  High biomass of tussock.

Fig. 2.4 Distribution of major vegetation types in the study area.

production in the cleared country to the east of Wallaby Creek.

Logging in the forest is controlled by the Forestry Commission of New South Wales, which permits periodic extraction of good quality trees of merchantable species and quota size (40 cm diameter under bark or greater). The forest was last logged in 1950-52. Management of the forest between logging events is limited to some planting of trees along logging tracks and loading ramps where natural regeneration is not expected to occur, and occasional fuel-reduction burns. The Forestry Commission also permits light grazing of cattle in the forest under leasing agreements with local cattlemen. Trees are occasionally felled on the pastoral lands for millable timber or fence posts.

The cleared land east of the creek is privately owned and managed. Regular pasture management associated with cattle raising here takes two forms : burning and hay-making. Cool fires are set in late winter to encourage spring growth and to reduce the risk of later wildfires. These fires tend to be small, especially in the southern half of the study area, and are set in different places each year so that any one place tends to be burnt at least once every four years, and in any year recently burnt and unburnt patches form a mosaic. Burning tends to be more irregular, extensive and synchronous in the northern half of the pasture area. The paddocks on the alluvial flats of the southern half of the study area are mown for hay several times each summer, removing mature leaf and stem of pasture grasses and stimulating new growth. Clovers have been sown on these paddocks. The whole cleared area is divided into several large paddocks by post-and-wire fences, which allow free passage of red-necked wallabies, and other macropods. There are no dingo fences in the valley. Dingoes *Canis familiaris*, are occasionally trapped and shot if they become very abundant and begin to kill calves, but the macropod population has been left essentially undisturbed since the 1950s. Three dams have been constructed to provide extra watering points for cattle. Wallaby Creek always holds some water, and the gullies also flow for parts of the year. Stocking rates vary from time to time, but average approximately one beast per hectare.

2.1.5 Fauna. The study area carries a diverse vertebrate community (Calaby 1966 gives a general account of the mammals of the region), including a number of species which are likely to interact directly or indirectly with red-necked wallabies in a number of important ways. Eastern grey kangaroos, rufous rat kangaroos and brush-tailed possums *Trichosurus vulpecula* are common and feed on the pastures used by red-necked wallabies; whiptail wallabies sometimes venture into the eastern part of the study area, and black-striped wallabies and red-necked pademelons *Thylogale thetis* sometimes venture onto the pastures near the creek. Dingoes regularly enter the study area from the forest to the north and have been seen chasing red-necked wallabies, and have sometimes been disturbed from fresh wallaby carcasses. Wedge-tailed eagles *Aquila audax* may also occasionally prey on wallabies.

2.2 Data collection and classification of study animals

The study began in March of 1981, and intensive data gathering ceased in March, 1984.

2.2.1 Recognition of individuals. Because they have been left undisturbed by humans for many years, and because I deliberately set about habituating them to my presence when my study began, the red-necked wallabies of Wallaby Creek can be approached closely enough to make recognition of individuals possible. I refined this technique in preference to methods of capture and marking, because the minimal disruption it causes does not disturb the indifference with which the wallabies, for the most part, regard me : many can be approached to within ten metres and show no apparent response (some individuals have remained steadfastly shy, and become nervous if approached to within 30 m or so; however, all can easily be recognised at this distance). Differences between individuals' facial characteristics were most useful for their identification : I found ear size and shape; notches or tears in the ears; spots or irregular markings in the ear; depth of colour, thickness and length of the dark margins of the ear; face colour; bone structure of the face; length, thickness and clarity of the black forehead stripe; distribution of colour on the face;

presence of dark lines under the eyes; and length and distinctness of the white cheek stripe, to be particularly variable. When becoming familiar with a new wallaby, I began by making a sketch of his or her face, showing which of these characteristics or combinations of characteristics differed most sharply from the 'average', but after I had encountered the wallaby several times and spent some time observing it closely, instant recognition from the appearance of the whole face, rather than from any particular unusual feature, became easy. At this point I became confident that I 'knew' the wallaby, as each characteristic, especially ear notches or tears, may change but the conformation of all the features of the face is not thereby seriously disrupted. When I had become so familiar with some wallabies that they entered my dreams as distinct individuals I found myself able to recognise them by subtle differences in their demeanour and response to me (but always confirmed such identifications by close inspection of their faces before recording them).

The validity of this technique was confirmed in late 1984, when Karen Higginbottom had been learning to recognise individuals in the same population for three months, and I had taught her my names for the ones who had been residents in 1983 and early 1984. During November we spent two and a half days searching through the study area, comparing our identifications of the same individuals. Because the composition of the population had changed somewhat during the preceding months, Karen was familiar with some wallabies I did not know, but in 65 sightings of wallabies with whom we both judged ourselves familiar, our initial identifications differed only once. In that one case, one of us misidentified a wallaby from a distance, but corrected the identification after a closer inspection. This sample included 35 individuals, some of whom were seen more than once. Individuals were always identified consistently in repeated sightings.

I began the study in 1981 by learning to recognise all of the wallabies in the north western part of the study area, then expanded my area of knowledge until, by 1983, I was confident that I knew all of the wallabies living in the 216 ha mapped in Fig. 2.4, a standing population of 98 individuals, not counting pouch young and young-at-foot. Infants kept entering the population, of course, and

had to be learned, and strange wallabies occasionally moved in from outside and became resident. Over the three years of intensive study, I learned to recognise a total of 145 individuals, 68 males and 77 females (again, not counting young-at-foot). The distribution of the frequencies with which these animals were seen is shown in Fig. 2.5. Individuals who were seen infrequently were either young wallabies who had died soon after weaning, or wallabies who lived near the southern or eastern edge of the study area, and were first identified relatively late in the study.

2.2.2 Collection of records. This section gives a general outline of the methods employed; more detailed descriptions are given where appropriate in the results chapters.

I visited the study area once every month, usually for periods of ten to twelve days. Data were collected in two ways : monthly censuses of the study population were taken, and sustained observations were made of individuals and groups. To obtain census data, I systematically searched the whole of the study area at least three times each month; in this way I was able to find each resident wallaby at least once every month, and keep regular records of the reproductive states of females. In addition to this reproductive data, I recorded the localities, and identities of all individuals seen, together with their group size, spacing within the group (where possible), and the time of day and date. All searches (indeed, all of my work) were conducted on foot. Because wallabies were encountered in many different vegetation types, from wet forest to open pasture, and were often in gullies and under creek banks, I searched most intensively in areas where visibility was poor and wallabies could easily be missed. Locations were recorded, to within ten metres, as grid references. A grid, with one ha grid cells, has been established on the study area by Peter Jarman, Gordon Wyre, Colin Southwell and Robyn Stuart-Dick : grid points are marked in the field by stakes in the ground, this grid is represented in Fig. 2.1. These censuses provided information on the intensity of use by wallabies of different parts of the study area, the home ranges of individuals, grouping and associations between individuals. The same kinds of data were

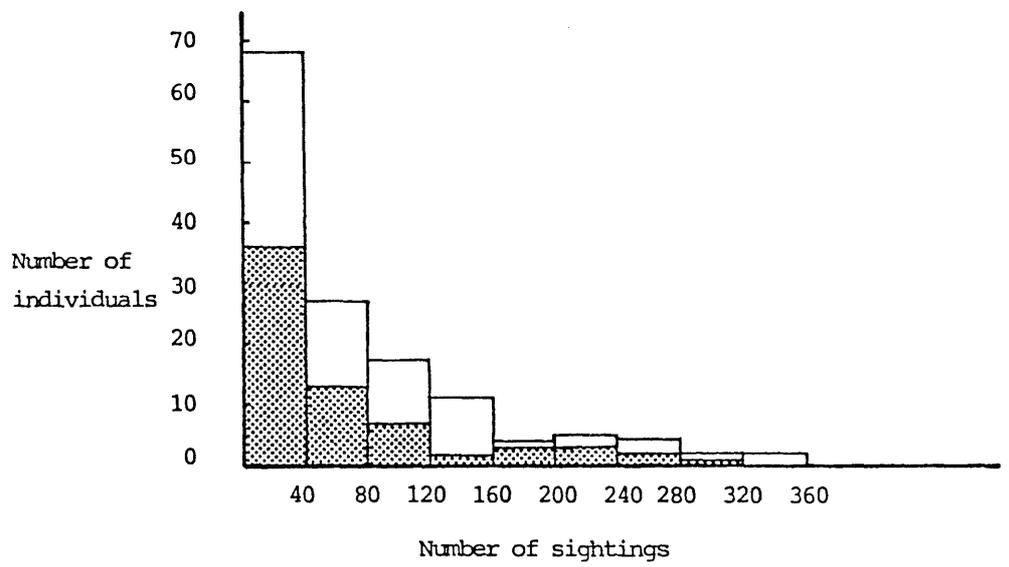


Fig. 2.5 Numbers of sightings made of known individual males (stipled bars) and females (open bars).

opportunistically collected at other times during the field trips, but data collected systematically were kept separate in the records from those obtained opportunistically.

During sustained, systematic observations of groups and individuals, I recorded social interactions, group dynamics, spatial relationships between individuals, rates of progression of individuals and activity of individuals.

Observations were usually made at close range (20 to 60 m) through binoculars, and were recorded in notebooks or on tape-recorders. Most of the data were subsequently stored on the DEC20 computer at U.N.E.

2.2.2 Age, size and reproductive classifications of wallabies.

Broad age classes. All wallabies were assigned to one or other of the following three broad age classes:

Infants (0-14 months of age): includes all ages between birth and weaning. This interval has two distinct phases : young resident in the pouch were called **pouch young**; those who had left the pouch but were still suckling were **young-at-foot**.

Subadults (weaning - adulthood at approx. 24 months of age): includes weaned but sexually immature wallabies. Males usually disperse at 24 months of age, just after their testes descend, and are thereafter termed adults. Females reach sexual maturity, as defined by their first parturition, at ages varying from 19 to 30 months (mean = 25 months, median = 26 months, n=7).

Adults (greater than 24 months of age): sexually mature females, and dispersed, apparently physiologically mature males.

Reproductive states of females. Females' reproductive cycles usually last ten months : just over nine months carrying a pouch young, and about three weeks from the permanent emergence of one young from the

pouch to the birth and entry to the pouch of another (the beginning of a new cycle). This whole cycle was divided into discrete stages, so :

females with small pouch young (fsy): first three months after parturition.

females with medium pouch young (fmy): months four to six of pouch life.

females with large pouch young (fly): the remainder of pouch life.

parturient females (fpt): females in the month after an infant has permanently left the pouch, during which time they give birth again.

Size and age classes of males. As adult males were very variable in size (Fig. 1.2), I tried to objectively record differences in size. This was attempted in two ways : by assigning males to broad size classes; and by ranking them according to relative body size.

Males were assigned to the following size classes:

Small males (sm): adult males similar in body size to, or only slightly larger than, females; larger small males show some lengthening of their forearms.

Medium males (mm): males significantly larger than females, with forearms longer, in proportion to body size, than females': larger medium males show some thickening of their upper forearms.

Large males (lm): males very much larger than females, with

heavily muscled forearms, and the development of heavy muscles on the shoulders and the nape of the neck.

Obviously, this classification is an attempt to subdivide a continuum, and the boundaries between classes cannot be precisely defined. Nevertheless, I found that with experience I was able to classify males consistently. Peter Jarman and Colin Southwell (pers. comm.) have independently devised a very similar classification for male eastern grey kangaroos.

Over the three years of this study, some males passed from one size class to another. Information on the time taken for them to do so can be used to judge the range of ages encompassed by each size class. One male of known age was observed to pass from subadult, through small to medium male status. He remained in the small male class for almost two years, and was four years old when he became a medium male. Given that there is little variation in male weight for age up to four years of age, I regard this observation as a good indication that medium males were at least four years old. No male was observed to pass from small, through medium to large size, but five remained in the medium size class for at least two years. The scattering of the plot of male weight on age that begins to develop after five years of age suggests that males pass through the medium size class at varying rates, but most probably took at least two years. I therefore assume that most large males were over six years of age.

Continuous size rankings of males were constructed by recording, whenever I saw two males together, which was larger, then compiling these two-way comparisons for each six month period of the study to order all of the males according to their body size. Males who could not be separated by size were given the same rank. The rankings for each period were converted to a standard 20-point scale; males given the lowest rank of 20 were the smallest of small males, those close to one were the largest of large males. The transition from small to medium size was at about rank 15.0, while medium males became large at

about rank 7.0. Although these rankings are less useful than would be absolute measurements of size, they at least treat size as a continuous variable, and proved useful in showing how male behaviour changed with body growth.

2.2.4 A note on statistical analyses. As much of my data fell into distributions that were skewed, often violently so, I used non-parametric tests except where the data could actually be shown to be distributed normally. I used standard procedures, as set out in Siegel (1956), Conover (1980), Roscoe (1975) and Gibbons(1976).

CHAPTER THREE

Home Range and Habitat Use

3.1 Introduction

Red-necked wallabies reach their highest densities close to the edges of dry sclerophyll forests and woodlands, in which they shelter during the day, and from which they move to feed during the late afternoon, night and early morning (see Calaby 1983). Although this habitat preference is well known, there are no published studies to show precisely which features of their habitat are most important in limiting the abundance of the wallabies. However, Southwell (in prep.) has measured the densities of red-necked wallabies in relation to several vegetative and topographic variables within a 3.6 km² study area at Wallaby Creek, and has shown that the wallabies reached high densities where grasses other than *Poa* and bladey grass were tall but of low biomass, the biomass of bladey grass and forbs and the number of trees were low, and a forest edge or a gully was nearby.

My study area lies within Southwell's, and in this chapter I extend his findings by describing the home ranges and locations of the wallabies in my intensively studied population, analysing the habitat preferences of the whole population in relation to the movements of individuals, and showing how habitat influences breeding.

3.2 Data analysis

3.2.1 Home ranges. The size of an individual's home range was measured as the area of the smallest convex polygon which could enclose all the sightings of that individual. Fig. 3.1 shows that at least 25 determinations of location were necessary to use this method to estimate the size of an individual's home range with reasonable accuracy. Home range estimations made from less than 25 locations

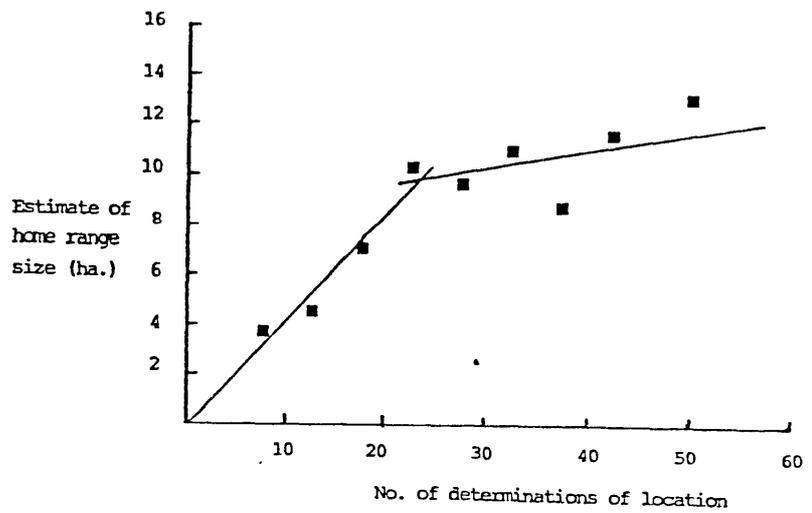


Fig. 3.1 Relationship between sample size and estimate of home range size.

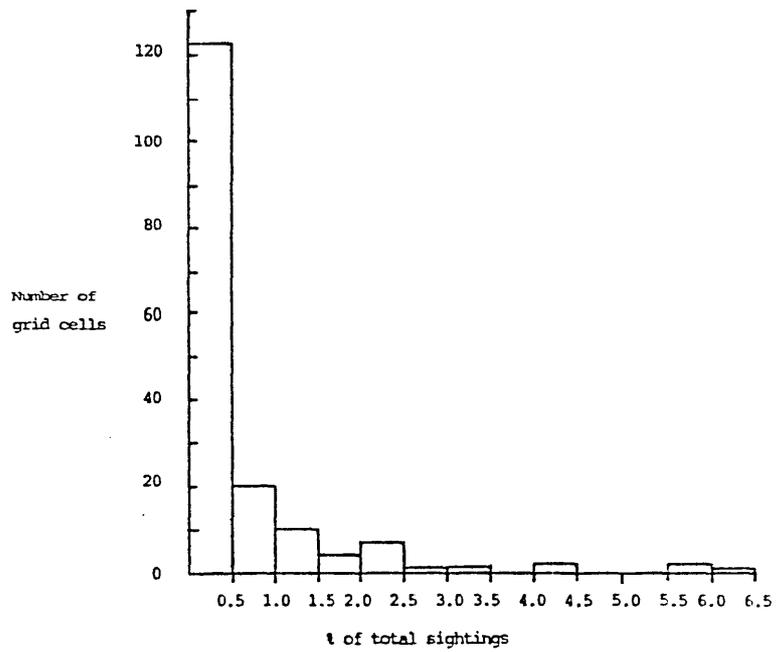


Fig. 3.2 Distribution of occupancy of grid cells, 1983.

were excluded from subsequent analyses. A centre of activity was computed for each home range - this was a location having the average of all the coordinates used to map the home range - and the mean and median distances of all the wallabies' sightings from this centre of activity were found.

3.2.2 Distributions. The results of systematic censuses of the study population were used to calculate, for a given time period or class of wallaby, that percentage of the total number of sightings which were made in each 1 ha. grid cell. These relative measures of the intensity with which each grid cell was used by wallabies are summarised in distribution maps (see Fig. 3.4 etc.). Maps were prepared showing the distribution of wallabies at each season or period of the day and of each class of wallaby (all males, large males, females with large pouch young, and so on). The degree to which any two distributions resembled one another was quantified by calculating a coefficient of the correlation between the relative intensity of use of the same grid cells across the two distributions. The distributions tended to be very patchy, with many cells under-used (i.e. having percentage shares of the total number of sightings less than would have been expected had the wallabies been using the study area in a perfectly uniform fashion), while a few cells were very heavily used (see Fig. 3.2). Moreover, many cells were under-used by all classes of wallabies over all time periods and seasons. I discarded from the statistical comparisons of any two distributions those cells that were under-used in both distributions - this exclusion lifted from the analysis the weight of the many cells that were consistently avoided.

Correlation coefficients calculated in this way provide useful and simple measures of the similarity of distributions, but some caution must be exercised in interpreting the levels of significance of the differences. The reason for this is that each distribution has been constructed from the locations of repeated sightings of the members of a set of individuals. Each wallaby contributes a cluster of inter-dependent data points to the analysis, whereas the statistical testing assumes that all data points are independent. This problem is

likely to be serious when the distributions of small sub-sets of the population (e.g. small or medium males) are being compared. In such cases the contributions of one or two exceptional individuals could produce apparently significant differences. I have therefore used the correlation analyses of the various patterns of habitat use as procedures for generating hypotheses, which can then be tested by statistical comparisons which treat each individual wallaby as a single independent datum.

3.3 Characteristics of home ranges

3.3.1 Size and heterogeneity of use. Individual red-necked wallabies in this study area usually live in roughly circular or elliptical home ranges, each of which is made of a central, heavily used "core area" (sensu Kaufmann 1962) and a surrounding zone of lightly-used ground. The entire home range might be as small as 5.6 ha or as large as 54.0 ha with a median size (in 1983) of 15.2 ha (n=62). The home ranges of sub-adults tended to be smaller than those of adults (median for sub-adults 7.40 ha (n=9); for adults 16.35 ha (n=53)). Other differences between sex- and age- classes in the sizes of their home ranges will be discussed below.

The heterogeneity of use of a home range - the degree to which its occupant's activity concentrated in one central part of it - can be conveniently measured as the ratio of the mean to the median of the distances of all the wallaby's sightings from its centre of activity. As Fig. 3.3 shows, the frequency with which wallabies were sighted tended to fall rapidly with increasing distance from their centres of activity : the females in the sample used to construct Fig. 3.3 spent, on average, 50% of their time in the central three ha of their home ranges. The skew in this distribution of sightings causes the mean of the distances of all sightings from the centre of activity to exceed the median. The greater an individual's tendency to make heterogeneous use of its home range in this fashion the more will its mean distance from its centre of activity exceed its median distance, while a mean to median ratio of unity indicates a uniform distribution of activity throughout the home range : this measure will hereafter be referred to as the "heterogeneity of use". The average heterogeneity

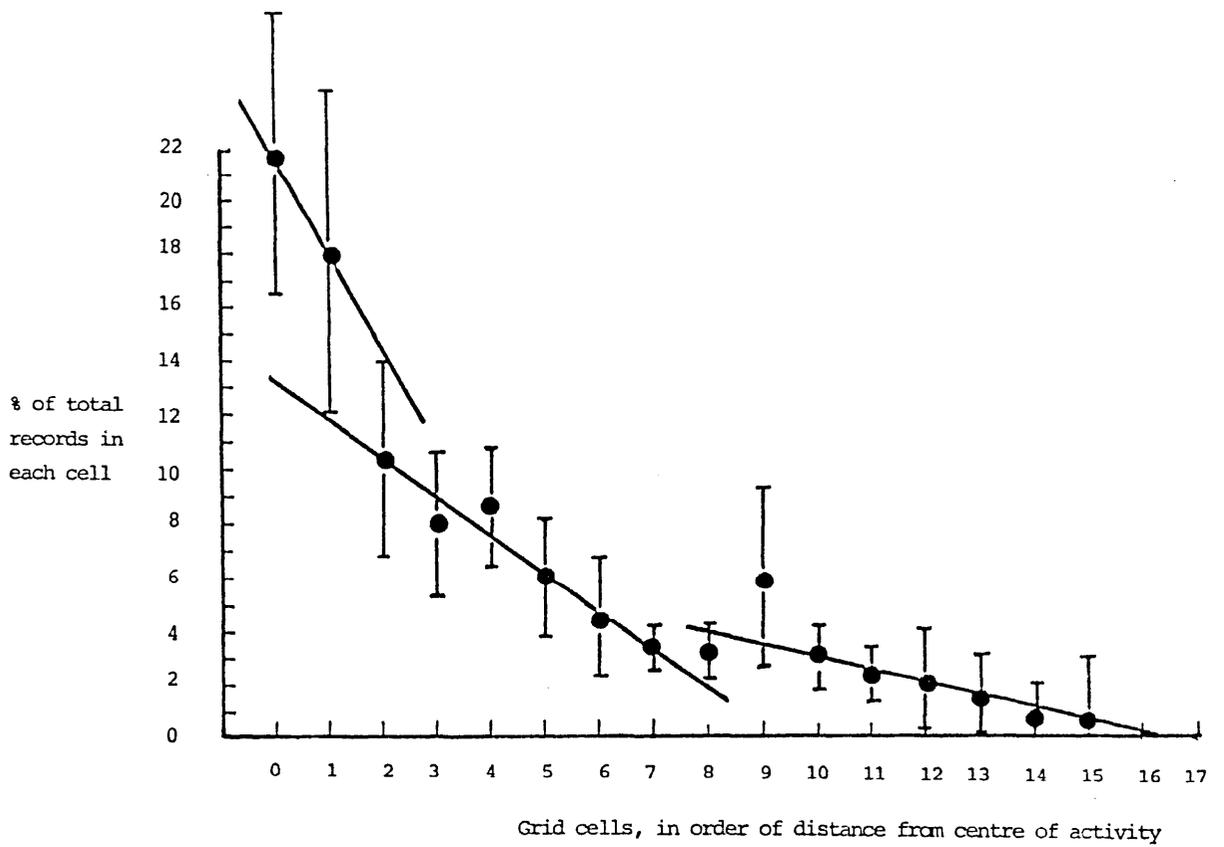


Fig. 3.3 Distribution of intensity of use within the home range, females (means with 95% C.I.s).

of use for female wallabies was 1.27, that for males was 1.32.

Inter-individual variations in home range size and heterogeneity of use were correlated in opposite directions for females and for males ($r=0.37$, $n=34$, $P<0.05$ for females, $r=-0.50$, $n=29$, $P<0.01$ for males). Thus, females with large home ranges tended to make heterogeneous use of them, while males with large home ranges tended to use them more uniformly. However, both correlations, particularly the one for females, are quite weak.

3.3.2 Stability. There was very little drift in the locations of the home ranges of adult wallabies from year to year. Sixteen of the adult females and nine of the adult males whose home ranges were mapped in 1981 were still present in the study area in 1983. None of these animals had shifted their centres of activity by more than 30 metres over this period. Some wallabies, particularly young males, do make dispersive movements (see Ch. 7), but apart from such movements, the annual home ranges of all wallabies are remarkably constant in location.

3.4 Habitat preferences

The distribution of sightings, made during systematic censuses in 1983, of all classes of wallabies at all times of the day and year, is shown in Fig. 3.4. This distribution map was compiled from 3071 sightings of 96 individual wallabies, an average of 32 sightings per individual. Wallabies were most frequently seen along the creek and on the alluvial flats just to the east of the creek, and in or close to gullies on the patchily wooded eastern side of the valley. The centres of activity of individual wallabies are also plotted in Fig. 3.4; these also tended to be close to the creek or along the gullies. The heaviest concentrations of wallabies were found in areas where deep-soiled lightly-wooded flats carrying pastures of soft grasses and herbs lay close to densely vegetated patches of country dissected by gullies. Figs. 3.5 and 3.6 summarize the tendency for wallabies' centres of activity to be near the creek, or close to a cover edge.

Fig. 3.7 contrasts the distribution of wallabies during the middle of the day (i.e. from three hours after dawn to three hours before

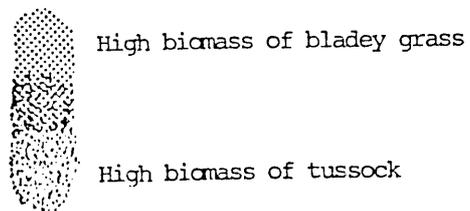
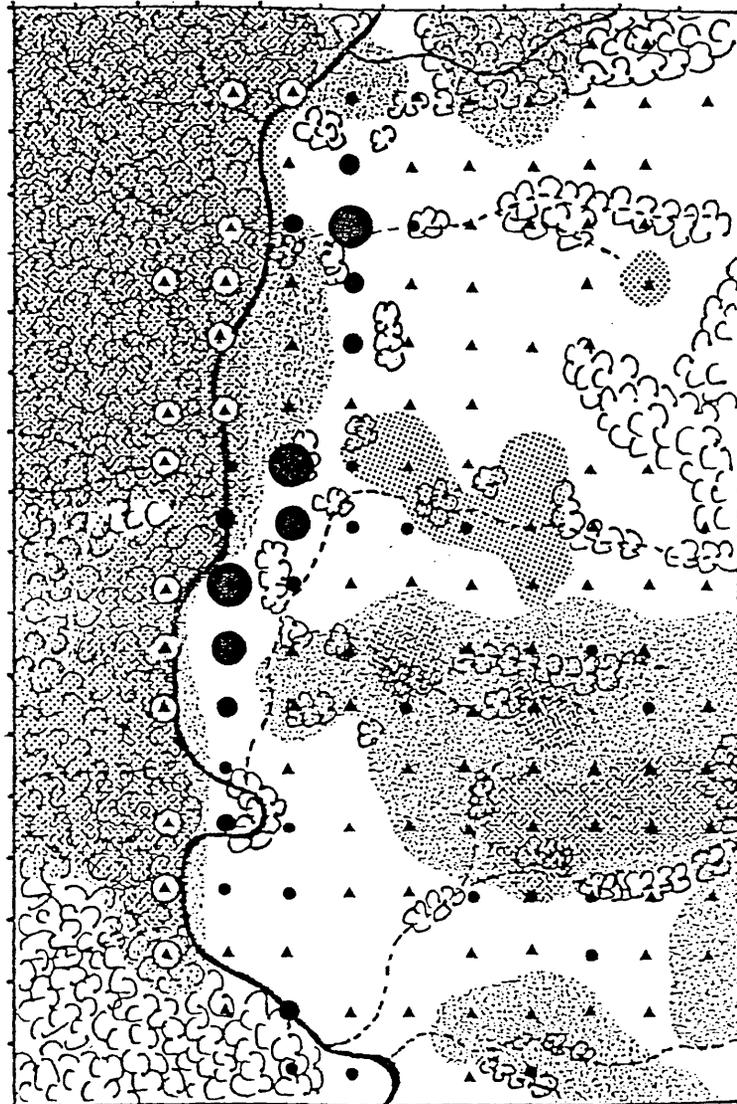


Fig. 3.4a Locations of centres of activity of male (■) and female (●) adults and subadults, 1983.



▲ < 1%
 ● 1-2%
 ● 2-3%
 ● 3-4%
 ● > 4%

% of total number of sightings
 falling within each grid cell:
 (cells in which no wallabies
 were seen are left empty).

Fig. 3.4b Distribution of sightings of wallabies, all classes, seasons and times of day, 1983.

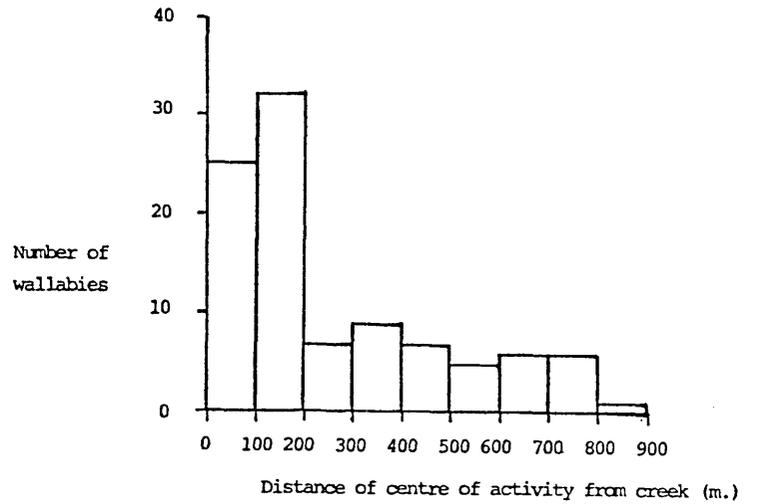


Fig. 3.5 Distribution of centres of activity in relation to the creek (differs from uniform: $\chi^2=78.4$, $P<0.001$)

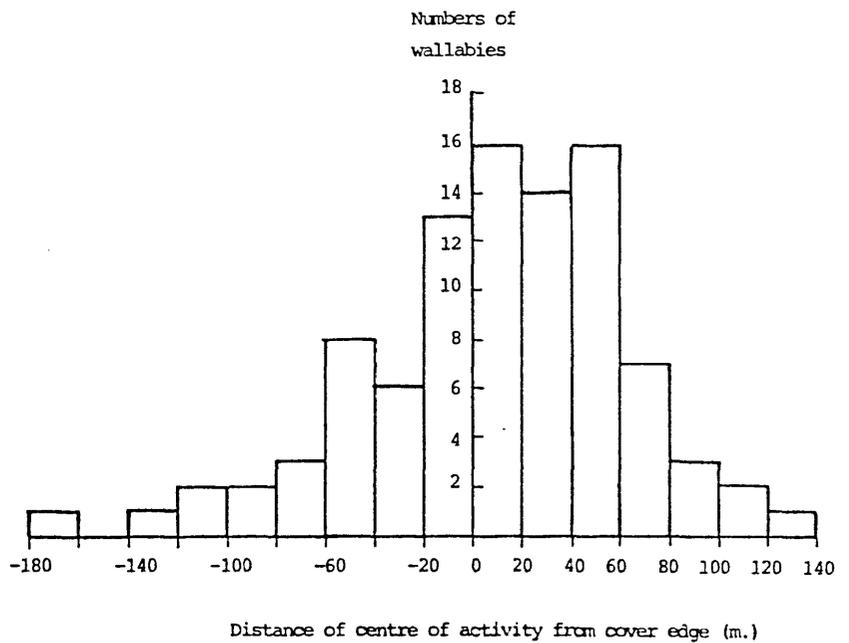


Fig. 3.6 Distribution of centres of activity in relation to cover edges ($\chi^2=83.8$, $P<0.001$). Negative values are for centres of activity within cover, positive values in the open.

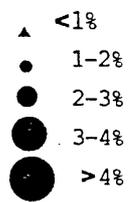
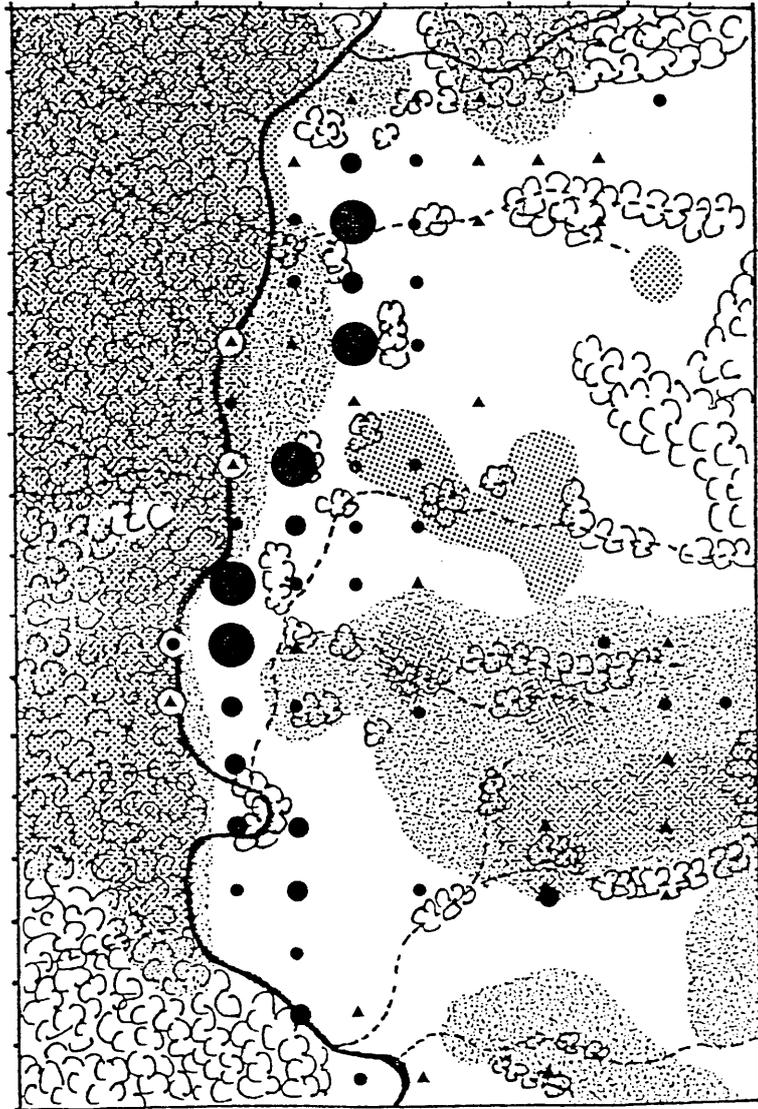


Fig. 3.7a Distribution of sightings during the morning, evening and night, 1983.

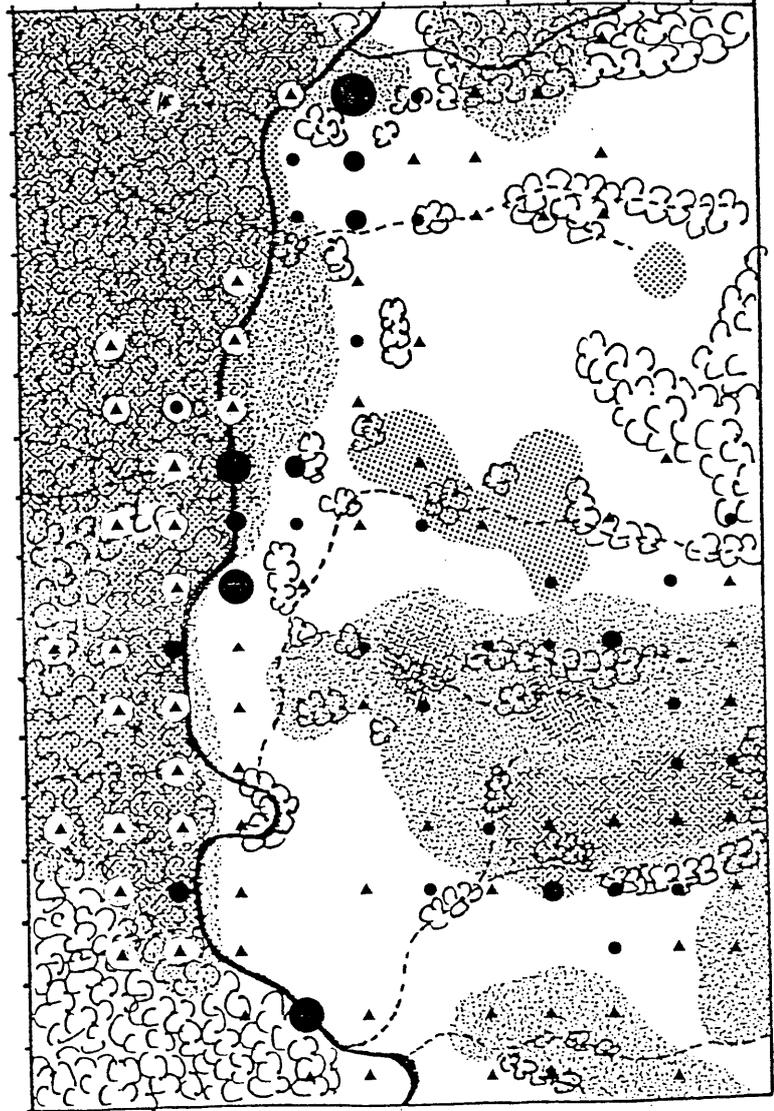


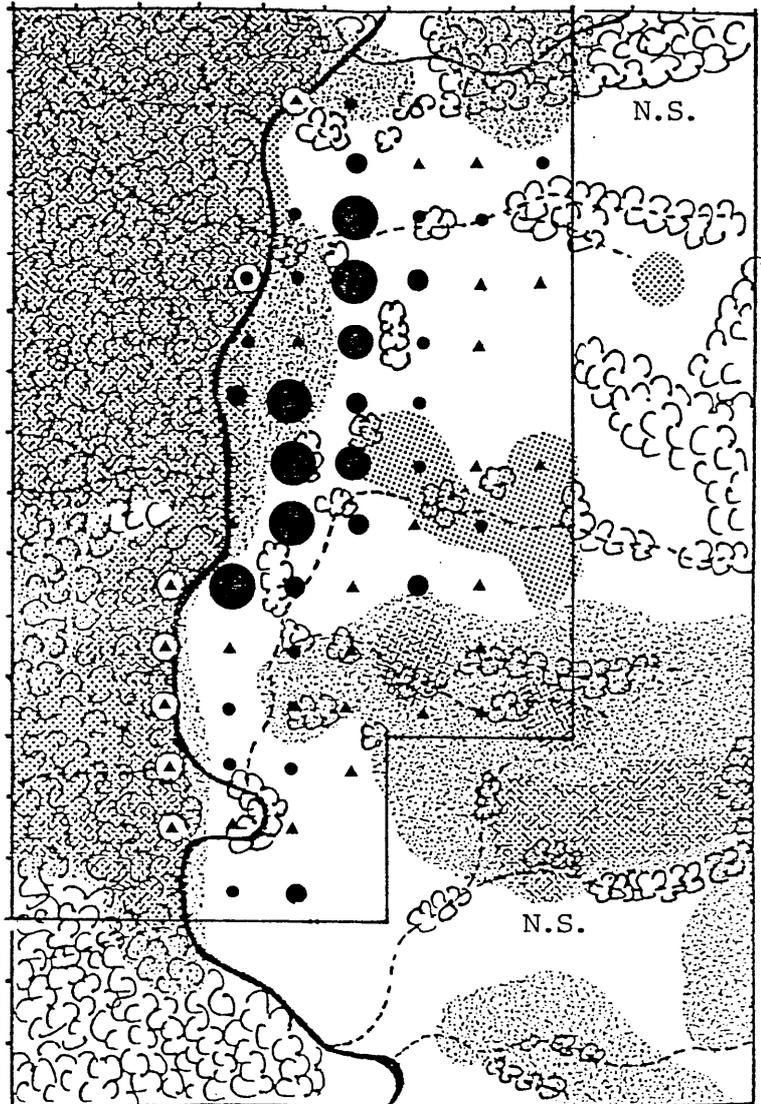
Fig. 3.7b Distribution of sightings during the day, 1983.

dusk), when they were resting for most of the time, with their distribution during the evening, night and morning (i.e. from two hours before dusk to two hours after dawn) when feeding was the dominant activity. The two distributions were weakly correlated ($r=0.19$, 55 cells compared). During the middle of the day the wallabies were most often seen in the forest or on its edge, or on the densely vegetated floors of gullies on the eastern side of the valley, where they sat or lay down while resting. The wallabies moved out into more open areas to feed, although they usually stayed within a hundred metres or so of the cover provided by a bed of tussocks or bladey grass and the floor of a deep gully. If disturbed while feeding, they would quickly dash back into cover. A wallaby could disappear most effectively by fleeing down into a deep gully or by hopping along it and losing itself from sight around bends in the gully.

On only two occasions did I see a red-necked wallaby drink, both were in dry periods, one during a dry summer, the other during a dry winter.

3.5 Seasonal variation in habitat use

Fig. 3.8 shows the distribution maps for wallabies of all classes and at all hours of the day during the summer (Dec. 1981, Jan., Feb., March 1982) and winter (May, June, July, August) of 1982. The seasonal distributions in 1982 have been analysed in detail because in that year the seasonal variation in rainfall most nearly approximated the long-term average pattern (the summer was wet and warm while the winter was dry and cold, see Fig. 2.2). The correlation between the two distributions was weak ($r=0.23$, $n=44$ cells compared). In winter the wallabies were concentrated on a number of small isolated patches of pasture and adjacent cover, mainly along the creek flats, while in summer they were less patchily distributed and tended to be further to the east of the creek, on higher ground. Seasonal variation in habitat use in 1983 followed a similar pattern, but was less pronounced ($r=0.35$, $n=55$ cells). The sites preferred so strongly in winter were flats where, because their soils were especially deep and cultivation or grazing by cattle kept the pastures growing, feed remained relatively green through the winter.



- ▲ <1%
- 1-2%
- 2-3%
- 3-4%
- >4%

Fig. 3.8a Distribution of sightings during summer, 1981/2.

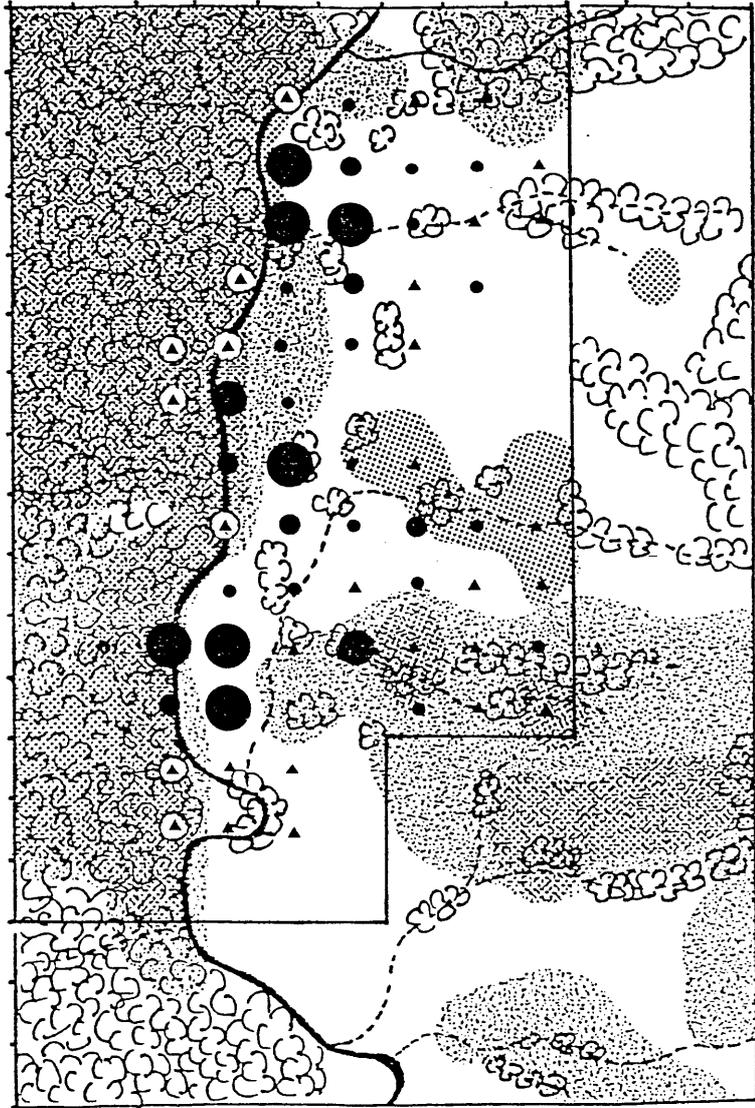


Fig. 3.8b Distribution of sightings during winter, 1982.

The data in Table 3.1 show how the home ranges of individual females varied from summer to winter in 1982. The females have been divided into two groups : those whose annual centres of activity were within the areas of winter concentration (defined as cells receiving more than 2% of the total winter use) and those whose annual centres of activity were elsewhere. Females whose centres of activity were not within winter concentrations used significantly larger home ranges in winter than they had in summer ($U=15$, $P<0.05$), they also made more heterogeneous use of their home ranges, although this increase was not significant. Females whose centres of activity were within winter concentrations showed no significant seasonal variations in home range size or heterogeneity of use. The changes came about because females whose centres of activity were not within winter concentrations increased their use of those areas, but did so without abandoning their summer home ranges; rather, they made daily movements to feed on the green flats, returning to rest within their traditional home ranges. Some females moved as far as two or three home range widths over what must have been unfamiliar ground to fulfil this daily routine during winter.

The centres of activity of all females in summer tended to be significantly east (i.e. up-slope) of their winter centres of activity (by Wilcoxon Matched-Pairs Signed-Ranks test, $T=34.5$, $P<0.05$, $n=17$). These females' centres of summer activity were a median of 40 metres to the east of their centres of winter activity.

There were no significant seasonal changes in the sizes or heterogeneities of use of the home ranges of males (see Table 3.2), nor did the tendency for their summer centres of activity to be to the east of their winter centres of activity reach significance ($T=13$, $n=11$, n.s.).

3.6 Differences in habitat use between classes of wallabies

The similarities of the dispersions of each class of wallaby to all of the others are shown in Table 3.3. The closest correlations were between sub-adults and females with young-at-foot, females with medium pouch young and females with large young, respectively; the weakest correlation was between the distributions of large and small

males. The dendrogram of Fig. 3.9 summarises all of the information in Table 3.3, and shows that sub-adults and all females except oestrous females fall into a cluster of similar distributions, to which large males also belong. Medium males and oestrous females have somewhat similar distributions, which differ from the dispersion of large males, other females and sub-adults, while small males do not closely resemble any other class.

These classes of wallabies also differed in the patchiness with which they were distributed. Patchiness can be measured on the skew in the frequency distribution of cell occupancy rates (see Fig. 3.2), which in turn is indicated by the value of the ratio of the mean to the median frequency of occupation of grid cells - a very patchy distribution results in a high value of this ratio. The results in Table 3.4 show that although all classes of females (except oestrous females) had closely correlated dispersions, females with young-at-foot were much more patchily distributed than were any other class of females, and females with medium pouch young had the most uniform distribution of all.

The significance of the difference between the distributions of all males and all females was tested by comparing the proportions of their time that individuals spent in areas that were heavily used by females. For the purpose of this analysis, a grid cell was considered to be heavily used by females if it contained more than 1% of the total number of sightings of females. Variation in the intensity of use of parts of the study area by females in 1983 is illustrated in Fig. 3.10. Naturally enough, adult females tended to spend high proportions of their time in these female-preferred areas (median of 76.9%, $n=23$ females) but individual adult males spent significantly less of their time there than did females (median of 54.6%, $n=24$, a significant difference : $U=164.5$, $Z=-2.37$, $P<0.01$). Females concentrated on pastures and adjacent cover on creek flats and gully floors; clearly, males also used these areas but tended to spend more of their time than did females in the spaces between gullies and above the creek flats. The same standard of comparison was used to show how individual males varied in their use of habitat. Large males spent, on average, a significantly greater proportion of their time in areas

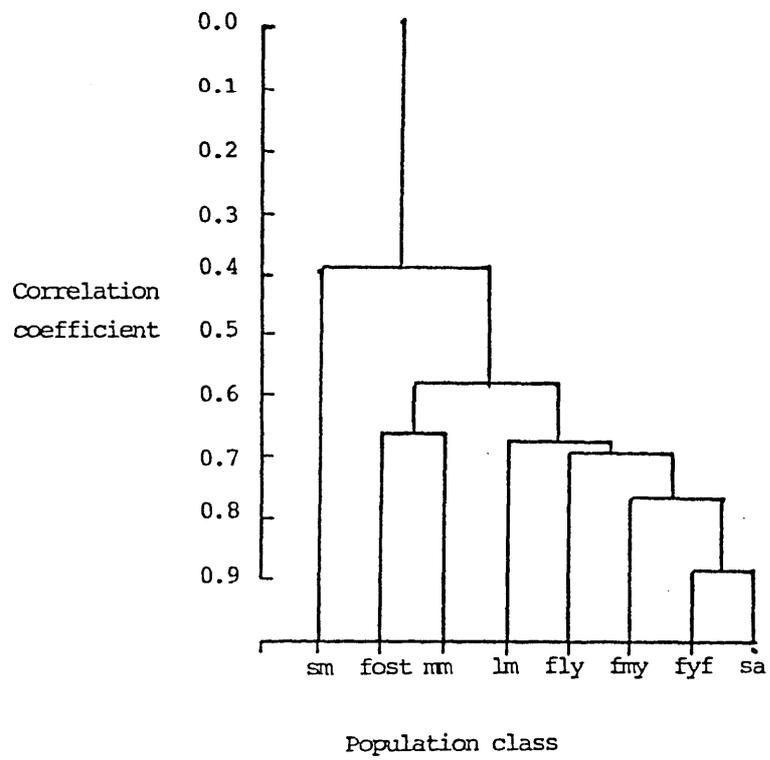


Fig. 3.9 Dendrogram of similarities between distributions of classes of wallabies (see ch.2 for explanation of abbreviations).

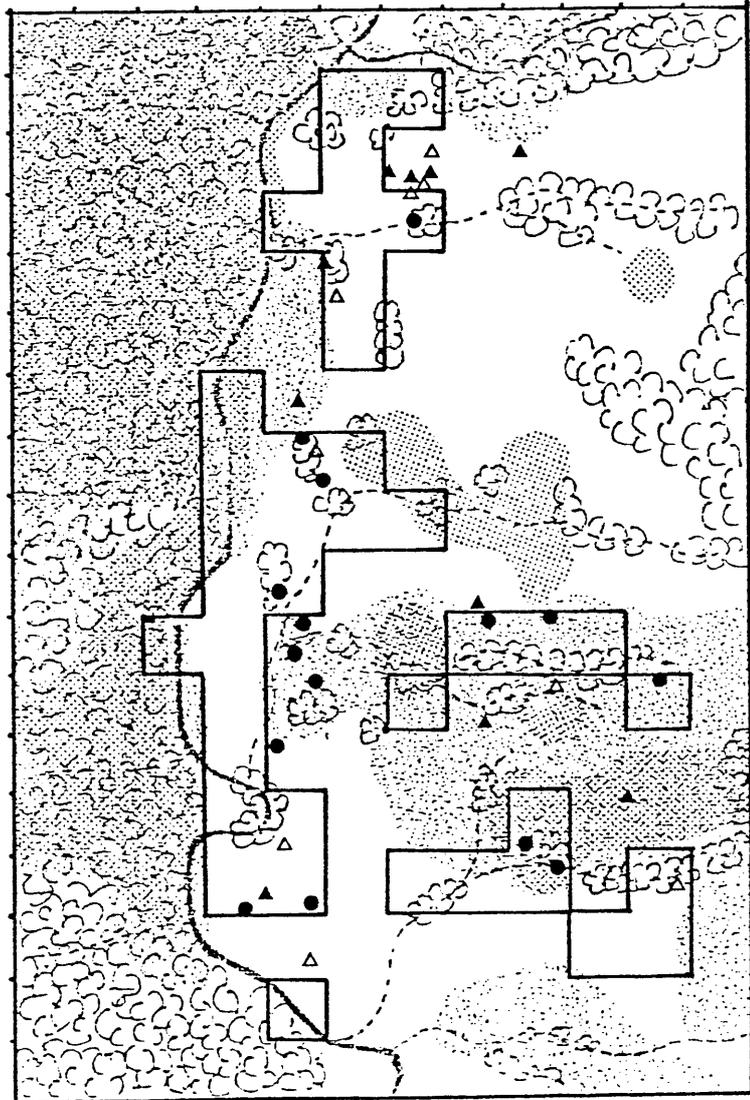


Fig. 3.10 Locations of the centres of activities of large (●), medium (▲) and small (△) males, in relation to areas of intense female use.

heavily used by females than did medium males (median for large males=66.1%, n=12, for medium males 41.7%, n=12, U=34, P<0.05). The distribution of centres of activity of large and medium males reflects this : large males tended to have centres of activity within or very close to peaks of female density, whereas the centres of activity of medium males were more likely to be peripheral to these peaks (see Fig. 3.10). Usage of female-preferred areas by small males (median=60.4%, n=6) was similar to that for large males, yet the dispersion of small and large males appeared to be very different (Fig. 3.9). This effect may have been due partly to the relatively low number of small males in the sample, and also to the smallness of their home ranges (see below) : the resulting dispersion was apparently unusually patchy and erratic, but this may have no special significance.

Males and females also differed in the average sizes of their home ranges (Fig. 3.11). The median size of home range used by adult females was 11.8 ha (n=32) while that for adult males was 31.6 ha (n=22), a significant difference (U=220, Z=-3.49, P<0.001). The home ranges of males were very variable in size (see Fig. 3.11). Much of this variability can be accounted for by a relationship between body size and home range size in males. Large males tended to have large home ranges (see Fig. 3.12 : $r_s=0.77$, n=29, P<0.01); the largest males in the population had home ranges up to five times the average for females. The heterogeneity with which males used their home ranges tended to decline with increasing body size, but this tendency did not reach significance ($r_s=-0.32$, n=29, n.s.).

Table 3.4 shows how home range use differed between females with young-at-foot, females with medium pouch young and females with large pouch young. To prevent seasonal effects from confounding this comparison, I calculated the home range data for females of different reproductive classes during the same season (summer 1982/83). Home range size did not vary significantly between these three classes of females, but there was significant variation in heterogeneity of home range use ($\chi^2=9.74$, 2 d.f., P<0.01, Kruskal-Wallis test). Females with large pouch young, and especially females with young-at-foot, made significantly more heterogeneous use of their home ranges than

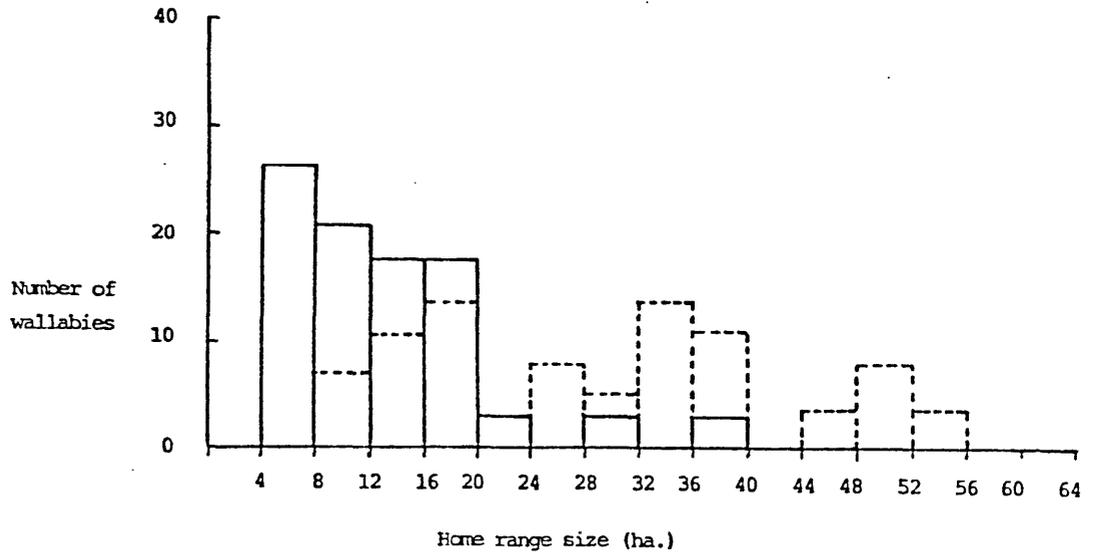


Fig. 3.11 Sizes of the home ranges of male (dashed lines) and female wallabies (solid lines).

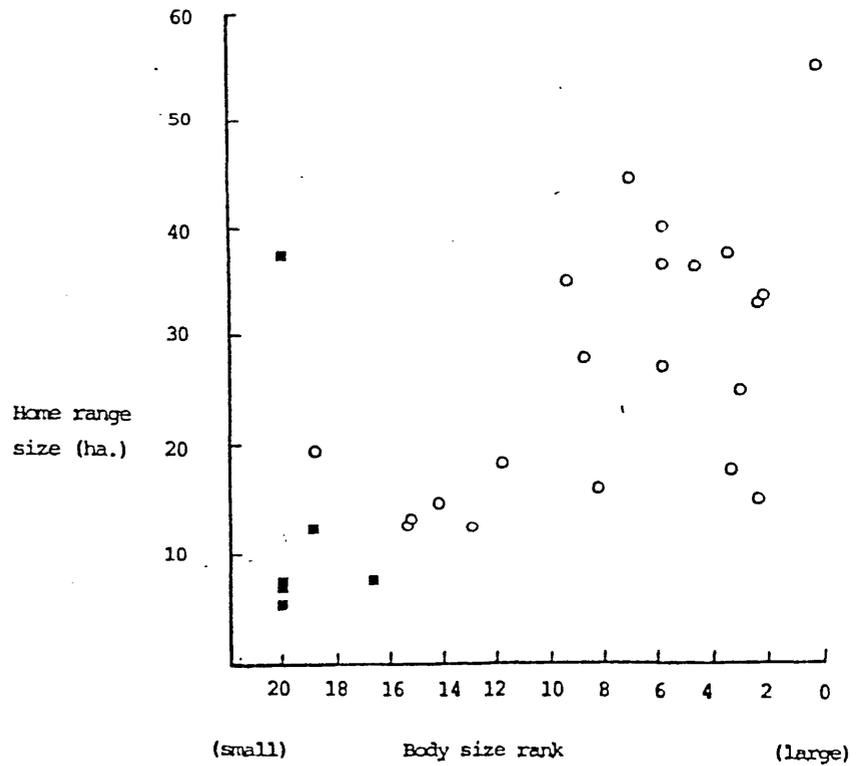


Fig. 3.12 Relationship between body size and home range size, male wallabies (squares represent subadult males).

did females with medium pouch young.

Fig. 3.13 shows that females often shifted their home ranges over relatively great distances as their young grew from the medium pouch young stage, and left the pouch. The 15 females whose home range shifts are illustrated in Fig. 3.13 moved a median distance of 125 metres over this period : such shifts are large by comparison with seasonal movements and inter-annual drift. The 12 females who moved more than 50 metres all moved from uniform or open areas towards the treed edges of large patches of bladey grass or beds of tussocks. These movements also took the females closer to feeding areas preferred by the population as a whole (see above).

Females with young-at-foot apparently spent much of their time in small areas where feeding sites were close to cover in which the young could hide and gullies which the young could use as escape corridors when alarmed (see Ch. 6). When with medium-sized pouch young, and not accompanied by young-at-foot, females seemed to make less discriminating use of the micro-habitats available to them.

3.7 Habitat preferences and the reproductive performance of females

Fig. 3.14 shows that the ages at which young females gave birth for the first time were significantly correlated with their distances from the creek : females who lived on the creek flats first gave birth when up to 11 months younger than females who lived away from the creek on the valley slopes ($r=0.92$, 5 d.f., $P<0.01$). Habitat preferences may have influenced reproduction by females in other ways. The infants of females whose annual centres of activity were within winter concentrations were more likely to survive to weaning age than were the infants born elsewhere (65.4%, $n=26$, vs. 44.1%, $n=34$; $\chi^2=2.61$, n.s. ($P<0.20$)); and their mothers tended to breed according to a rather more seasonal pattern (see Fig. 3.15). These effects are interesting, though with the data currently available neither of them is significant.

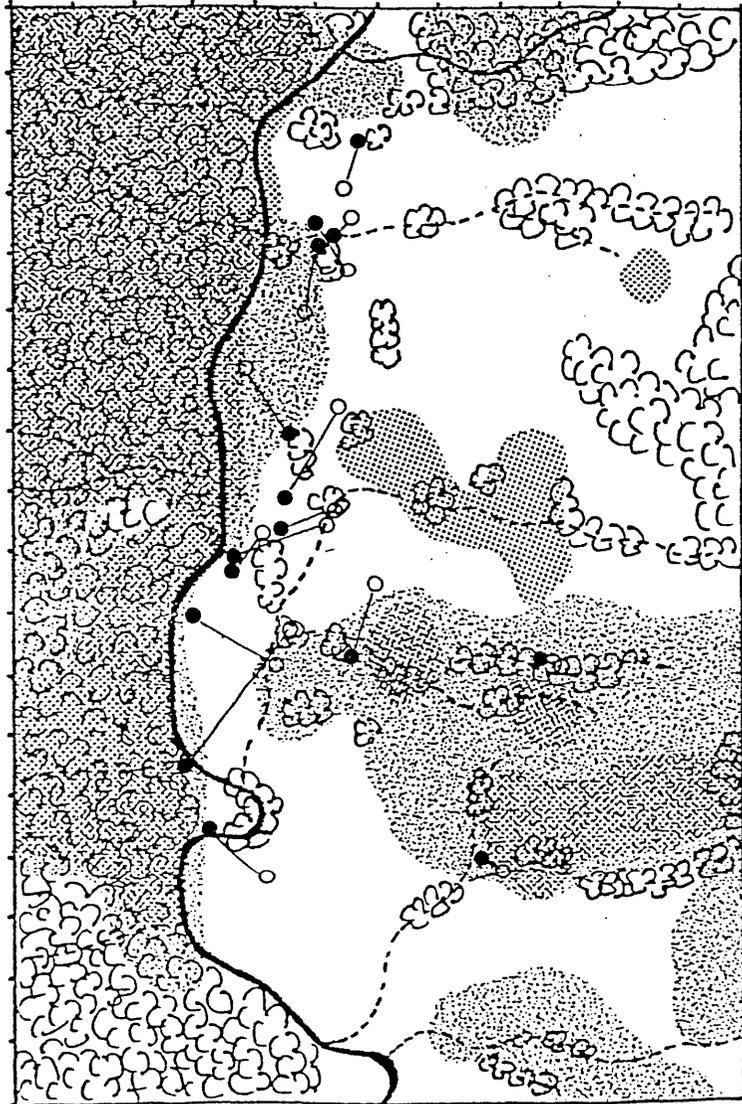


Fig. 3.13 Shifts in the centres of activity of females passing from having medium pouch young (o) to having young-at-foot (●).

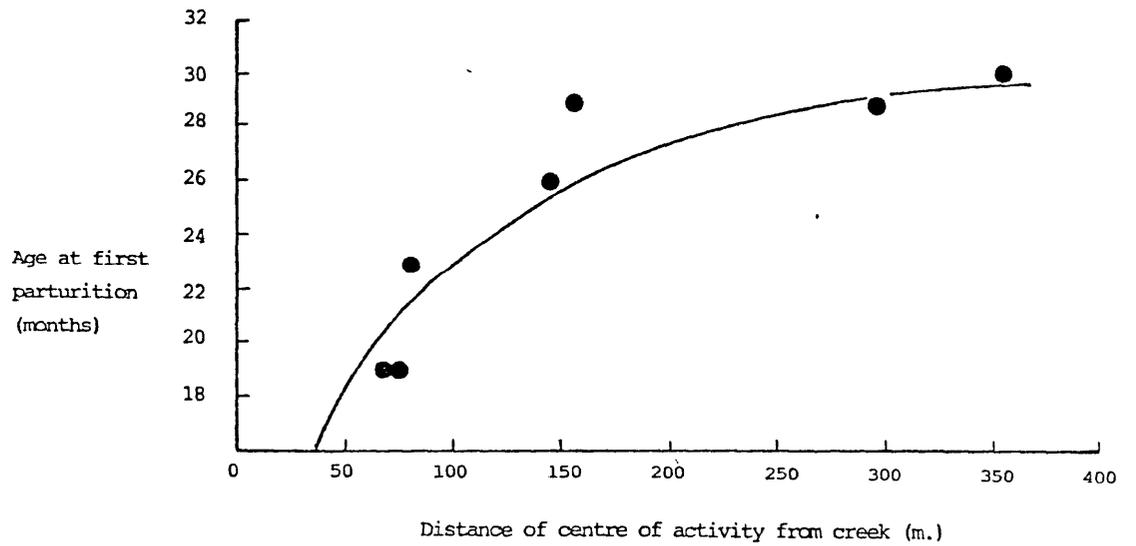


Fig. 3.14 Relationship between location of centre of activity and age at first breeding, female wallabies. ($y = 6.47 \ln x + 6.86$; $r = 0.92$, $P < 0.01$)

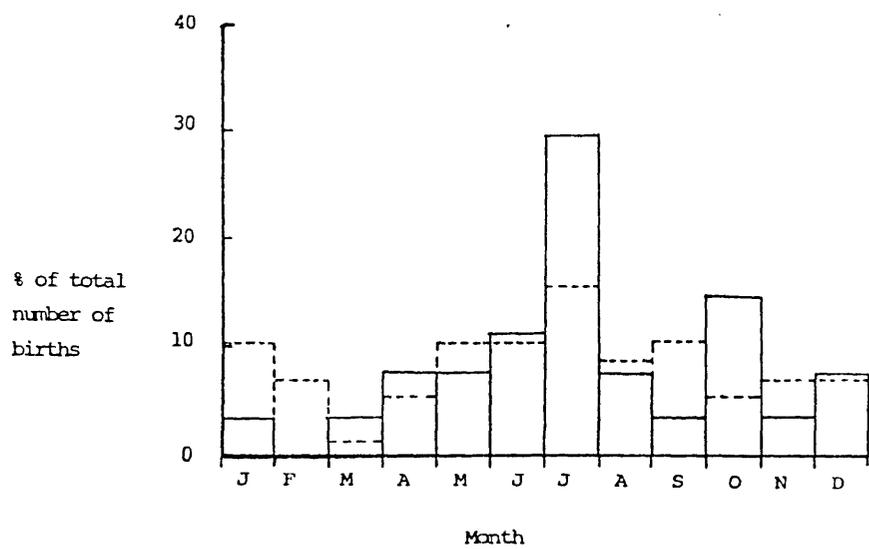


Fig 3.15 Seasonality of breeding of females with annual centres of activity within (solid lines) and outside (dashed lines) areas of winter concentration.

3.8 Discussion

Red-necked wallabies in my study area reached their highest densities on the flats beside Wallaby Creek, that is, at the base of the local catena. A catena is a connected series of soil types, grading from light, shallow soils on ridge tops to heavy, deep soils on valley floors. Soils at the base of the catena receive and retain moisture for longer periods than do soils higher on the catena, and therefore are likely to sustain plant growth through longer dry spells. It is evidently because of the potential of the creek flats to support some plant growth during the dry, cool winters experienced at Wallaby Creek, that so many wallabies live there. Indeed, the wallabies concentrate most heavily on the flats during the winter, but tend to use slightly higher positions in summer. In many species of large, mobile mammals, seasonal changes in the use of soil and vegetation types follow quite simple catenary patterns, with animals moving up the catena during wet seasons and down during dry seasons. Movements of this kind have been shown to occur in many African ungulates (see P.J. Jarman 1972, Bell 1971, M.V. Jarman 1979, Maddock 1979), and in red and western grey kangaroos (Priddel 1984, Johnson and Bayliss 1981, Newsome 1965b). Such patterns of movement allow animals to take full advantage of rainfall high on the catena, particularly when plant communities capable of rapid responses to rainfall grow there, and to use lower levels of the catena when moisture has drained down from higher soils and plant growth on them has ceased.

It is evidently the strong attachment of individual red-necked wallabies to their home ranges that prevents them from making more pronounced seasonal movements. Even individuals who made what were by wallaby standards extensive movements to reach heavily used winter feeding areas on the flats, did not abandon their summer home ranges to do so, but instead extended their daily ranges of movement. Those characteristics of the creek flats which made them so favourable to red-necked wallabies had some important effects on the breeding performance of individual females : females who lived perennially on

the creek flats bred for the first time when almost a year younger than females who lived on the valley slopes. This difference of a year is a large proportion of the lifespans of wallabies at Wallaby Creek, which are almost always less than ten years (see Appendix I).

Red-necked wallabies also occur on ridge-tops at Wallaby Creek, and sometimes reach high densities there. Southwell (in prep.) found that they were the most widely distributed species of macropod in the valley. Finlayson (1929) has described how, prior to settlement in south eastern Australia, red-necked wallabies were found both on low-lying country and on dry ridge-tops, but were in greater numbers on the former type of country. With close settlement of low-lying ground the wallabies' numbers were reduced, but they retained their hold on the dry, relatively inhospitable ranges. Red-necked wallabies are evidently able to use a wide range of forested habitat types, and are probably equally sedentary in all of them. Further information on the reproduction and population dynamics of wallabies in different habitats should prove helpful in understanding the processes of population regulation in each.

The other important factor determining the distribution of wallabies was the availability of cover, in the form of patches of forest, beds of baldey grass or *Poa* tussocks or densely vegetated gully floors. The centres of activity of individual wallabies clung to the edges of patches of cover, and tended to follow gullies up towards the ridges. The heaviest concentrations of wallabies occurred in patchy microhabitats, where good cover abutted tracts of relatively short open pasture : in such places the wallabies could feed without moving far from cover, and flee quickly back into cover if disturbed. Although many wallabies had favourite resting places in cover, they did not depend on particular sites for refuge. This is in contrast to most smaller species of macropodoids, for whom certain sheltering and hiding places have critical value. Burrowing bettongs *Bettongia lesueur*, for example, dig burrows in which they spend the day (Finlayson 1958, Burbidge 1983): so to a lesser extent, do rufous hare-wallabies *Lagorchestes hirsutus* (Burbidge and Johnson 1983). Potoroos *Potorous* spp., other bettongs and rufous rat kangaroos construct nests in which they remain hidden during the day (see Calaby

1966, Christensen 1980, Johnson and Rose 1983, Schlager 1981). Each individual appears to maintain several nests within its home range, and if approached very closely will burst from cover, flee from sight and enter another of its nests or some other type of refuge. Rock wallabies *Petrogale* spp. will only live on steep cliff faces or rock piles where they can retreat to certain inaccessible caves or sheltered ledges if disturbed by predators (Short 1982, Joblin 1983).

The refuge sites used by these animals provide them with concealment from predators and a stable thermal environment. Each individual must make a considerable investment of time and effort in the construction or defence from conspecifics of its refuges, and must possess precise knowledge of their location within the home range and of the preferred routes to and between them. It is probably for these reasons that some small macropodoids show very strong fidelity to their home ranges. For example, Christensen (1980) has shown that woylies *Bettongia penicillata* do not abandon their home ranges during fires; instead, they escape fires by seeking refuge on small unburnt patches within the home range, or by doubling back through the flames.

Red-necked pademelons, which are nearer in size to red-necked wallabies than are bettongs, potoroos, and hare wallabies, make daily movements from shelter in rainforest to feeding areas on adjacent pastures (Johnson 1980) in a similar fashion to red-necked wallabies, but remain closer to the forest edge and are less likely to emerge from the forest during the day. The members of larger species such as the whiptail wallaby (Kaufmann 1974) and the eastern grey kangaroo (Southwell, in prep.; my observations) make less pronounced daily movements, which do not necessarily involve passage from one vegetation type to another.

It seems clear, therefore, that the dependence of the members of a species on fixed hiding places or refuge habitats within their home ranges is very strong in small species of macropodoids but diminishes with increasing body size; red-necked wallabies lie near the mid-point of this continuum. Probably the strength of the attachment of individuals to their home ranges also declines with body size. There could be several reasons for this scaling of the style of home range use to body size. It could be that small size allows animals to

easily enter and conceal themselves in nests, burrows or caves, and therefore to consistently exploit them to avoid environmental extremes and conceal themselves from predators. It may also be important that the mass-specific energy costs of locomotion fall, and the maximum attainable velocities rise, with increasing body size (Taylor et al. 1970, Bonner 1965, Peters 1983). Large animals may therefore be better able than small to outrun predators over long distances. These relationships have been deduced over many orders of magnitude of variation in body size, and can be expected to apply only loosely over the relatively narrow body size range which contains the macropodoids; however, they may predispose the members of small species to remain concealed for as much of their time as is practicable and to flee only short distances into cover or to a refuge, or from one hiding place to another, while larger species may venture much further into the open to feed, remain on the alert so as to detect predators from a distance, and outrun them if necessary (see also Jarman 1974, Jarman and Jarman 1979).

The habitat preferences I have been describing for red-necked wallabies were not expressed equally by all classes of wallabies. Females tended to stay closer to the edges of large belts of dense cover when with young-at-foot than at other times. The distribution of females, which very closely followed the creek flats and gullies, was imperfectly matched by males. This difference was almost entirely due to the tendency of medium males to spend large proportions of their time outside areas of high female density.

Infant wallabies, particularly during their first months out of the pouch, spend almost all of their time in dense vegetation and gullies (see Ch. 6). Mothers probably shifted their own home ranges towards these areas so that their young could live within cover while still having regular contact with their mothers. This habitat preference by mothers and their infants probably made the infants less vulnerable to predation than would have been the case had they ventured often into open areas. A similar, but more dramatic shift in habitat use by mothers with young has been observed in the moose *Alces alces* of Isle Royale by Edwards (1983). Cows swim to small wolf-free islands just before giving birth, and remain on them while their

calves are small and vulnerable to predation; this in spite of the lower quality of food available on small islands.

I suspect that medium males were partially displaced by large males from places preferred by other classes of the population. Large male red-necked wallabies were dominant to smaller males (see Ch. 8) and tended to direct much of their aggression towards medium males. Medium and large adult males sometimes fed together in relative peace, but if the smaller male made any movements or took any actions which drew the attention of the larger male, he was likely to be attacked. Harassment of this kind could have led medium males to avoid contact with large males by shifting slightly away from areas heavily used by them (and by females). These males may have moved back into preferred areas when larger, and able to prevail over a greater proportion of the adult male population. More complete separations of the habitats used by dominant and subordinate adult males are found in some of those species of ungulates in which males defend territories. For example, dominant male vicunas *Vicugna vicugna* defend territories for their groups of females on fertile meadows, and thereby force bachelor males onto barren, stoney ground (Franklin 1978, 1982).

TABLE 3.1: Seasonal variation in home range size and heterogeneity of use, female wallabies

A Females with annual centres of activity within winter concentrations

	Summer 1982 (n = 5)	Winter 1982 (n = 6)	
Home range size (medians, ha)	4.06	6.90	U = 10, n.s.
Heterogeneity (medians)	1.20	1.08	U = 11, n.s.

B Females with annual centres of activity outside winter concentrations

	Summer 1982 (n = 8)	Winter 1982 (n = 9)	
Home range size (medians, ha)	6.45	14.89	U = 15, P < 0.05
Heterogeneity (medians)	1.16	1.32	U = 21, n.s.

TABLE 3.2: Seasonal variation in home range size and heterogeneity of use, male wallabies

A Males with annual centres of activity within winter concentrations

	Summer 1982 (n = 7)	Winter 1982 (n = 6)	
Home range size (medians, ha)	10.56	13.50	n.s.
Heterogeneity (medians)	1.06	1.14	n.s.

B Males with annual centres of activity outside winter concentrations

	Summer 1982 (n = 5)	Winter 1982 (n = 4)	
Home range size (medians, ha)	10.12	11.47	n.s.
Heterogeneity (medians)	1.17	1.05	n.s.

TABLE 3.3: Coefficients of correlation between distributions of classes of wallabies (see text 3.2 for details; **Fost** are females in oestrous, other abbreviations explained in Chapter 2)

	Fly	Fmy	Fyf	Fost	M _L	M _M	M _S	SA
Fly		0.58	0.66	0.55	0.67	0.52	0.16	0.69
Fmy			0.73	0.43	0.40	0.40	0.37	0.76
Fyf				0.47	0.55	0.58	0.34	0.88
Fost					0.47	0.66	0.23	0.44
M _L						0.32	0.15	0.55
M _M							0.39	0.61
M _S								0.39
SA								

TABLE 3.4: Patchiness (mean/median cell occupancy rates) of distributions of classes of wallabies

Class	Fyf	M _S	Fly	Fost	M _L	SA	M _M	Fmy
Patchiness	2.53	2.37	1.71	1.38	1.36	1.22	1.12	1.08

TABLE 3.5: Reproductive condition and home range use by females, summer 1982/83. Kruskal-Wallis test for heterogeneities: $\chi^2 = 9.74$, 2 d.f., $P < 0.01$ (vertical lines to the left of the columns of figures join medians which do not differ significantly)

Reproductive class	Medians of:		n
	Home range size (ha)	Heterogeneity	
Fmy	5.50	1.00	6
Fly	4.37	1.12	9
Fyf	4.15	1.28	6

CHAPTER FOUR

Group Size and the Dynamics of Grouping

4.1 Introduction

Many ecological pressures may influence gregariousness in animals, but perhaps the two most general and powerful factors are, firstly, the effects of group size on the vulnerability of group members to predation, and, secondly, the effects of food quality, density and distribution on grouping behaviour (see Alexander 1974, Jarman 1974, Bertram 1978, Clutton-Brock and Harvey 1978).

Grouping may protect animals from predation not only because an individual who is surrounded by companions can be warned of the approach of a predator earlier than if it were alone, but also because its companions are alternative victims for the predator and (in certain species) the whole group may engage in coordinated defensive or evasive tactics (Wilson 1975, Hamilton 1971, Bertram 1978). Reductions in the vulnerability to predation of individuals living in groups have been demonstrated in free-living populations (e.g. Kenward 1978, Treherne and Foster 1980), and it has also been shown for a number of species that groups are most likely to form in places where either the densities of predators, or the exposure of animals to potential predators, is high (Lott 1984).

There are several ways in which the distribution and quality of food items can influence grouping behaviour. In species for whom each food item is both valuable and rare, or otherwise difficult to obtain, feeding interference between group members will be severe, and individuals may feed less efficiently when with others than when alone: at some point the company of others becomes, on balance, a liability rather than an asset, and the animals therefore remain solitary and rely on strategies other than grouping (crypsis, for example) to avoid being killed by a predator (see Jarman 1974, Clutton-Brock and Harvey 1977, 1978, Van Schaick 1983). On the other hand, an even, dense dispersion of easily collected food items may facilitate the maintenance of groups because in such circumstances group members need not sacrifice much feeding time in order to coordinate their speeds

and directions of travel so as to remain in constant, close contact (Jarman and Jarman 1979). A clumping of food items, however, such that many individuals or small groups are attracted to each food source but none is able to defend exclusive access to it, will promote the formation of large groups (Clutton-Brock and Harvey 1978, Strushaker and Leyland 1979, Wilson 1975, Lott 1984).

In this chapter I use the term 'group' to describe any gathering of wallabies in one place. The problem of whether certain individuals occur together in groups more often than would be expected by chance will be taken up in Chapter 7; for now, I will describe variations in group size and group dynamics in red-necked wallabies in order to provide material for a discussion of the ecological pressures likely to be regulating group size in this species. The analysis proceeds by first considering inter-population variation in group size; then describing seasonal variation in group size at Wallaby Creek in relation to spacing within groups, rates of movement of group members and rates of group flux; and concludes by showing how the activities of group members vary with group size. These comparisons permit a partial assessment of the effects of resource quality and distribution on grouping behaviour, and the relationships between group size on the one hand and the feeding activity and vigilance of group members on the other.

4.2 Data collection and analysis

Data on group sizes were collected during searches of the study area. Two wallabies were regarded as belonging to the same group if they were within 30 metres of one another when first sighted. As Fig. 4.1 shows, nearest neighbours within groups were rarely more than 24 metres apart; the chosen distance criterion should therefore allow accurate determinations of the sizes of natural groups of wallabies. The distance from each wallaby to its nearest neighbouring group member was recorded whenever I was satisfied that the wallabies had not been disturbed by my approach before I had sighted them.

Continuous observations of groups were broken up into half-hour bouts, wherein I recorded all arrivals to and departures from the group; the activity of each member at one-minute intervals; and the distance moved by each wallaby over the entire half-hour. Groups of oestrous females and attendant males, and females with young-at-foot,

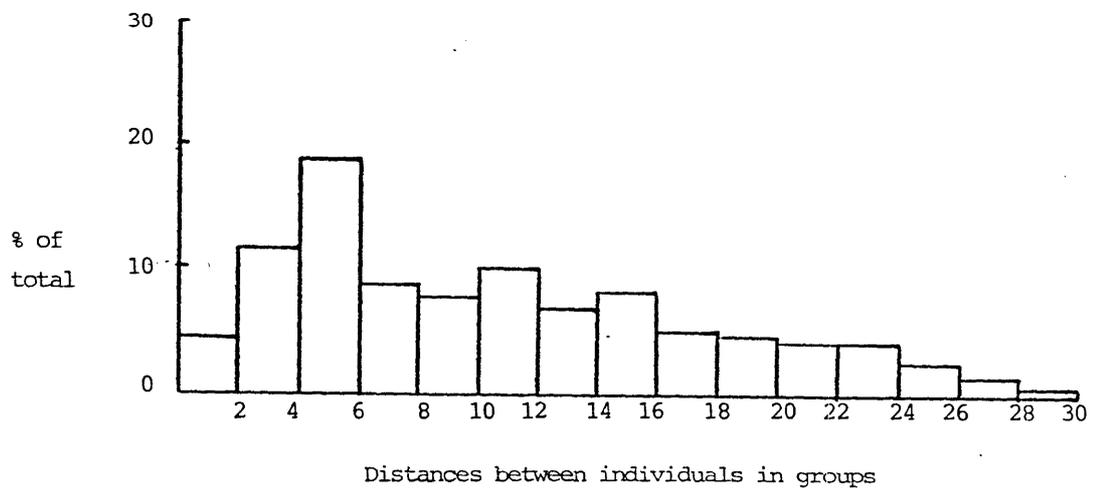


Fig 4.1 Frequency distribution of nearest neighbour distances within groups (n=418).

were excluded from this analysis : details of the structure and dynamics of such groups can be found in chapters 6, 8 and 9. Most of the data on rates of group flux and rates of progression of group members were collected during 1982 and the first half of 1983.

4.3 Inter-population variation in group size

The mean and typical group sizes (see Jarman 1974) of red-necked wallabies observed at six sites in southeastern Australia are shown in Table 4.1. Group sizes were similar at all sites excepting the Grampians in western Victoria, where the wallabies were unusually solitary. All of the other populations are in the coastal ranges : it may be that red-necked wallabies become more solitary as one moves from the eastern ranges towards the drier inland of Australia.

Estimates of the densities of red-necked wallabies are available for Southwell's two study sites in the Styx River area, and for my Wallaby Creek study area. The Wallaby Creek area can be divided into two density strata : a low density ($33.3 \text{ animals/km}^2$) stratum to the east of 13 E (see Chapter 3) and a high density stratum ($65.7 \text{ animals/km}^2$) to the west of this line. The mean group sizes in these two strata are plotted, with Southwell's data, against their respective densities in Fig 4.2. Group sizes of red-necked wallabies clearly do not increase with density. This non-relationship is contrasted in Fig 4.2 with the positive relationship between group size and density established for the eastern grey kangaroo by Southwell (1984a).

The frequency distribution of the sizes of groups observed at Wallaby Creek is shown in Fig 4.3 : 61% of all sightings were of solitary individuals, and the frequency with which larger groups were sighted declined with group size. The distribution of group sizes in other areas also takes this form (see, for example, Kaufmann 1974b, Clancy 1982).

4.4 Seasonal variations in grouping behaviour

4.4.1 Group size. The monthly mean and typical group sizes recorded over the two and a half years of intensive data gathering at Wallaby Creek are shown in Fig. 4.4; the sample sizes used to calculate these averages varied from 59 to 352 groups sighted in each month, with a

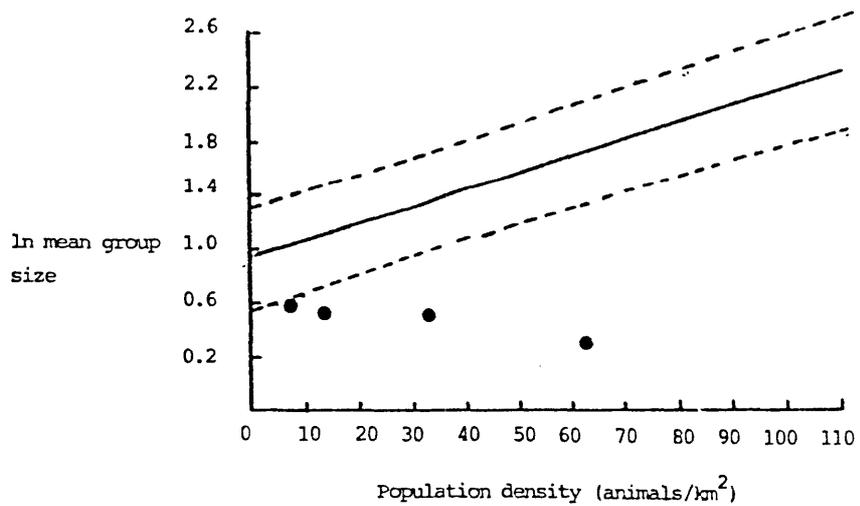


Fig. 4.2 Group size and density in red-necked wallabies and eastern grey kangaroos (least squares regression with confidence limits); data on red-necked wallabies represented by points, data on eastern grey kangaroos (from Southwell 1984a) represented by lines.

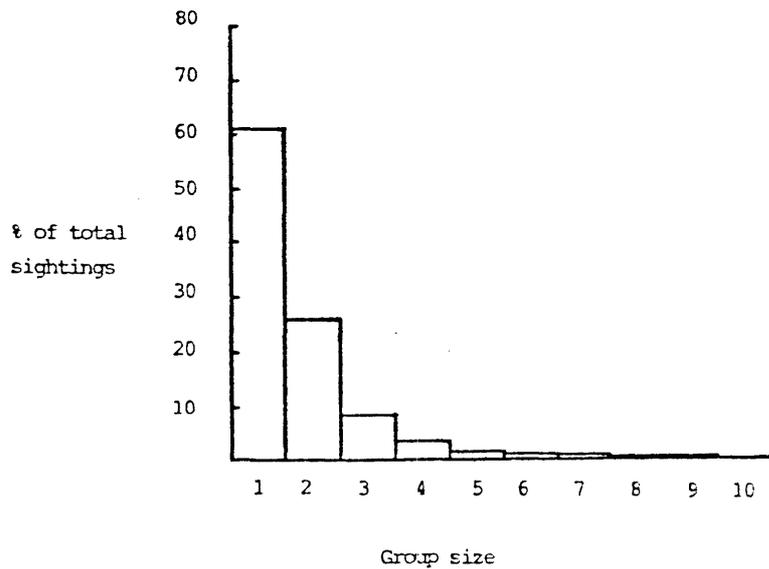


Fig 4.3 Frequency distribution of group sizes of red-necked wallabies at Wallaby Creek (n=6924).

mean of 229. In each year, the wallabies were most gregarious in winter and most solitary in summer.

4.4.2 Spacing within groups. Fig. 4.5 shows how the median nearest neighbour distances within groups varied throughout the year : nearest neighbours in groups of two tended to be closer together in summer but became on average, more distant through the autumn and winter. The analysis was restricted to groups of two to avoid the confounding influence of seasonal changes in group size distributions.

4.4.3 Rates of progression by feeding wallabies. An individual wallaby's rate of progression was measured in the field as the distance it covered during one half-hour observation period. The medians of these estimates for feeding wallabies in each calendar month are plotted in Fig. 4.6 (resting wallabies had very low rates of movement). Rates of progression while feeding were lowest in summer and peaked in late winter and early spring.

4.4.4 Group flux. Group flux was measured as the number of animals joining or leaving a group during a half-hour bout of observation, divided by the number of animals who had been in the group at the beginning of the bout. Because a solitary wallaby cannot leave itself, values of this group flux index for groups of different initial sizes are not directly comparable. Calculating group flux indices for each group size class (1, 2 or >2 group members) and averaging these for each time period, however, gives a standard measure of group flux in that time period, which is independent of seasonal variations in group size frequency distributions. As Fig. 4.7 shows, this standard measure of group flux was maximal in winter and reached its lowest value in summer. Winter groups were, therefore, much less stable, regardless of their size, than were summer groups.

4.5 Feeding activity in relation to group size.

Table 4.2 shows that wallabies in large groups spent a slightly lower proportion of their time feeding than did solitary wallabies, although this difference does not reach significance. There was no apparent relationship between group size and time spent

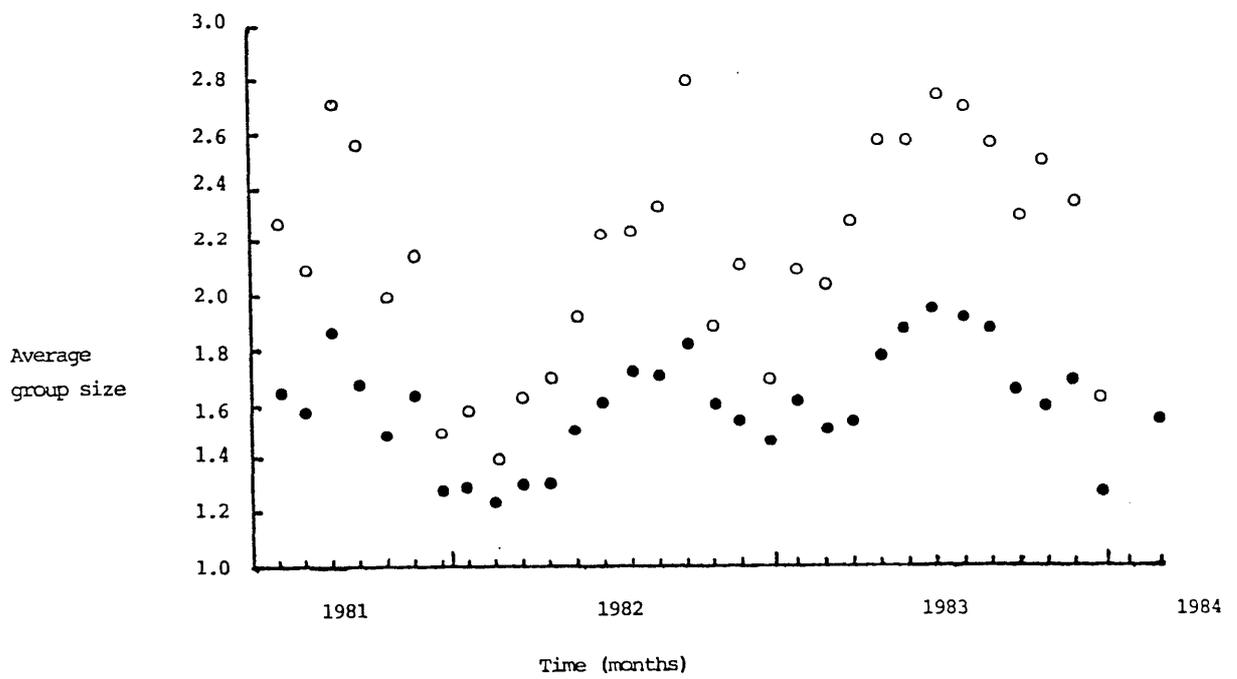


Fig 4.4 Monthly variation in mean (●) and typical (○) group sizes of red-necked wallabies at Wallaby Creek.

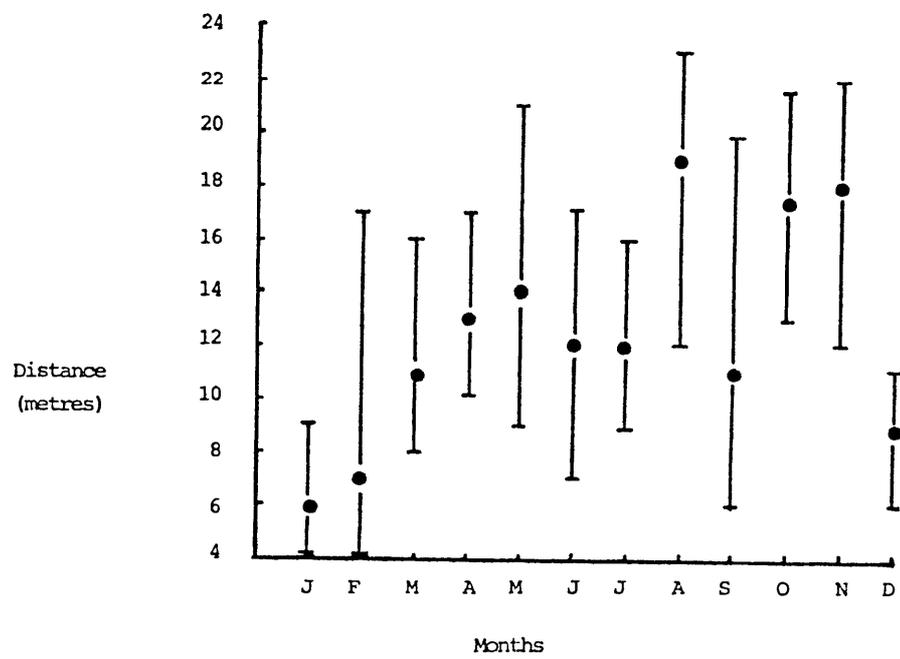


Fig. 4.5 Monthly variation in inter-individual distances (medians, with 95% C.I.s) within groups of two.

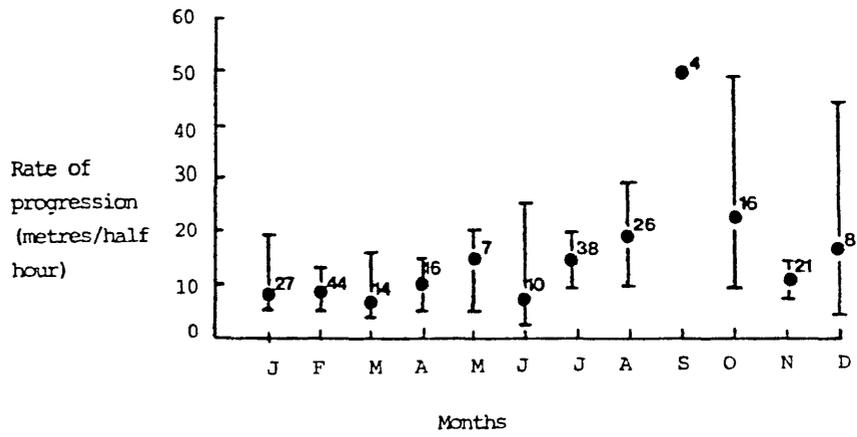


Fig. 4.6 Monthly variation in rates of progression of feeding wallabies (medians with 95% C.I.s and sample sizes).

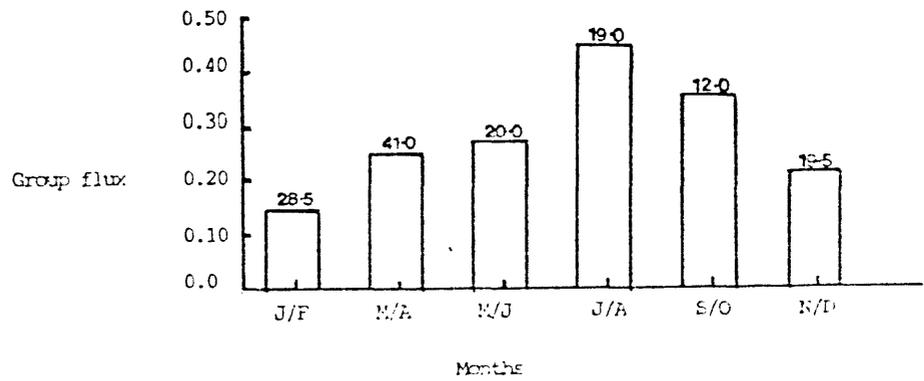


Fig. 4.7 Seasonal variation in rates of group flux (numbers above the bars are hours of observation), feeding wallabies. See text for explanation of calculation of group flux index.

alert. The entries in Table 4.2 are means of the proportions of their time spent by wallabies in each activity during half-hour observation bouts. The observation bouts included were all conducted during the first three hours after dawn and the last three hours before dusk, when feeding was the predominant activity. Summer and winter values were similar, and have therefore been combined in Table 4.2.

Although the apportionment of time into coarse categories of activity was not significantly affected by group size, rates of progression while feeding did vary significantly. As Fig. 4.8 shows, rates of movement by feeding wallabies were higher in large groups than in small. The effect was evident during that half of the year when rates of progression were low (January to June), but was only strongly significant during the latter half of the year, when rates of movement tended to be high (July to December, by Kruskal-Wallis : $\chi^2 = 11.28$, 2 d.f., $P < 0.01$).

4.6 Discussion

Red-necked wallabies are among the least social of the members of the genus *Macropus* and, in contrast to their more gregarious congeners, their tendency to spend their time alone or in small groups is unmodified by population density (cf eastern grey kangaroos Southwell 1984a, Taylor 1982a; wallaroos Taylor 1982a; and red kangaroos Johnson 1983). In high density populations, the frequency of chance encounters between individuals should also be high and should lead, other things being equal, to the formation of relatively large groups : the fact that this does not occur in red-necked wallabies implies that they somehow resist this process of the random formation of large groups in high density populations. Comparisons of group dynamics in high and low density populations will be required to show how this comes about - such comparisons cannot be made with the data currently available.

The prospects for accounting satisfactorily for the seasonal variations in grouping behaviour at Wallaby Creek are rather better. The quality of the wallabies' food there is subject to strong seasonal variation : pasture plants grow very rapidly during the warm, wet summer months, but plant growth slows as rainfall eases during autumn, and practically ceases after the first frosts fall in May or June ; summer conditions do not return until November or December. During

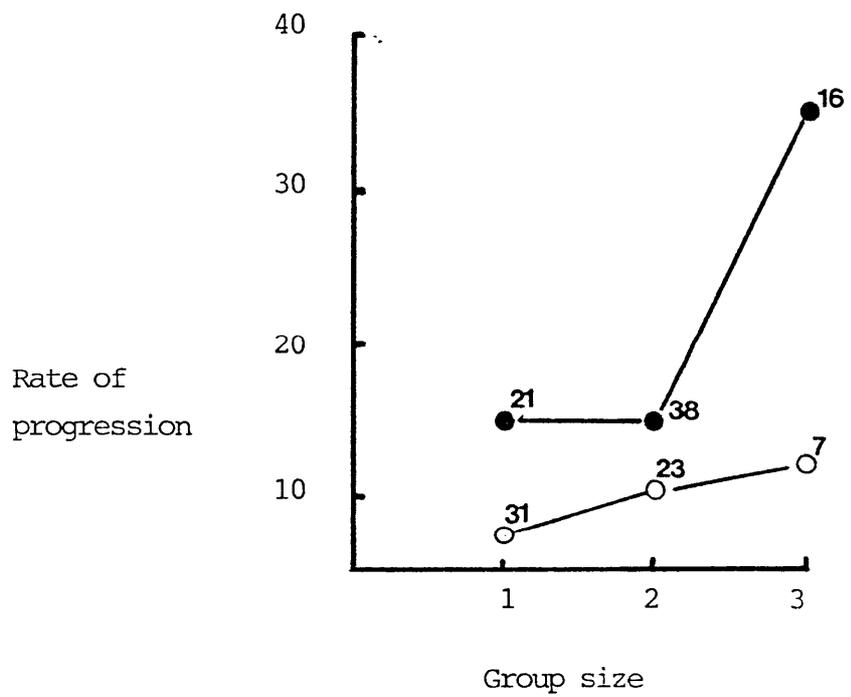


Fig. 4.8 Rates of progression of feeding wallabies in relation to group size, with sample sizes (nos. of half-hour bouts of observation). Summer (o) and winter (●) observations.

summer, plant growth rates obviously exceed herbivore offtake, and the pastures grow long, but are quickly grazed down in winter.

The observation that the wallabies' rates of progression while feeding rose as the quality of their food declined during winter suggests that they were being forced to increase the proportion of their feeding time devoted to searching for food items of acceptable quality. As their rates of progression while feeding rose, the spacing between individuals in groups increased, and groups became less stable. This loss of coordination within groups should have resulted in a fall in average group size : however, groups actually became larger in winter. This increase in group size was probably a response to an exaggeration in the clumping of relatively high quality food resources in winter. During the winter, the wallabies concentrated their activities on a series of relatively small and isolated patches of pasture on deep soils close to the creek (see Ch. 3, Fig. 3.8). The suggestion that the increase in group size during winter was due to the concentration of many animals on small patches of habitat is strengthened by a comparison of changes in habitat use and concomitant trends in group size in 1982 and 1983. Seasonal changes in habitat use were most pronounced in 1983 (see Ch. 3) and in that year typical group sizes varied two-fold (Fig. 4.4) ; the less dramatic seasonal concentration of wallabies in 1983 was associated with that year's relatively narrow (1.6- fold) range of variation in typical group size.

My observations show that wallaby groups in summer were small, relatively compact, and stable, whereas in winter groups were larger, straggling, more loosely organised aggregations. The functional explanation I have offered for this change is based on evidence that is largely circumstantial - more data are needed on seasonal variations in feeding behaviour, food quality and food quality gradients.

Evidence on direct feeding interference between group members is likewise circumstantial. The amount of their morning and evening time that wallabies devoted to feeding was not strongly influenced by group size; if anything, wallabies in large groups fed a little less intensively than those in smaller groups. The proportion of time spent alert was also nearly constant in groups of various sizes. Again, more refined data on feeding intensity and efficiency would be

worthwhile, but the apparent non-relationship does contrast interestingly with the results of studies on more gregarious species of animals. A number of authors have shown that in social species the average proportion of time that individuals devote to feeding increases, while time spent alert drops, with increases in group size. Solitary eastern grey kangaroos, for example, spend approximately 58% of their time feeding and 36% of their time alert, while kangaroos in large groups of 12 or more members spend about 80% and 5% of their time in the same activities (Southwell 1981). Similar trends have been documented in bighorn sheep *Ovis canadensis* (Berger 1978), pronghorn antelope *Antilocapra americana* (Lipetz and Bekoff 1982), ostriches *Struthio camelus* (Bertram 1980), house sparrows *Passer domesticus* (Elgar et al. 1984) and other species. Data of this kind have generally been interpreted as showing that individuals in large groups take advantage of the cumulative vigilance of other group members by reducing their own watchfulness (see Pulliam 1973; the argument assumes, of course, that animals in groups can quickly detect the alarm reactions of other group members). For such species grouping not only confers added protection from predators through early warning of their approach, it also allows them to be rather less vigilant and thus to spend more time gathering food.

It is probably because group members so often drift apart that red-necked wallabies do not also follow the pattern discussed above. Southwell's (1984b) measurements of group flux in the eastern grey kangaroo show groups of this species to undergo fewer changes of membership per unit time, despite their larger size, than do groups of red-necked wallabies.

The positive relationship between rate of progression while feeding and group size in red-necked wallabies can plausibly be viewed as a consequence of direct interactions resulting in displacements of wallabies, or of more subtle adjustments of the positions of feeding wallabies maintaining inter-individual separations beyond some acceptable minimum. Both kinds of interactions, if they occur often enough, could restrict the freedom with which individuals in groups search for food items, and therefore the efficiency with which they gather food. That this sort of thing can happen is shown by Van Schaick et al.'s (1983) detailed study of feeding activity, social interactions and group size in the long-tailed macaque *Macaca*

fasicularis. Individual macaques avoid very close association with neighbours while searching for food, and tend to move aside if approached by another animal. Probably as a consequence of this, individuals in large groups spend more time travelling and searching for food, and less time resting and feeding, than do individuals in small groups, and large groups go on longer day-journeys than do small. Wyre (1981) has shown that swamp wallabies, which are even less gregarious than are red-necked wallabies, spend less of their time feeding and engaging in 'relaxing' activities, and more time grooming and moving, when in groups than when alone.

Whatever the causes of the faster rates of progression of red-necked wallabies in relatively large groups, it doubtless contributes to the instability of larger groups, and is a force inclining the animals towards a solitary existence.

TABLE 4.1: Records of group size from several populations of red-necked wallabies

Locality	Group size:		Source
	Mean	Typical	
Wallaby Creek	1.63	2.25	This study
Bonalbo, Nth N.S.W.	1.50	2.10	Kaufmann (1974b)
Styx River, Nth N.S.W. (I)	1.82	1.99	Southwell (1981)
Styx River, Nth N.S.W. (II)	1.70		Southwell (1981)
Grampians, W. Victoria	1.24	1.54	Coulson (pers. comm.)
Nile District, Tasmania	1.56	2.13	Clancy (1982)

TABLE 4.2: Group size and feeding activity of red-necked wallabies (entries are means of proportions of each ½-hour observation spent feeding and alert)

Group size	% of time devoted to:		n (observation bouts)
	Feeding	Alertness	
1	76.7	14.2	8
2	78.6	17.0	31
≥3	72.6	16.7	15