

CHAPTER FIVE

Inter-Birth Intervals and Seasonal Breeding in Relation to Sex of Offspring

5.1 Introduction

The patterns of seasonality of breeding by macropodid marsupials vary widely, from populations in the tropical north, and the arid centre and north west of Australia, wherein breeding is completely aseasonal, to populations inhabiting the far south of the continent in which all young are born within clearly defined breeding seasons. Between these two extremes lie many populations in the non-arid mid-latitude regions of Australia where some young are born in all seasons although births are distributed unevenly through the year - breeding patterns of this kind are here referred to as 'partially seasonal'.

Completely aseasonal breeding occurs where individuals breed opportunistically in response to seasonally unpredictable environmental variables, such as are found in the non-seasonal arid regions of Australia and the monsoonal tropics (where conditions may be unfavourable to infant survival in wet and dry seasons), (see Newsome 1964, Frith and Sharman 1964 and Sadleir 1965 on red kangaroos; Ealey 1963, Sadleir 1965 and Russell and Richardson 1972 on euros; and Bolton *et al.* 1982 and Kirkpatrick and Johnson 1969 on agile wallabies). Populations in which breeding occurs only at certain regular times of the year are found in areas receiving cold, wet winters, and in these populations births are timed so that most young leave the pouch during spring and summer - any young born outside the breeding season would presumably have severely reduced survival prospects (see Berger 1966 and Inns 1980 on tammar wallabies; Merchant and Calaby 1981 and Catt 1977 on Bennett's wallabies; Rose and McCartney 1982a, b on red-bellied pademelons ; and Pearse 1981 on eastern grey kangaroos). The mechanism responsible for maintaining the seasonal pattern of breeding of tammar wallabies is now well known. All female tammars enter a seasonal quiescence which begins around the winter solstice and ends at the summer solstice; during

this period females are in anoestrous and the blastocysts they carry remain dormant regardless of the presence or absence of a young in the pouch. During the breeding season blastocysts may reactivate and oestrus cycles recommence in females who lose young from the pouch. These two forms of fertility regulation - seasonal quiescence during periods of increasing day length and lactational quiescence during periods of decreasing day length - differ in their endocrine control mechanisms, and the former is clearly a special adaptation to limit births to late summer and autumn (Tyndale-Biscoe and Hinds 1981, 1983). The breeding season is restricted by similar means in Bennett's wallaby (Merchant and Calaby 1981).

Partially seasonal patterns of breeding may evidently be stable from year to year. Such stability can be inferred from the fact that in all of five studied populations of eastern grey kangaroos in New South Wales and Queensland, frequencies of births were highest during the spring and summer months (Taylor 1982, Kavanagh 1977, Caughley 1962, Kirkpatrick 1965; see also Poole 1983); this is apparently also generally true of western grey kangaroos (Poole 1973, 1976; Bayliss 1980). Much remains to be understood about the maintenance and significance of stable patterns of partially seasonal breeding in macropods, particularly in species such as red-necked pademelons (Johnson 1977) and red-necked wallabies (see below) where females' inter-birth intervals are less than twelve months in duration. In populations where average inter-birth intervals differ from one year in length, females will breed in different calendar months in successive years, and thereby drift out of the peak birth season. If partially seasonal patterns of breeding are to be maintained in such populations this must either be because some of the females undergo a seasonal quiescence (in which case we would need to know what factors determine whether or not a given female will give birth in the 'non-breeding' season, and what effect this will be likely to have on the outcome of that breeding effort); or the length of a female's interval must vary seasonally for other reasons. Either of these phenomena - facultative seasonal quiescence, or seasonal variation in the time taken to complete a normal reproductive cycle - would be of considerable ecological and physiological interest. Alternatively, partially seasonal breeding could be produced and maintained if breeding were dominated by first-time breeders, who enter breeding

condition in synchrony, but drift out of the birth peak in later years.

This chapter examines fecundity and inter-birth intervals in the study population of red-necked wallabies, in order to show how the observed pattern of partial seasonality of breeding is maintained. I also look at the effects of season on infant survival, and compare the breeding patterns of females bearing male and female young.

5.2 Data collection and analysis

Females who had been observed monthly over periods including at least one complete reproductive cycle (birth/mating - pouch life - pouch vacation - birth/mating) were included in this analysis. Because females give birth about three weeks after an infant leaves the pouch, and mate within a day or two of giving birth (Merchant and Calaby 1981) parturition dates can be estimated to within half a month using records of pouch vacation, or to within a few days using observations of courtship. These determinations were used to estimate durations of pouch lives of infants and inter-birth intervals for adult females. Under normal circumstances, infants became visible to me as a bulge in the pouch three months after their birth and entry to the pouch. A delay in the appearance of a bulge in the pouch alerted me to the possibility that a female had become reproductively inactive, or that a very small pouch young had died and been replaced without me seeing the episode of courtship which would have heralded the birth of the succeeding infant.

5.3 Seasonal variation in frequencies of births, and continuity of breeding

The monthly frequencies of births recorded during the three years of this study are shown in Fig. 5.1; these frequencies are expressed as the proportion of the females present in the study population in a given month, who gave birth in that month. The data have been combined into bi-monthly periods to reduce sampling variation, which may have been particularly high during the first year of the study when a relatively small number of females was recognisable. Frequencies of birth varied substantially within each year, and were typically high in mid-winter or early spring (July to October) and low in autumn (March and April). In 1982 there was also

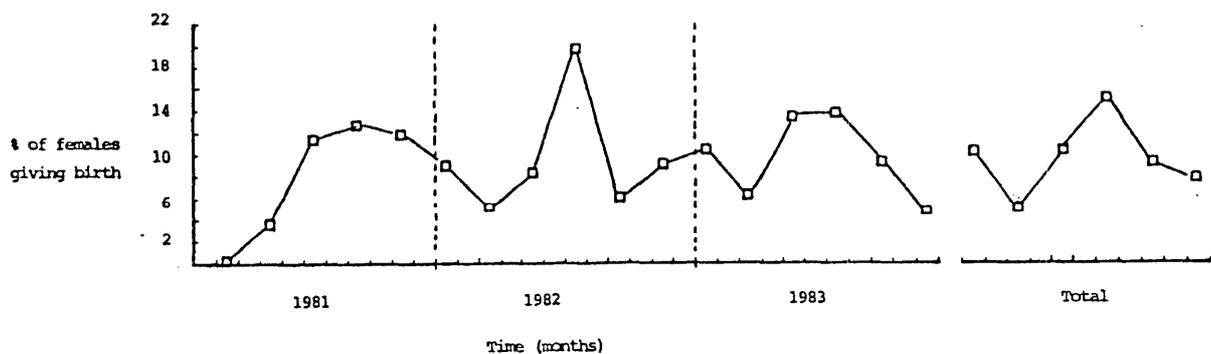


Fig. 5.1 Seasonal variation in birth frequencies.
(n = 115 births)

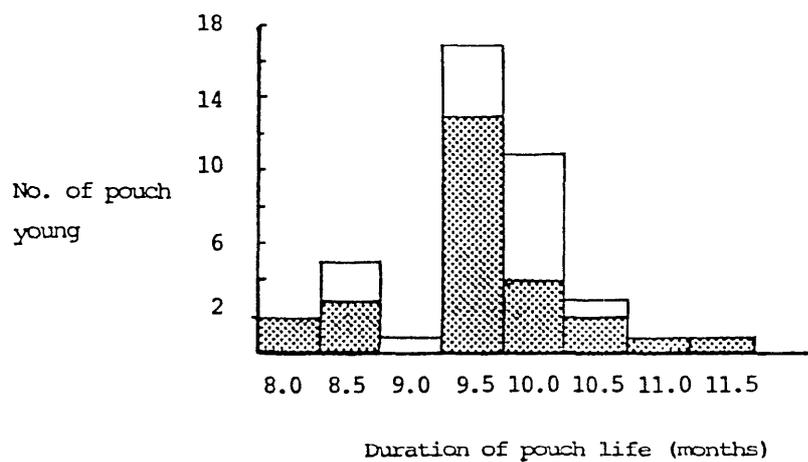


Fig. 5.2 Distributions of durations of pouch lives of young seen to be alive after leaving the pouch (stipled bars) and those not (open bars).

a faint birth peak in mid-summer. The total number of births occurring in each bi-monthly period differed significantly from the number which should have been given, had there been no seasonal variation in birth frequency ($\chi^2 = 11.36$, 5 d.f.; $P < 0.05$).

Female red-necked wallabies, when breeding without pause, should have young in the pouch continuously except for the three-week period between the vacation of the pouch by one infant and the birth and entry to the pouch of the next. Only four of the 76 females included in this analysis gave evidence of having spent more than a month at a time with an empty pouch. I could find no other evidence that some adult females undergo any form of reproductive quiescence between normal cycles. If this does occur in this population it is certainly of minor significance, at least under the environmental conditions that obtained during my study, and in any case is apparently not seasonal in its occurrence.

5.4 Variation in the Durations of Pouch Lives

5.4.1 Breadth of variation. Observed durations of pouch lives varied widely, from as short as eight months to as long as 11.5 months (see Fig. 5.2). However, before anything can be made of this, the data should be checked for two possible sources of bias.

Firstly, it is possible, given the way the data were collected, that some of the pouch lives which seemed unusually short might actually have been cases where a large pouch young died and was abandoned by its mother before the time it would have left the pouch had it survived. To test this, I compared lengths of pouch lives of infants who were seen to be alive, and following their mothers as young-at-foot, after leaving the pouch, with those who were not seen after disappearing from the pouch. These two classes of infants are separated in Fig. 5.2. Clearly, there was no tendency for infants who died before being seen as young-at-foot to have disappeared from the pouch earlier than those who survived for some time after leaving the pouch. Mortality in the pouch appears to be very low in this population (see Appendix I); I suspect that most of the infants who were not seen after they left the pouch died during their first month out of the pouch, when mothers and young spend most of their time apart, and the infants are rarely seen because they live among dense

vegetation (see Ch. 6).

It is also possible that the long pouch lives I recorded were in fact cases where a very small pouch young had died and was replaced, and I did not see the courtship that would have accompanied the birth of a new young (some cases of possible, but unconfirmed, infant mortality in early pouch life are not included in any of the analyses presented in this chapter). However, as the data in Table 5.1 show, the median duration from the (assumed) birth of an infant to the time at which I first saw it put its head out of the pouch was similar for young who ultimately experienced short, intermediate and long pouch lives - the progress of pouch life for all three classes of infants was similar up until the time this first landmark was passed.

The amount of time spent by infants looking out of the pouch increased steadily from the sixth month of age, and began to fall only as they started to leave the pouch for short periods (Fig. 5.3). The proportion of time spent outside the pouch increased in its turn until the young was spending all of its time out of its mother's pouch. Although all of the wallabies started to look out of the pouch at the same age, those who were to reside in the pouch for long periods were first seen outside the pouch when slightly (but significantly) older than others (see Fig. 5.3 and Table 5.1).

5.4.2 Seasonality of variation. Fig. 5.4 shows the relationship between environmental temperature during the eighth and ninth months of pouch life (when some infants stay in their mother's pouch while others leave) and the ultimate duration of pouch life, for 36 infant wallabies. Temperature is measured as the average of the mean minimum temperatures for each month, and the relationship is significant for the whole sample by simple linear regression ($y = 10.3 - 0.65x$, $r = -0.3784$; 34 d.f.; $P < 0.05$ for regression coefficient, $P < 0.05$ for r). A better accounting of the data can be had by applying a cubic transformation to the temperature data ($y = 9.95 - 0.0002x^3$, $r = -0.4311$; $P < 0.01$ for regression coefficient, $P < 0.01$ for r). However, there was a stronger relationship between temperature and length of pouch life for male young only ($y = 11.0 - 0.095x$; $r = -0.6894$; 10 d.f.; $P < 0.05$, and $P < 0.02$). There was no apparent relationship between the two variables for female young, and a relationship of intermediate strength for young of unknown sex ($y = 10.37 - 0.085x$, $r = -0.5918$, 6

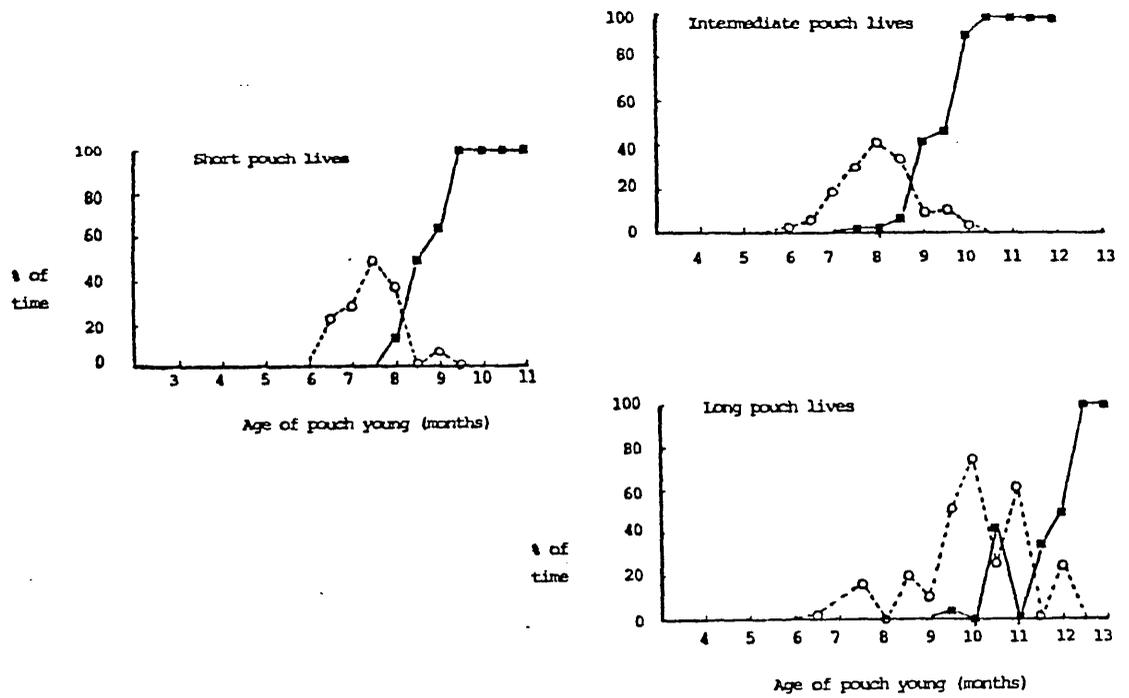


Fig. 5.3 Proportions of time spent by pouch young with head out of the pouch (o) and standing outside the pouch (■) in relation to age, for short (<10.0 months, n=5 infants), intermediate (10.0 and 10.5 months, n=6 infants) and long (>10.5 months, n=5 infants) pouch lives.

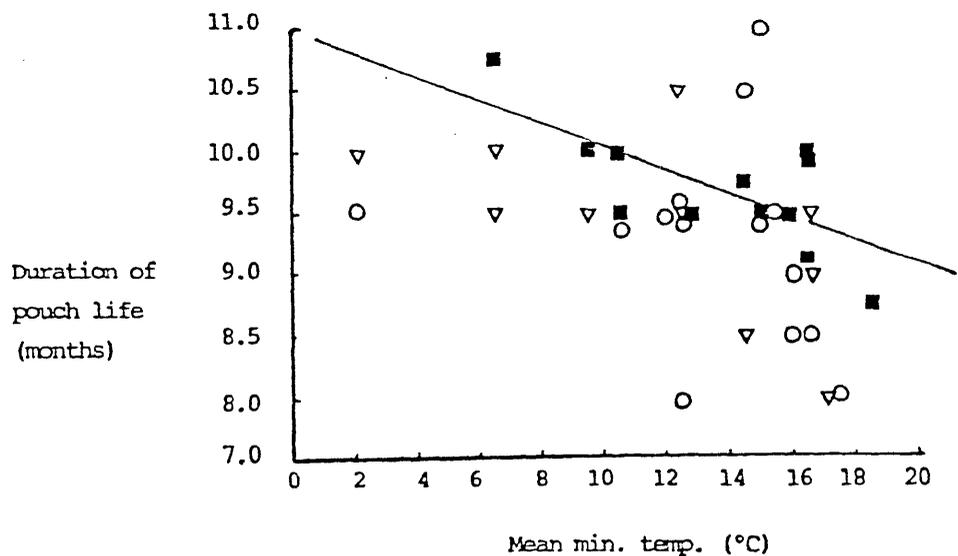


Fig. 5.4 Relationship between temperature during months eight and nine and ultimate duration of pouch life for male pouch young (■), female pouch young (o) and those of unknown sex (∇). The line shown is the regression for male young (see text).

d.f.; n.s.).

In Fig. 5.5, mean durations of pouch life, with 95% confidence limits, are plotted against month of pouch vacation for male infants, and for males, females and infants of unknown sex combined. As the relationship of Fig. 5.4 would suggest, young leaving the pouch in late winter, after several months of cold weather, tended to have had longer pouch lives than young leaving the pouch in late summer or early autumn, after several months of warm weather. The exaggeration of the pattern in the male-only curve suggests that the general pattern was due to the influence of variation in male pouch lives. Pouch lives of male and female young were similar in length (Fig. 5.6). No correlation could be found between rainfall in months eight and nine, and ultimate duration of pouch life.

5.4 Inter-birth intervals

I saw approximately half of the courtships of female wallabies that follow the emergence of one young from the pouch and the birth of the subsequent young. These all took place within a month of pouch vacation, regardless of the duration of that pouch life. It follows that, for female red-necked wallabies, the length of the interval from one birth to the next is (on average) dependent on season. The data on 36 inter-birth intervals of known duration have been used to construct Fig. 5.7, which relates the month in which a female gives birth in one year to the number of calendar months earlier (the 'drift') she will give birth in the next year. So, for example, a female who gives birth in August of one year will probably give birth just over one month earlier, in July, of the following year, whereas a female who gives birth in April one year will probably do so again in January of the following year.

5.5 Seasonal variations in infant survival

Table 5.2 shows the numbers of infants who emerged from the pouch during each of six bi-monthly periods and who survived to weaning. These numbers are compared with the numbers expected to have survived had there been no seasonal variation in survival probabilities. Of the 80 infants who emerged from the pouch during this study and whose fates I was able to ascertain, 40 survived to weaning, and there was little evidence that this survival rate varied substantially through

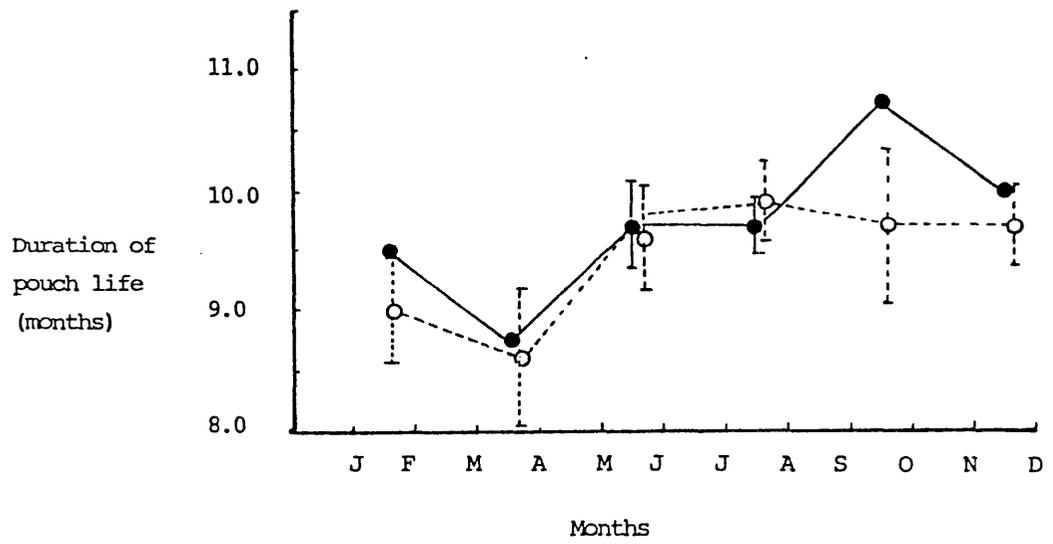


Fig. 5.5 Relationship between month of pouch vacation and duration of that pouch life (means with 95% C.I.s) for male infants (●) and all infants (○).

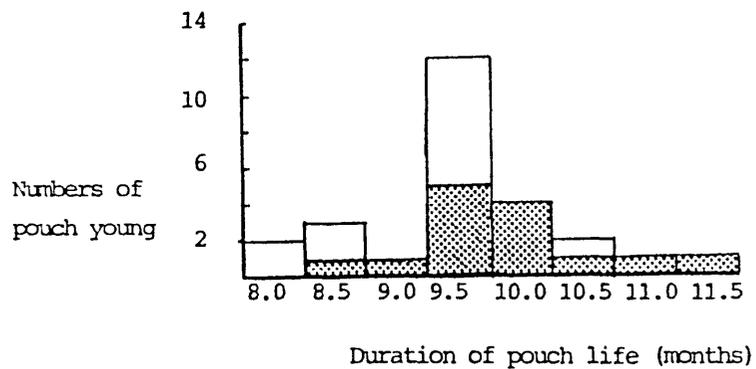


Fig. 5.6 Distributions of durations of pouch lives of male (stippled) and female (open) infants.

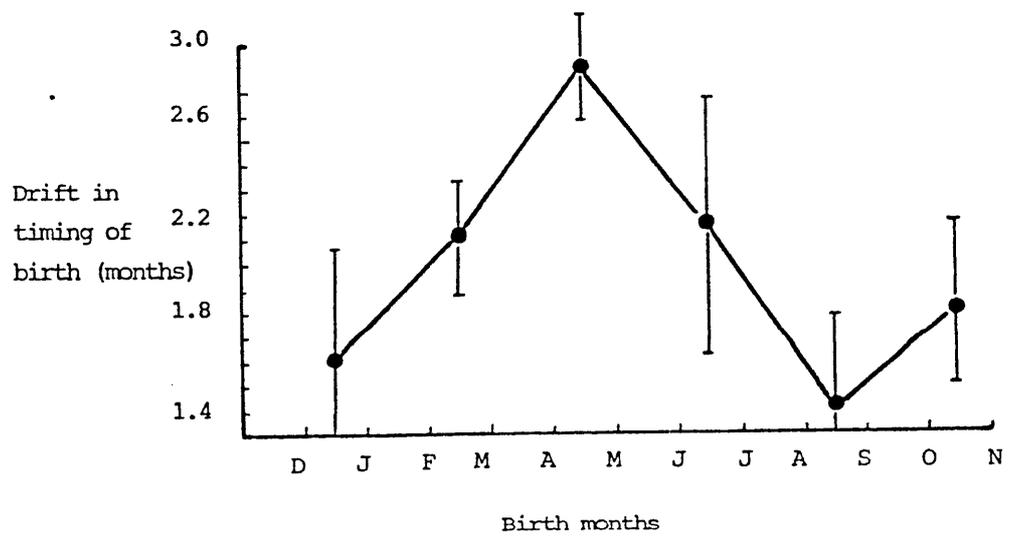


Fig. 5.7 Relationship between the month in which a female gives birth in one year, and the number of months earlier (means with 95% C.I.s) she will give birth in the following year.

the year : the observed and expected distributions in the table are similar ($\chi^2 = 1.90$; $P > 0.80$, < 0.90).

5.6 Timing of first parturition date for young females

The dates on which twelve young females gave birth for the first time were recorded. Half of these first parturitions took place during only two months of the year, January and July, which were both peak breeding months (see Fig. 5.1).

5.7 Discussion

The females of many species of macropods retain dormant embryos while also carrying young in the pouch (Renfree and Calaby 1981). The time at which these females give birth is determined by the action of the factors responsible for maintaining the embryo in diapause. Sharman (1963) inferred that it is the tactile stimulus of the mammary gland provided by a suckling young in the pouch which is primarily responsible for keeping the embryo in its quiescent state. He also demonstrated (Sharman 1963, 1965) that the period of diapause of the embryo in the female red kangaroo could be extended beyond its normal duration if the frequency of suckling was increased (by the fostering of a second young-at-foot to the female). Further experimental verification of the critical role of tactile stimulation of the mammary gland came from Renfree (1979), who showed that development of the diapausing embryo in lactating tammar wallabies could be resumed if the gland was denervated, even though the gland continued to function normally and the pouch young continued to suckle.

The timing of events in the reproductive cycle of the red-necked wallaby suggests that the quiescent embryo resumes development close to the time at which the pouch young permanently leaves the pouch (Merchant and Calaby 1981). The frequency with which the infant suckles almost certainly falls abruptly at this time. Even while they were temporarily outside the pouch, large pouch young had their heads inside the pouch for 33% of the time (see Ch. 6) and it is probable that they grasped the teat for much of this time. However, during their first month after leaving the pouch, infants suckled at a rate of only 0.14 bouts of, on average, about nine minutes each, per hour (Ch. 6). This change in suckling frequency is initiated by the mother when she refuses to allow her infant back into the pouch after one of

its excursions. The mother's behaviour is therefore in large measure also responsible for determining the length of the interval from one of her parturitions to the next. The burden of this chapter has been to show that the duration of this interval may vary widely under natural conditions.

There are some comparable data in these areas for eutherian mammals, particularly humans. It has been shown that the duration of lactational amenorrhoea in women is variable, and the most important factor controlling its length appears to be suckling frequency (see McNeilly 1979). It has also been shown that high suckling frequencies per se are associated with high levels of circulating prolactin in women (Delroye et al. 1977) and red deer *Cervus elaphus* hinds (Louden et al. 1983), although the role of prolactin in fertility regulation in these and other species of eutherians is somewhat unclear (Albon and Iason 1984, Louden et al. 1984, Webster and Haresign 1983). In women, post-partum lactational amenorrhoea is regarded as a variable pause between normal breeding cycles; I have considered the variation in inter-birth intervals of female red-necked wallabies to be due to differences in the lengths of uninterrupted normal cycles because the same factor - the tactile stimulation of the mammary gland - appears to control the return to oestrus throughout; it is the duration of its action which varies.

The seasonal pattern of the variation in the average length of the inter-birth interval is probably sufficient to account for the partially seasonal pattern of breeding found in this population, for the reason that females breeding in late winter of one year are likely to give birth at nearly the same time in the next year, whereas females breeding in autumn one year will give birth up to three calendar months earlier in the next year (see Fig. 5.7). In other words, females tend to drift out of late winter or early spring breeding more slowly than they drift out of autumn breeding, and therefore in any year more females will be giving birth in late winter and early spring than in autumn (Fig. 5.1).

This seasonal pattern has its origin in the tendency for infants whose pouch lives are well-advanced during cold months to remain in the pouch for longer than average, so that some infants who would otherwise have left the pouch during autumn and winter do not do so until late winter or early spring. This could be because such infants

have slower than normal rates of growth in the pouch, or are less active in getting out of the pouch, or because their mothers do not exclude them from the pouch until they are relatively old. Data collected by Clarke (1984) suggest that, in Bennett's wallabies, the quality of the resources available to adult females can affect the growth rates of their pouch young. Although growth rates of pouch young may well have varied during my study, I suspect that this is not the whole explanation of the variability in pouch lives, if only because some infants who left the pouch while still relatively young were also unusually small - this was something I noticed (and was astonished by) in the field, before I had begun to analyse data on the durations of pouch lives. Growth rates of all classes of infants were certainly uniform up until the sixth month, when they started looking out of the pouch; subsequent differences in their appearances outside the pouch could have been due either to differences in growth rates during this phase of pouch life or to subtle differences in the activity and behaviour of mothers or young.

Whatever the causes, the outcome for infants whose pouch lives were extended through winter was that they became more likely to be approaching weaning during late spring or early summer, when pasture conditions were improving.

The fact that this description applies only to males makes simple explanation of the adaptive significance of the phenomenon difficult. Perhaps young males benefit more from access to high quality pasture at weaning (or are more severely affected by relative food shortages earlier on) because of differences in their food requirements, metabolism or growth rates, which prepare them for the costs of dispersal and sustained growth into adulthood (males rather than females disperse, they grow larger than females, and the ultimate size a male reaches is critical in determining his reproductive success (see Chs. 7 and 8)). Clutton-Brock *et al.* (1985) have shown that in species where adult males are larger than adult females, juvenile males are likely to store less fat than females, and die in greater numbers during adverse conditions. The durations of females wallabies' pouch lives were as variable as those of males, but I could find no pattern to their variation.

One immediate consequence of the relationship between season and the probability of pouch vacation by males should be a seasonal

variation in the sex ratio of young leaving the pouch : males should be in excess at those times when a high proportion of young are leaving the pouch. I was able to sex only 58 young-at-foot, and failed to sex many of the ones who apparently died in their first month out of the pouch. This is an unsatisfactorily small sample for comparing monthly ratios. However the correlation between the total proportion of females whose young left the pouch in the bi-monthly periods of Fig. 5.1 and the sex ratio of those young, was in the expected direction ($r = 0.79$; 4 d.f.; $P < 0.1$; > 0.05) and approached significance.

Infants have moderate chances of survival regardless of the season at which they leave the pouch (Table 5.2). It is probably for this reason that strictly seasonal breeding has not evolved in red-necked wallabies living in this part of Australia. However, this chapter suggests that the wallabies' breeding biology is flexible enough to respond to relatively minor seasonal variations in resource quality, and to the sex of the current offspring.

TABLE 5.1: Passage of landmarks by infant wallabies experiencing short, intermediate and long pouch lives

Duration of pouch life (n = number of infants)	Age at first appearance of head out of pouch (median in months)	Age at first excursion from pouch (median in months)
Short (8.5-9.5 months) (n = 5)	7.0	9.0
Intermediate (10-10.5 months) (n = 16)	7.5	9.5
Long (11-11.5 months) (n = 7)	7.5	10.5
Significance of differences (by Kruskal-Wallis)	T = 1.253 P>0.50;<0.70	T = 9.04 P<0.02

TABLE 5.2: Monthly variation of infant survival rates ($\chi^2 = 1.90$, n.s.)

	Months :					
	D/J	F/M	A/M	J/J	A/S	O/N
Number surviving						
- observed	6.0	1.0	11.0	10.0	8.0	4.0
- expected	5.5	1.5	9.0	8.5	8.5	6.5
n	11.0	3.0	18.0	17.0	17.0	13.0



Plate 3. Female red-necked wallaby, with large pouch young temporarily outside the pouch.

CHAPTER SIX

Relationships Between Mothers and Infants

6.1 Introduction

The relationships between mother kangaroos and wallabies and their infants have been systematically observed in the wild in only three species (the whiptail wallaby, kaufmann 1974a; the euro croft 1981b; and the red kangaroo croft 1981a). Infants of these species follow their mothers closely from the time they leave the pouch. Ungulates similar in body size and habitat use to these species of macropods are usually 'hidiers' (Walther 1965, 1969, Lent 1974), that is, their newborn young spend long periods lying apart from their mothers in dense vegetation. Kaufmann (1974a) suggested that this apparent difference in behaviour between macropods and ungulates is a consequence of differences in their modes of reproduction : he argued that the period just before the permanent emergence of the young macropod from the pouch, when it may spend long periods outside the pouch but return to it when alarmed, takes the place of the hiding phase in the lives of many species of ungulates.

In this chapter, I describe behaviours akin to hiding in infant red-necked wallabies, then review the distribution of hiding-type behaviour in ungulates and macropods and compare the behaviour of newborn ungulates and infant macropods at comparable stages of development. The results of these comparisons and the detailed observations of mother-young relationships in red-necked wallabies are used to show how the pouch influences the survival strategies that young macropods adopt as they pass through it on their way to complete independence from their mothers.

6.2 Data collection

The locations and associations of mothers and young were recorded

during searches of the study area. A mother and her infant were deemed to be in association if within 30 metres of one another; exact distances between the two were estimated whenever possible. During systematic observations I recorded all interactions between mothers and young; their activities every minute; and the distances between them every ten minutes. Changes in the spatial relationships between mothers and young were measured by recording the numbers of approaches and withdrawals each made to or from the other. An 'approach' was defined as a movement by one wallaby from a distance of more than, to a distance of less than 20, 10, 5 or 2 metres from the other; withdrawals were defined as the converse of approaches. In addition to behaviour recorded systematically, bits and pieces of behaviour of mothers and infants were observed during searches of the study area.

6.3 Relationships between mothers and pouch young

6.3.1 Activities of pouch young. During the early part of its pouch life the infant wallaby is permanently attached to a teat (see Merchant and Calaby 1966), but it begins to put its head out of the pouch during its sixth month of life. The proportion of time spent by the infant with its head out of the pouch, and later the time spent altogether out of the pouch, increased steadily over the subsequent months (see Fig. 5.3). Excursions from the pouch varied in duration: they were usually brief if the mother was feeding in the open when her young left the pouch (mean = 8.0 min; n=8) but were often much longer if the mother was resting in cover, particularly if she was in a deep gully. The durations of these extended out-of-pouch excursions by infants were often difficult to measure, because the mother and young were usually both very alert while the pouch young was abroad, and the infant always leapt very quickly back into the pouch if disturbed in any way by the observer. However, three out of four excursions from the pouch made by young whose mothers were resting in cover lasted more than thirty minutes.

While temporarily out of the pouch, infants usually stayed within two metres of their mothers, except for brief exploratory dashes to 25 metres or so from them. They spent much time grooming themselves, and occasionally groomed or were groomed by their mothers. Pouch young

also spent a good deal of time in bodily contact with their mothers while out of the pouch, often with the head actually in the mothers' pouch (this was so in 33.3% of 63 minute-scans of the activity of infants temporarily abroad). For the rest, the infants intently smelled and examined objects close to their mothers, and occasionally nibbled at vegetation.

6.3.2 Interactions between pouch young, mothers and other adult females. If the mother and young became alarmed while the young was out of the pouch, the mother would lean forward, spread wide her forearms, and relax the muscles around the opening of her pouch to allow her infant to dart back in. By adopting this posture the mother was able to signal very effectively to her young that it should get back into her pouch, and so control the amount of time it spent outside. It is possible that mothers could at times hold their young in the pouch by tightening the muscles around the pouch opening, but I was unable to see whether they actually did this.

Infants who had not yet permanently left the pouch could easily become confused as to their mother's identity if other females were nearby when they hopped out of the pouch. On the two occasions when I watched a pouch young get out of the pouch while another adult female was feeding close to its mother, the infant hopped up to the other female and tried to enter her pouch. This caused the other female considerable alarm, and in each case she hopped away from the strange infant, which then tried to catch up with her. The infant's mother also became alarmed and hopped after it until she could stand in front of it and let it back into her pouch. This kind of retrieving of infants by their mothers has not previously been observed in macropods (see Russell 1982). Perhaps because of the possibility of confusion and even loss of the pouch young if it followed a strange female away from an inattentive mother, infants were rarely seen to leave the pouch if their mothers were close to other wallabies (in only 2 (12.5%) of 16 half-hour bouts of observation of females with large pouch young in which the mother was within 30 metres of another wallaby did I see the infant get out of the pouch, compared with 38.0% of 34 observation bouts during which the mother was alone; this

difference approaches significance, $\chi^2=3.43$, $P>0.05$, <0.1). It was not clear to me whether mothers actually prevented their pouch young from going abroad while other wallabies were present, or whether mothers induced their young to get back into the pouch so quickly if they did leave it that some very short excursions escaped observation. The former possibility is suggested by an observation of a closely-watched female whose young remained in the pouch while two other wallabies were nearby, but got out as soon as the others left her mother. Infants who were a month or two older and had permanently left the pouch had no apparent difficulty in identifying their mothers, and although they occasionally approached strange females, did not try to follow them or enter their pouches. Interestingly, females did not become alarmed by the approaches of strange, older infants, and either ignored them, or cuffed them indifferently if they came very close.

Observers of other species of macropods (Russell 1973 and tamar wallabies and red kangaroos; R. Stuart-Dick pers. comm. and eastern grey kangaroos) have seen mothers groom their pouch young around their cloacas while the young stand outside the pouch (infants may also be groomed in this way while in the pouch); this grooming stimulates the infant to produce urine and faeces, which the mother apparently consumes. I did not see this in my animals, but this may have been because I was often observing them at a distance and while they were partly concealed in long grass. However, an orphan pouch young which we reared was stimulated to defecate and urinate by gentle rubbing of his cloaca, and always stood still while this was being done to him.

6.4 Permanent vacation of the pouch

Infants seven months old or older seemed eager to get out of the pouch, and spent increasing amounts of time out of the pouch as their pouch lives progressed. However, once an infant had left the pouch it could re-enter it only at its mother's discretion: if she tightened the muscles around her pouch opening, her infant would be unable to climb back in. In some cases, I determined that there was a short transitional period of no more than a week or so at the end of pouch life during which the mother sometimes allowed her young back into the pouch and sometimes not. However, if the mother consistently

prevented the infant from returning to the pouch for more than a few days, it stopped attempting to do so. All of the occasions on which I saw a mother disallowing the entry of her infant to her pouch were when I approached a female with a large pouch young standing beside her; the infant would become alarmed and try to force its way into her pouch while its mother stood inscrutably by. If I continued to approach, the infant would be obliged either to leave its mother and flee alone into cover, or follow her if she hopped away. Incidents of this kind mark the end of pouch life for the young wallaby.

6.5 Relationships between mothers and young-at-foot

6.5.1 Frequencies of association. The frequencies with which mothers associated with their young-at-foot during the six months following permanent vacation of the pouch are shown in Fig. 6.1. Mothers associated relatively infrequently with their infants during the first three weeks or so after permanent vacation of the pouch, but from then until weaning, spent most (but not all) of their time with their young-at-foot. Mothers spent significantly more time with male than with female offspring during the five months after they left the pouch (median association for 13 males was 56.0%; for 11 females it was 38.0%; $U=27.0$, $P<0.01$). The initial period of separation was longer, the subsequent levels of association lower, and the drop in association frequency during months five and six more precipitate, for female than for male young. Sons also tended to stay closer to their mothers while associating with them than did daughters, although closeness of association between mothers and young declined with age at similar rates for sons and daughters (see Fig. 6.2; during the first five months after pouch vacation sons were at a median distance of 5.41 m ($n=9$) from their mothers, compared with 8.27 m ($n=6$) for daughters; $U=2.0$, $P<0.005$). The modal distance (less than two metres apart) between mothers and young when in association was similar for sons and daughters, but daughters spent more time than sons at greater than two metres from their mothers (see Fig. 6.3).

6.5.2 Maintenance of association. I collected 43 hours of systematic observations of mothers with young-at-foot, during which changes in

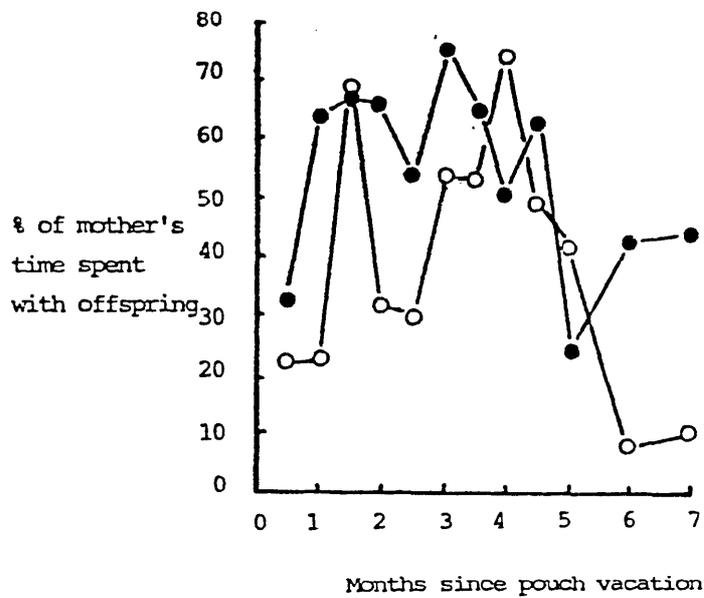


Fig. 6.1 % of time spent by mothers with male (●) and female (○) young-at-foot. Data from 1306 sightings of the mothers of 13 male and 9 female young, % of time estimated as % of sightings.

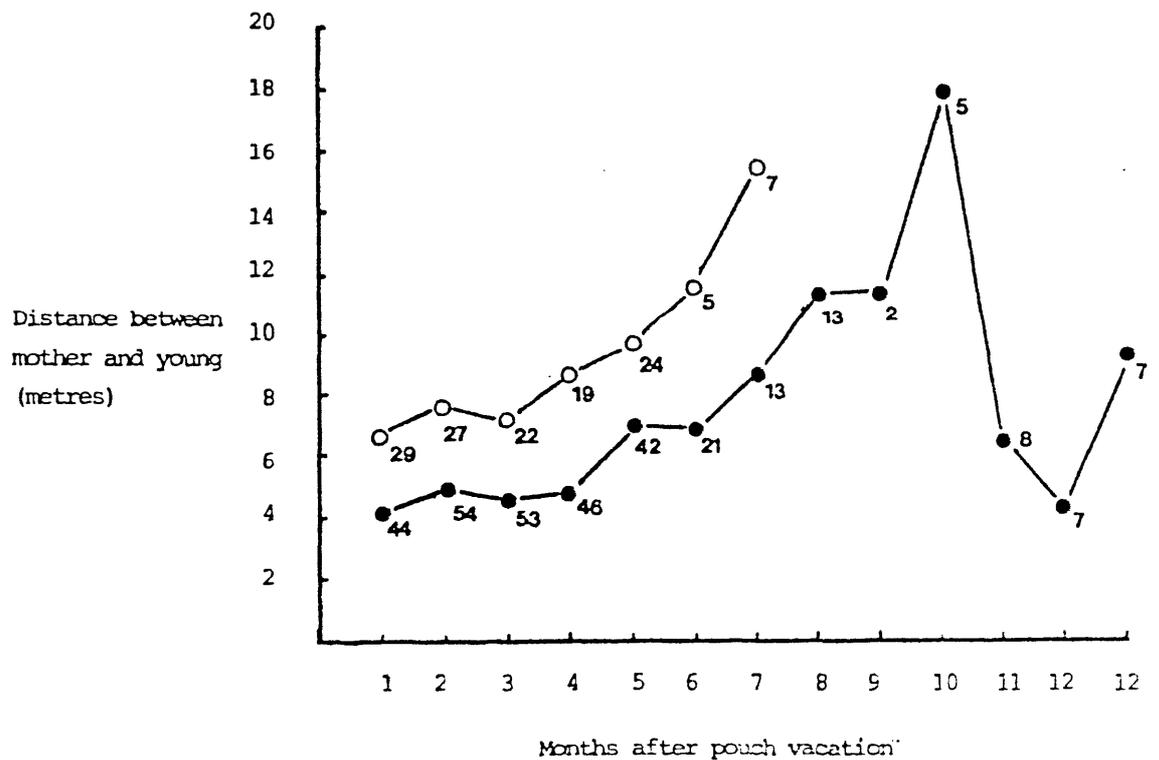


Fig 6.2 Closeness of association between mothers and their male (●) and female (○) young-at-foot. Numbers entered on the graph are numbers of records for each sex-and-age class of young.

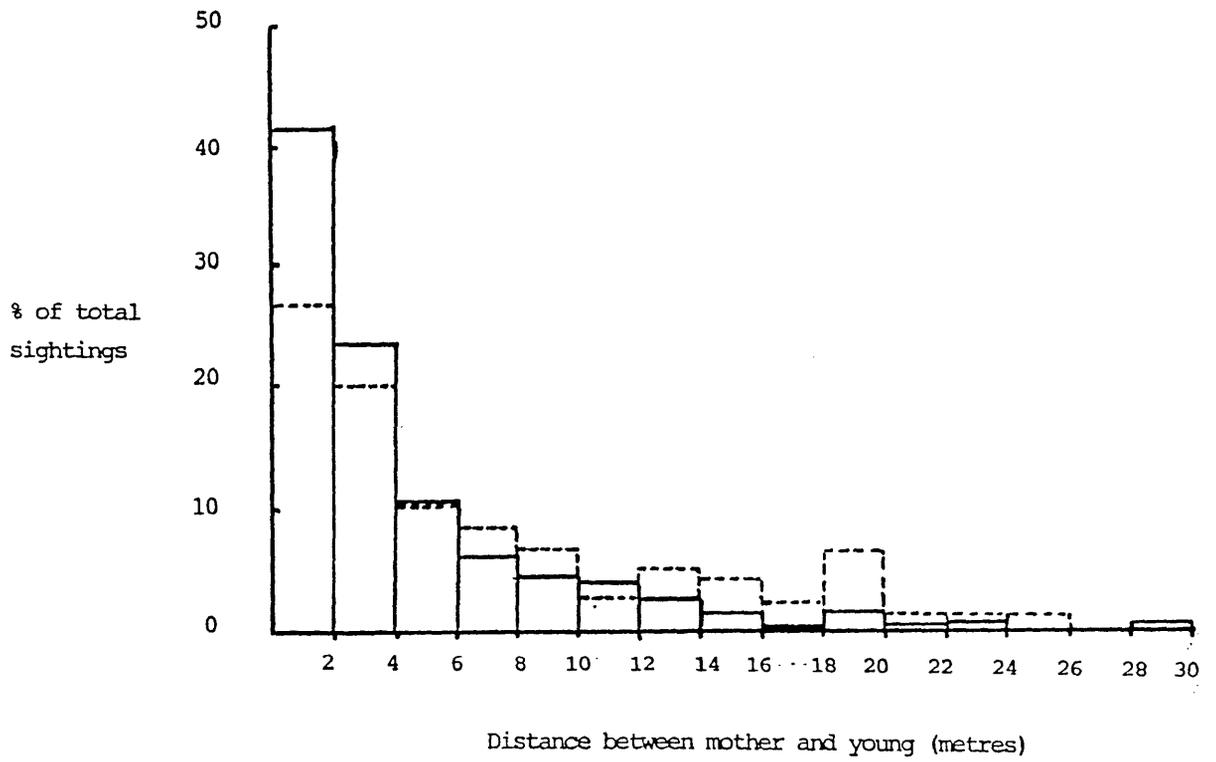


Fig. 6.3 Frequency distribution of distances separating associating mothers and young-at-foot (solid lines are male young-at-foot, dashed lines females; n=241 and 120 sightings respectively).

the proximity of mothers and sons were made at a rate of 5.70 per hour, while changes in the proximity of mothers and daughters were seen at a rate of 7.84 per hour. Mothers initiated these changes at rates of 2.03 per hour when with sons and 2.32 per hour when with daughters. Sons were less likely to initiate changes in their proximity to their mothers than were daughters (3.67 changes per hour and 5.52 per hour for sons and daughters respectively).

In Fig. 6.4 are plotted estimates of the proportions of movements made by mothers or offspring which were approaches to the other, with male and female offspring considered separately. Mothers were more likely to withdraw from than to approach their infants (approach < 50), while offspring approached their mothers more often than they moved away from them. The median approach proportions for 13 mothers was 20.0%, and for their infants 63.6%, a significant difference ($U=0$; $P<0.01$). Fig. 6.4 also shows that, although mothers apparently behaved even-handedly towards their sons and daughters, male young-at-foot tended to have higher approach proportions than did female infants. The statistical significance of this difference was decided in the following way: average monthly approach proportions were calculated, using data from male and female offspring; approach frequencies were then calculated for each infant in each month that observations were made on it, and the magnitude and direction of the deviation of each infant's monthly approach proportion from the average for that age class was found; the averages of monthly deviations for individuals who had been observed in more than one month were then taken. The quantity thus calculated for each infant is a balanced measure of the degree to which its approach proportion differed from the average for all infants. The median of these deviations for male offspring (12.4%, $n=9$) was compared with that for females (-13.8%, $n=4$) using a one-tailed test (it was suspected that the greater association and closer proximity of male infants with their mothers was due to a stronger following response of males) and found to be significantly different ($U=5.0$, $P<0.05$).

It seems therefore that the responsibility for maintaining contact between mothers and young-at-foot rests primarily with the young, and that the sex-differences are due to more persistent following by male

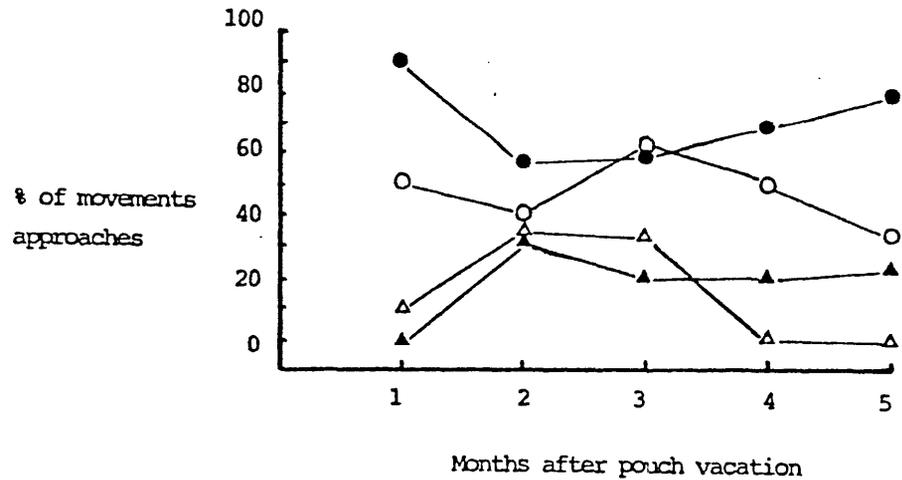


Fig. 6.4 Proportions of movements made by young-at-foot which were approaches to the mother, and vice-versa (mothers represented by triangles, young-at-foot by circles; male young-at-foot -mother pairs represented by closed symbols, female-mother pairs represented by open symbols).

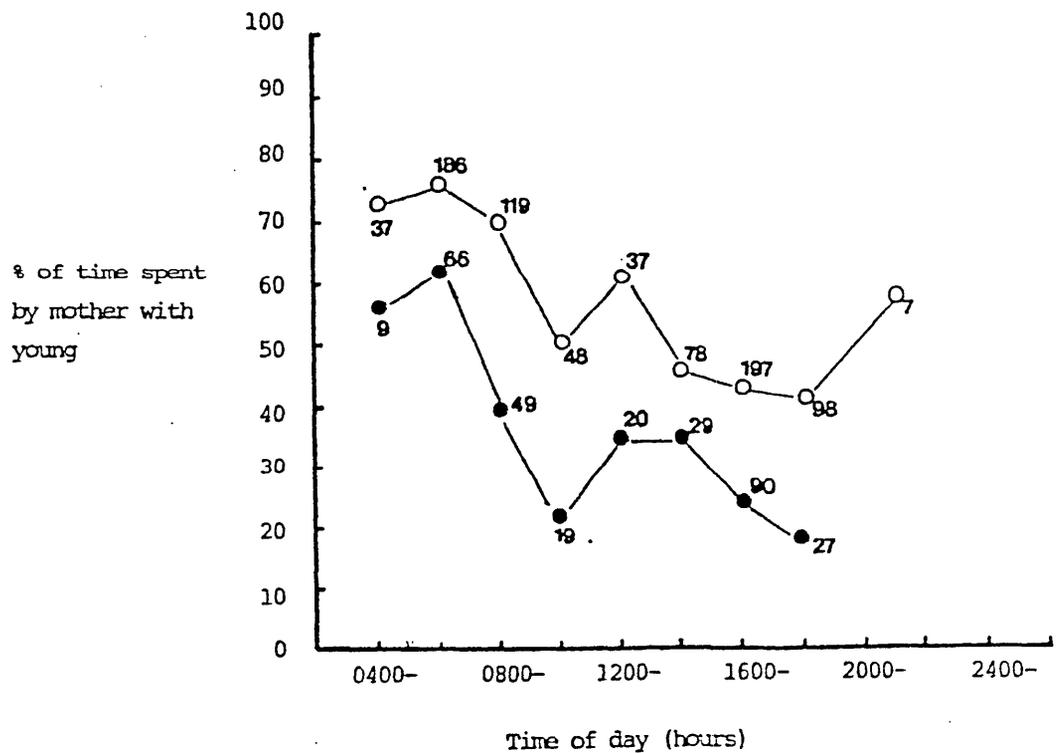


Fig. 6.5 Diurnal variation in proportions of time spent by mothers with their young-at-foot during their first (●) and subsequent (○) months out of the pouch. Sample sizes are numbers of observations of mothers.

young-at-foot.

6.5.3 Separations. I identified three different sets of circumstances under which mothers and their infants would temporarily part company. These were, a) when mother and young were both undisturbed and the young entered cover while the mother went to feed in the open ('routine separations'); b) when the two of them were disturbed and separated while fleeing ('separations in flight') and c) when the mother left an infant who was unaware of her departure ('accidental separations').

I watched twelve routine separations; in nine of these the infant first moved away from its mother rather than vice versa. Of these nine separations which were initiated by the young-at-foot, six involved young infants (i.e. in their first or second month after leaving the pouch). Typically, infants moved away from their mothers soon after a suckling bout and hopped into deep cover, the mother then hopped out into an open area and began feeding. It was more difficult to watch mothers and infants rejoining after a separation of this kind. However, repeated observations of the same infants showed that they used very small home ranges, particularly during the first month after leaving the pouch (see below); probably the infant stayed in hiding close to the point where it had last been with its mother until she returned, several hours later. Routine separations of young infants from their mothers probably largely account for the low frequency with which mothers were sighted with infants newly emerged from the pouch (see Fig. 6.1). The behaviour of lone infants will be described below. Mothers and young-at-foot associated with a relatively high frequency during the early morning, but were seen together less often as the day progressed; associations were evidently resumed during the night (Fig. 6.5). Apparently, infants were most inclined to go into hiding during the day, and if they were still with their mothers at the end of the morning's feeding, would rest with her during the middle of the day but stay in hiding rather than follow her back onto her feeding grounds later in the day.

Mothers and young-at-foot usually separated if seriously disturbed, particularly if the infant was a young one (my approach was

the source of all observed alarms; unfortunately I was never able to observe the reactions of a mother and infant to the approach of a genuine predator). However, the manner in which the two separated in flight varied. If they were disturbed while in the open, they fled in different directions; usually the infant fled before its mother did, although it is not clear if this was an adaptive tactic, or whether mothers fled later simply because they were more familiar with me than their offspring were. After separating, the mother and young-at-foot would flee to different patches of cover, or to different portions of the same gully or belt of forest (forked gullies seemed to be particularly useful for the separation in flight of mothers and young-at-foot : the mother could go into one arm of the gully and the infant into the other). I often suspected, and on several occasions was able to confirm by careful observation of and searching for mothers and young-at-foot who had separated thus, that the two rejoined soon afterwards. Both mother and infant seemed to be active in bringing about their reunion. Wallaby creek is, from the wallabys' standpoint, a heterogeneous place, and animals who had been disturbed rarely had to flee far to enter cover. Both mother and infant seemed to know the mothers' home range, particularly that part of it frequented by the infant, well enough that they could soon find each other again after separating in flight.

If it happened that the mother and infant were disturbed while standing together in long grass, so that the infant was wholly or almost wholly concealed, the mother would flee while the infant remained still, alert and hidden. If I then approached it to within four metres or so, it would break from cover like a quail, dash out of sight and into another patch of cover, and rejoin its mother after its fright subsided.

I saw only one accidental separation of a mother and young. In that case a female (Isabell) was with her young-at-foot male (Dama) while she was being courted, early in the morning, by two males. Isabell apparently became agitated by the males' attentions, and hopped to more than a hundred metres away, with the males following. Dama did not see her go, and became seriously alarmed when he realised she was no longer there. He spent about an hour searching the

vicinity, approached and was rebuffed by a female wallaby, followed an eastern grey kangaroo for a few hops, then hid in a patch of long grass where he had last seen Isabell. Isabell came back and found him there about ten hours later, (she had been watched intermittently during the intervening time, and did not appear to have been searching for him). This was the only time I heard a contact call between an infant and its mother : Isabell went to a spot about 25 metres from where Dama was standing in long grass; he stood sniffing the air and gave two hoarse, breathy little coughing sounds; his mother then hopped towards him and he came out of cover and hopped up to her.

6.6 Behaviour of lone infants

While apart from their mothers, infants stayed in or close to screening vegetation; it is for this reason that I refer to them as being in hiding. They usually chose to stay within beds of *Poa* tussocks, patches of tall bladey grass or thickly growing shrubs. These kinds of cover seemed to be particularly attractive to young wallabies as hiding places if they were in deep gullies, perhaps because the uneven terrain made it possible for an infant to get very quickly out of view of a predator if disturbed, and also interrupted the lines of sight into the hiding place. While in hiding, infants did not adopt a specific hiding posture, they simply stood, sat, crouched or lay down in the same manner as adults. Nor did they freeze if disturbed : when I approached infants in hiding they became very alert and peered towards me while crouching, again much in the same way that adults do. They usually allowed a closer approach than did unhabituated adults, but this varied according to the degree to which they were concealed - if I was clearly visible to them, infants rarely let me get to within four metres of them before they burst explosively, but almost noiselessly, from cover and disappeared at speed. By carefully following some young wallabies who had been put to flight in this way, I found that they usually fled far enough to get well out of my view, then went into another patch of dense vegetation.

Infants did not necessarily use the same patch of cover from day to day, or even remain within the same patch in a single period of

separation from the mother. They were sometimes quite active while apart from their mothers and hopped around somewhat, although remaining in cover. Lone infants were generally rather difficult to observe, so I have no quantitative data on their activity and the way in which it may have changed with time since pouch emergence. However, I formed the impression that they were least active and stayed most closely concealed during the first month, but that their activity increased thereafter, with a developing tendency to venture out of cover, although their home ranges remained considerably smaller than their mothers' (see below).

6.7 Suckling and weaning

Young-at-foot put their heads into their mothers' pouches only in discrete, uninterrupted and rare bouts, during which both mother and young stood still. I assume that infants were suckling when they did this.

While with their mothers, male infants suckled at a rate of 0.25 bouts per hour, females at a rate of 0.39 bouts per hour, a non-significant difference. If these rates are corrected for the proportions of time spent by mothers with their male and female offspring to give absolute suckling rates, the difference between male and female young vanishes (males and females both 0.14 bouts per hour). Durations of suckling bouts were also similar in both sexes (medians of 9.08 minutes for males, $n=10$; and 8.0 minutes for females, $n=6$; $U=19.0$, n.s.).

No detailed observations of interactions between mothers and young were conducted at night, but I looked for variation in suckling frequencies through the daylight hours by dividing the day into three periods (morning, midday, evening) of equal duration. Suckling frequencies per hour of observation of mother-young-at-foot pairs were 0.26, 0.32 and 0.42 for the morning, midday and evening periods respectively ($n=56$ hours of observation). If these rates are corrected for the proportions of their time that mothers spent with their young-at-foot during the three periods, they reduce to 0.19, 0.19 and 0.18 bouts per hour. The fact that suckling frequencies were so constant during the daylight hours, despite variation in the

activity of the mother and the association of mothers and young, suggests that suckling frequencies may remain similar during the night.

Data on the changes in suckling frequencies and durations of suckling bouts with time since permanent emergence of the young from the pouch are presented in Table 6.1. Suckling frequencies were nearly constant during the first four months, but dropped sharply to the fifth month. Frequencies of association also fell during the fifth month (see Fig. 6.1) and it is probable that most young were weaned some time during their fourth and fifth month after they permanently left the pouch. No suckling was observed beyond five months past permanent vacation of the pouch. There was a faint indication that males suckled more often than females during the latter part of infancy - during systematic observations of mothers and young and censuses of the study area, I saw eight young (i.e. in their first and second months out of the pouch) male and eight young female infants suckling, and seven old (months three, four and five) male and four old female infants suckling - but much larger samples would be needed to demonstrate such an effect. Durations of suckling bouts tended to increase with the infants' age, but suckling bouts by young infants were not significantly shorter than those by old infants ($U=21.0$, $n_1=9$, $n_2=7$; n.s.).

Suckling bouts were initiated by the infant, and apparently the infant always terminated them. Mothers stood still while their young-at-foot suckled, and at no time did I see a female display impatience while her offspring suckled. There are strong theoretical reasons for expecting to find weaning conflict in mammals (Trivers 1974) and its occurrence is widespread; its apparent absence in red-necked wallabies is therefore surprising. It should be recalled, however, that red-necked wallaby mothers usually exclude their infants from the pouch at an age when they clearly want to continue to reside there - this expulsion probably influences, among other things, the young's pattern of suckling. Fleming *et al.* (1983) observed free-ranging female Bennett's wallabies terminating their offsprings' suckling bouts; it may be that behavioural control of suckling patterns in late lactation by mothers varies from one population to

another, or from time to time within a population.

6.8 Other social interactions

At the end of a suckling bout, mother and infant usually groomed themselves, and sometimes one another. Other interactions involving physical contact between mother and young-at-foot were observed at a frequency of 0.6 interactions per hour (n=34 interactions) during systematic sampling of mothers with young. Of these interactions, 26.5% were grooming of one individual by the other; 26.4% were mutual grooming; and other forms of contact, usually brief naso-nasal touching, accounted for the remaining 47.1%. The frequency with which these interactions took place changed little during the first four months after pouch vacation (0.67, 0.56, 0.67 and 0.59 interactions per hour respectively) but dropped sharply in the fifth month (0.29 per hour; these frequencies have not been corrected for the proportions of time spent by mother and young together). For only 19 interactions could I be certain which of the two had been the initiator; 47.4% of these were initiated by the mother. Mothers became less likely to initiate interactions as their offspring grew : 77.8% (n=9) of non-suckling interactions between mothers and infants in their first two months after pouch-leaving were initiated by the mother, whereas she initiated only 20.0% (n=10) of interactions over the subsequent three months; these proportions differ significantly ($\chi^2=4.1$, 1 d.f.; $P<0.05$).

Male young-at-foot interacted with their mothers more often than did female young-at-foot (interaction frequencies of 0.68 per hour and 0.44 per hour respectively). When these frequencies are corrected for association time of mothers with their male and female offspring, they reduce to absolute rates of 0.38 per hour for males and 0.17 per hour for females, a more than two-fold difference. Unfortunately, my samples were not sufficiently large to allow me to compare the rates at which sons and daughters initiated interactions with their mothers. No aggressive interactions were observed, with the exception of a female who once lightly kicked her small young-at-foot aside when it got underfoot.

I saw two bouts of play between mothers and young (neither was

during a systematic observation period). In both cases the play was initiated by male infants, one of whom was in his fourth month after leaving the pouch, while the other had not yet permanently left the pouch. The descriptions of these incidents given below are taken directly from my field notes:

1800, Giselle with her y.a.f. standing in front of her and play-sparring with her, she responding by fending his arms gently with hers; he also moved around behind her and attempted to jump on her back.

0600, Twilight, with young out of pouch, it engaged in two bouts of play-fighting with her. The first time he jumped at her from the side, jumping up onto her shoulders, then confronted her and engaged her in sparring. She responded with light sparring. The second time (4.5 minutes later) he ran at her several times from the front, jumped at her and kicked her chest with adult-type fighting actions, immediately after this he got back into her pouch.

Both bouts of play were composed of actions used in serious fights between adult males (see Ch. 8), and Giselle's young-at-foot might also have been conducting a rehearsal of mating when he jumped onto her back. I once saw a 19 month old male press himself close to his mother's back as if trying to mount her, this may also be considered as mating play. Croft (1981b) found that infant male euros sparred with their mothers more frequently than did infant females; Kaufmann (1974a) also observed sexual play by male infant whiptail wallabies with their mothers.

Rates of social interaction involving contact have been measured for euros by Croft (1981a), and found to be much higher than the rate observed in red-necked wallabies (2.84 interactions per hour compared with 0.6 interactions per hour). Social interactions between mothers and young also seem to be more frequent in whiptail wallabies (Kaufmann 1974a) and red kangaroos (Croft 1981a) than in red-necked wallabies, and in eastern grey kangaroos, (R. Stuart-Dick pers. comm.) found small young-at-foot to be in physical contact with their mothers for 21% of their time. Adults of these larger species are more gregarious than adult red-necked wallabies. These comparisons suggest

that, in macropods, frequencies of interactions between mothers and young may be positively correlated with degrees of sociality among adults.

6.9 Activity budgets of mothers and young

Fig. 6.6 shows how the activity budgets of infant wallabies changed with time since emergence from the pouch, and compares them with the activity of the mother. The diagram refers only to the times when the mother and her young-at-foot were together. The data used to construct Fig. 6.6 were balanced in the following way. All observation bouts were allocated to one of the two time periods : morning and evening (0600-1000 and 1600-1800) when feeding was the predominant activity, and midday (1000-1600) when the animals were for the most part resting; the percentage of time spent by all individuals in each category of activity was found for each time period, and these were then averaged over both time periods to give the proportions depicted. While still young, infants spent most of their time while with their mothers resting, but as the months passed they spent more time feeding and alert, and less time resting, grooming, suckling and interacting, until in month five their activity budgets resembled those of their mothers. The proportions of time spent by male and female infants feeding, while they were with their mothers, were similar (36.35% and 33.73% respectively, all months combined).

6.10 Home ranges of young-at-foot

Fig. 6.7 shows how tightly small young-at-foot clung to cover : most of the sightings of infants in their first month after permanently leaving the pouch were on the edges of bladey grass patches or beds of tussocks, particularly if these were near a gully or a stand of trees. Large uniform tracts of dense vegetation, as well as open areas, were avoided. Because of this love of cover, young-at-foot wallabies usually had small home ranges : the average home range sizes for males and females were both 3.6 ha. (n=9 for males, 6 for females). These were 50.5% and 47.0% respectively of the average home ranges of their mothers over the same periods.

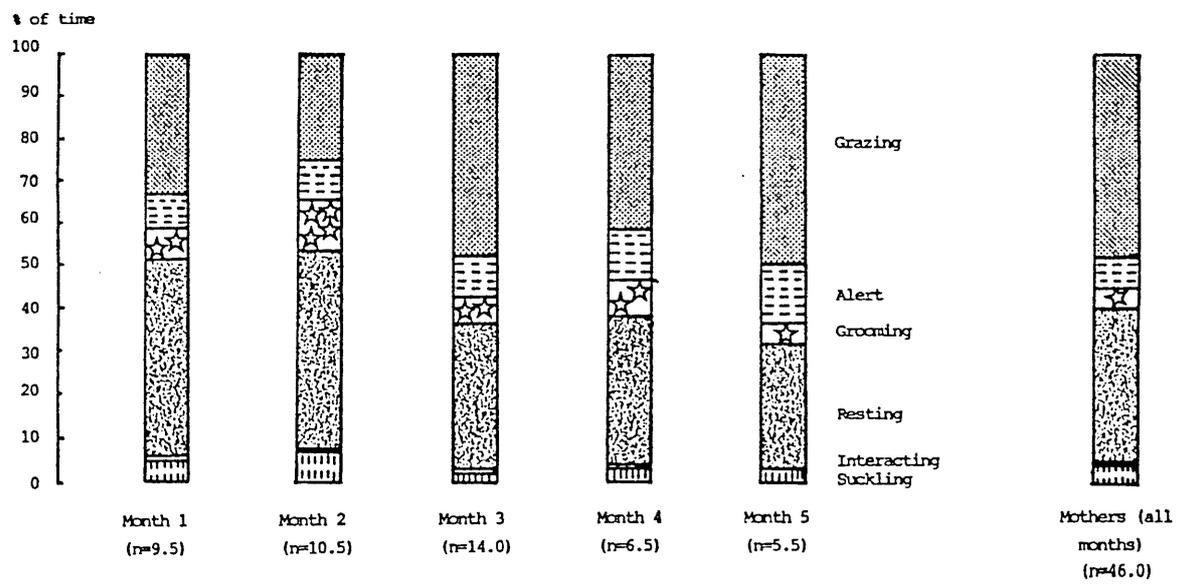


Fig. 6.6 Activity budgets of young-at-foot and mothers.
 Sample sizes are hours of observation.

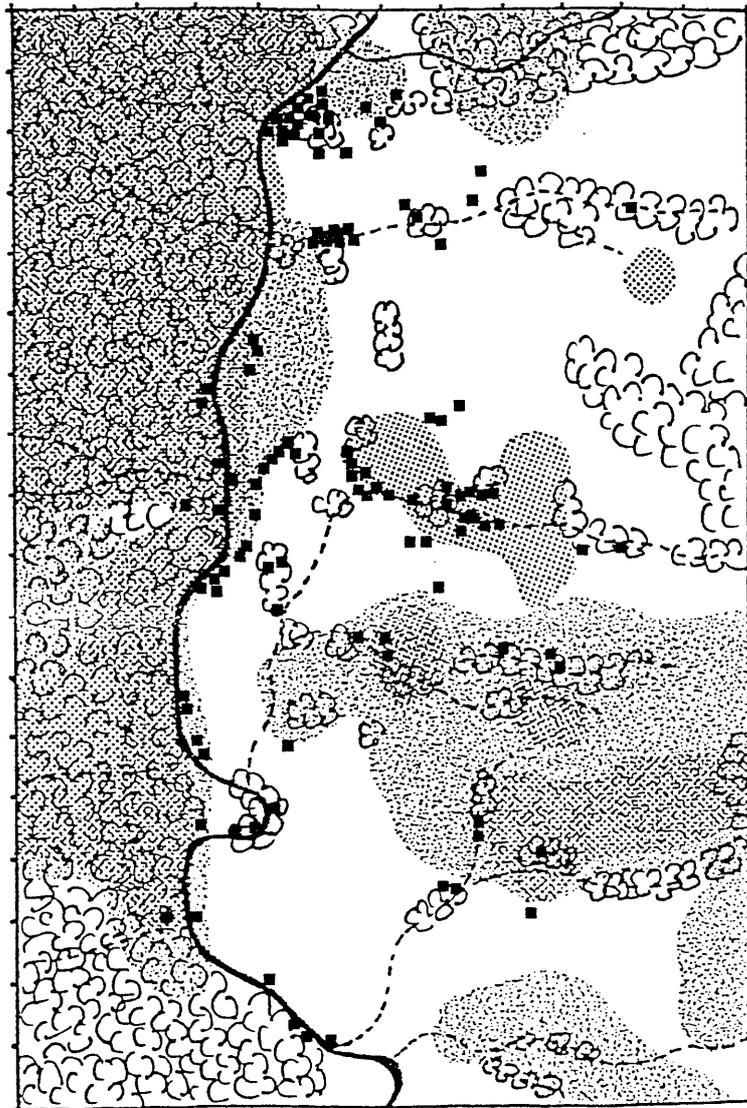


Fig. 6.7 Locations of sightings of infants during their first month out of the pouch.

6.11 Hiding and following in ungulates and macropods

The distinction between 'hider' and 'follower' species of ungulates was drawn for bovids by Walther (1965, 1969) and generalised to other families by Lent (1974) and Leuthold (1977). The behaviour of mothers and infants in the two groups differ strikingly in a number of ways. Mothers of hider species isolate themselves from conspecifics, and seek concealment in dense vegetation, before giving birth. They carefully clean their infants and the birth site, and expel and eat the placenta soon after parturition. Not long after it has first managed to suckle, the infant begins to wander away from its mother, and selects a site where it may lie in concealment. The mother is attentive to this movement of her infant, and she will return to its lying-out site after leaving the vicinity to feed for periods of an hour or more. When lying out, the infant presses itself close to the ground and, for the most part, remains still and silent. On her return, the mother usually does not go right up to her infant, but may call softly to it from several metres away, and allow it to approach her. The infant usually suckles immediately after reunion with its mother; the mother in her turn licks her infant's perianal area. This apparently stimulates the young to pass urine and faeces, which the mother then consumes. Periods of contact between mothers and small infants are usually terminated when the infant returns to hiding, often in a fresh hiding place. At some point the infant's desire for seclusion wanes, and it begins to follow its mother wherever she goes. All or parts of this suite of behaviours have been observed in field studies of Thomson's gazelle *Gazella thomsoni* (Walther 1969), Grant's gazelle *Gazella granti* (Walther 1965), reedbuck *Redunca arundinum* (Jungius 1970), hartebeest *Alcelaphus buselaphus* (Gosling 1969), waterbuck *Kobus ellipsiprymnus* (Spinage 1969), impala *Aepyceros melampus* (Jarman 1976), roe deer *Capreolus capreolus* (Espmark 1964) and pronghorn *Antilocapra americana* (Fichter 1974, Autenreith and Fichter 1975), among other species (see Lent 1974 and Leuthold 1977). Hiding is most characteristic of sedentary, solitary or moderately gregarious species living in habitats providing ample cover for the newborn, and the behaviour serves to keep them concealed and to minimise the scent they carry during the period in

which they are most vulnerable to predation. Byers and Byers (1983) also showed that pronghorn mothers move sufficiently far from their hiding infants that coyotes *Canus latrans* find it uneconomical to use the mother's location as the starting point of a search for the fawn.

Follower species, such as zebras *Equus* spp. (Klingel 1974, Penzhorn 1984), wildebeest *Connochaetes taurinus* (Estes and Estes 1979), caribou *Rangifer tarandus* (Lent 1966), African buffalo *Synceus caffer* (Sinclair 1977) and others are generally large-bodied, mobile, gregarious beasts of open country. Mothers of these species often give birth in the open and close to conspecifics; the expulsion of the placenta may be delayed and the after-birth not eaten (see Estes and Estes 1979). Infants follow their mothers as soon as they are able (which in wildebeest is a very short time after birth) and the mother then re-enters her herd if she has been left behind while giving birth. The close proximity maintained between mothers and young appears to make the infants less obvious to predators than they would be if they were left alone and unhidden, especially if, as in plains zebra *Equus burchelli* (Klingel and Klingel 1969) and wildebeest the mother places herself between her infant and a predator, and moves the infant to the opposite side of the herd. Wildebeest cows with calves associate preferentially (Estes and Estes 1979); this further protects newborn calves as they are likely to be surrounded by slightly older calves capable of out-running predators, and thus become still less likely to be singled out and pursued by a predator. The cover provided for neonates by other calves in this highly precocial species appears to have been an important factor in the evolution of its remarkable synchrony of breeding (Estes 1976). The ability of the mother to actively defend her offspring against predators may be an important condition (necessary but insufficient) for the evolution of following : saiga antelope *Saiga tartarica* live in open country, are very mobile and hugely gregarious, yet give birth to infants who hide as best they can for the first few days after birth (Bannikov et al. 1967). This may be because adult female saigas are probably too small (at 27 kg) to effectively defend their young against wolves. Most adult females of follower species of ungulates are large enough to defend their newborn young against some predators, and in certain

species individuals other than the mother may regularly take part in the defence of young. In plains zebra (Klingel 1967) and mountain zebra *E. zebra* (Penzhorn 1984) stallions will defend all members of their family group against predators, and all the members of a herd of African buffaloes will respond to the distress call of a calf (Sinclair 1974, 1977).

Some species of ungulates, such as bontebok *Damaliscus dorcas* (David 1975) and giraffe *Giraffa camelopardalis* (Pratt and Anderson 1979) are clearly intermediate between hider and follower types, so it appears that the classical hider and follower species stand at the end points of a continuum, rather than on the arms of a dichotomy (see also Lent 1974). Nevertheless, the distinction between hidiers and followers remains a useful one, in showing how the tactics used to minimise predation on infants may vary with the body size, habitat use and gregariousness typical of their species.

The behaviour of young red-necked wallabies after leaving the pouch is similar in many ways to that of newborn ungulates of hider species (but differs from them in a number of other ways which will be discussed below) while larger species of more open habitats, such as red kangaroos, euros (Croft 1981a, b) and eastern grey kangaroos (R. Stuart-Dick pers. comm.) behave in parallel with follower species. Some anecdotal evidence suggests that the young of other medium-sized and small macropods of closed habitats spend some time apart from their mothers after leaving the pouch. K.P. Joblin (pers. comm.) observed a female and young-at-foot swamp wallaby *Wallabia bicolor* at their resting place in a patch of long grass over a period of several days, and noted that the mother sometimes left the young-at-foot alone there. I once put an adult swamp wallaby to flight from a patch of long grass, while an infant which had been beside the adult remained there, and broke from cover only when I approached the place closely. J.C. Merchant (pers. comm.) noticed that captive infant agile wallabies sometimes tried to hide under tussocks though their mothers were in the same enclosures with them. Hornsby (1978) has seen young brush-tailed and yellow-footed rock wallabies left alone among the rocks in their home areas while their mothers moved down to drink. Captive red-bellied pademelon young separated from their mothers

during the day, but joined them at night (Clancy 1982), while a young captive parma wallaby observed by Stuart-Dick (pers. comm.) hid away from its mother for much of its time.

It seems likely that species similar in size to, or smaller than, red-necked wallabies behave in ways similar to hiding ungulates, while in larger species, infants continuously and persistently follow their mothers from the moment they leave the pouch. Female whiptail wallabies, which are slightly larger than red-necked wallabies and use somewhat more open habitats, spend about 10% of their time apart from their young-at-foot during the first month after they leave the pouch, one mother-young pair observed by Kaufmann (1974a) spent 39% of their time apart during this first month : perhaps whiptail wallabies are a 'follower' species with some tendency towards hiding. I suggest, therefore, that in macropods, as in ungulates, hiding gives way to following in larger, more gregarious species living in more open habitats, but that the threshold above which following appears is lower in macropods than in ungulates. Red kangaroos, whiptail wallabies and eastern grey kangaroos are more similar in habitat, body size and sociality to hider species of ungulates such as gazelles, roe deer and impala than they are to follower species, such as wildebeest, caribou and zebras.

The behaviour of infant red-necked wallabies when in hiding differs in several important ways from that of hiding newborn ungulates. Young wallabies, although they initiate separations from their mothers and remain in concealing vegetation, do not adopt a prone posture or freeze at the approach of something alarming. Instead, they adopt typical adult postures, stay alert, and will not allow an approach by a potential predator to a distance of less than four metres (especially if they are partly exposed). If approached as closely as this, the young wallaby breaks explosively, but without vocalising, from cover, and bounds out of sight of the disturbance and into fresh cover. Even when undisturbed, the infant does not necessarily sit still in a particular hiding place, but moves around within cover to some extent.

One of the most striking characteristics of newborn infants of hider species of ungulates is their adoption of a prone posture while

lying out, and their tendency, when alarmed, to freeze into this posture, thus allowing predators to approach them very closely. Kruuk (1972) and Walther (1969) have observed hyenas pass within two metres of hiding Thomson's gazelle fawns, without eliciting flight from the fawn. This tactic is effective provided the fawn is not located by the predator, but if it is it may fall prey very easily. Some gazelle fawns may simply be picked up and killed, others, if approached very closely, will break from cover, stotting and bleating. This apparently draws the attention of the mother, who may try to defend her fawn if the predator is a jackal, but if the fawn is being pursued by a hyena it has little hope of avoiding death. M.V. and P.J. Jarman (pers. comm.) have seen impala fawns freezing so persistently that they have been picked up and killed by predators. The alarming stimuli which elicit freezing into the prone posture by white-tailed deer (*Odocoileus virginianus*) fawns also evoke reductions in heart rates of up to almost 70% and depressions in breathing rates, especially in fawns less than a week of age and of low body weight (Jacobsen 1979). Observations by Truett (1979) of coyotes capturing white-tailed deer fawns suggest that these responses make them very vulnerable if they are located by a predator. Humans can easily capture by hand the newborn infants of a number of species of ungulates (e.g. white tailed deer, White et al. 1972; pronghorn, Autenreith and Fichter 1975).

These differences in behaviour could have arisen because macropods are more physiologically and behaviourally developed when they leave the pouch than are newborn eutherians of comparable species. An African artiodactyl of an adult body size similar to the red-necked wallaby would be born after a gestation of approximately six months (Western 1980), whereas red-necked wallabies have a one-month gestation and subsequently spend about nine months as pouch young. In parma wallabies (Wallis and Maynes 1973) quokkas (Shield 1966) and tammar wallabies (Setchell 1974), pouch young develop endothermy during a 40 to 50-day transitional period beginning after 62, 55 and 56% respectively of pouch life has elapsed; these authors (see also Maynes 1976) suggest that it is within or at the end of this transitional period that the pouch young is most nearly equivalent to

a newborn eutherian. It is also during this transitional period that the infant acquires its pelage, begins to put its head out of the pouch and prepares to begin leaving the pouch for short periods (Shield 1961, Murphy and Smith 1970, Maynes 1976). It has been shown that, during this same transitional period, the kidneys of young quokkas begin to function effectively (Bentley and Shield 1962), thyroid function develops in young tammars (Setchell 1974), and brain growth in the tammar passes from its rapid to its mature phase (Renfree et al. 1982). (It is also of interest that Hinds and Tyndale-Biscoe 1982 showed that after 140 days (56%) of pouch life in the tammar wallaby, much higher levels of prolactin are necessary to sustain lactogenesis than in the earlier phase of lactation; they suggested that this second portion of lactation may be equivalent to lactation in eutherians).

It is probable, therefore, that young red-necked wallabies are most equivalent to newborn ungulates during months six and seven of pouch life, just before they begin to leave the pouch for short periods. Subsequent to this the infant wallaby passes through a two to four month period during which it may leave the pouch for varying periods of time, but returns to it immediately when alarmed. Ungulates at the same stage of development are either hiding alone, or following their mothers. When red-necked wallabies finally leave the pouch, therefore, they are probably more mature than newborn ungulates and able to use more sophisticated means of escaping predators. This may be partly due to more advanced coordination and greater speed in flight, but also to information acquired during the preceding months on the characteristics of hiding places and their distribution within the mother's home range : recall that pouch-young spend long periods out of the pouch while their mother rests in cover, and often look out of the pouch as she travels about in her home range.

Kaufmann (1974a) was probably correct in suggesting that the later stages of pouch life serve the same functions of protecting very vulnerable young from predation as does hiding in newborn ungulates. During late pouch life the infant may be quite active outside the pouch, but benefits from the alertness of its mother and when alarmed can be quickly carried by her into cover or in flight from a predator.

These functions of the pouch can be used to explain the extension of the duration of pouch life in macropods relative to gestation in eutherians. It is obvious, however, that the pouch young may sometimes be a serious burden to the mother, especially if she is being chased by a predator, and it is known from experience with captive animals and in capturing wild macropods that mothers may lose pouch young when panicked. It is popularly believed that wild female kangaroos and wallabies with large pouch young will, when closely pursued by dingoes, quickly drop their young from the pouch and conceal it somewhere, to return and collect it afterwards (see Pedley 1924). As far as I know it has not been determined whether any macropods actually do this.

TABLE 6.1: Suckling rates and duration of suckling bouts, in relation to time since permanent emergence of the young from the pouch (suckling rates have been corrected for monthly variation in association between mothers and young)

	Months since pouch vacation				
	1	2	3	4	5
Suckling rate	0.18	0.19	0.10	0.20	0.07
Median duration of suckling bouts	8.25	8.00	9.33	10.50	19.58
n (number of bouts observed)	6.00	3.00	3.00	3.00	1.00
n (hours of observation)	13.50	10.00	16.00	9.50	7.00

CHAPTER SEVEN

Philopatry, Dispersal and Association

7.1 Introduction

The kangaroos and wallabies of the genus *Macropus* seem to have open societies, in which groups are in constant flux. I gave evidence of the fluidity of red-necked wallaby groups in Chapter 4 ; observations on the more social species suggest that, to varying degrees, they too live in unstable groups. In particular, Croft (1981a, b) found that the sizes and compositions of groups in which certain recognisable red kangaroos and euros occurred were likely to change from day to day. Kaufmann's (1975) and Grant's (1973) observations suggest that individual eastern grey kangaroos experience similarly frequent changes in the identities of their companions. Kaufmann (1974a) showed this to be true also of whiptail wallabies, although he pointed out that, because the population he studied was broken up into a series of large, stable, discrete assemblages of animals, individuals associated repeatedly with familiar wallabies (a similar kind of dispersion may occur in populations of eastern grey kangaroos, see Kaufmann 1975, Jarman and Taylor 1983). Within these assemblages, however, Kaufmann could detect no stable, preferential associations between particular individuals, beyond the strong relationship between mothers and their infants.

Indirect evidence of the instability of groups in populations of *Macropus* comes from Caughley's (1964) analysis of group size frequency distributions for red and eastern grey kangaroos, which suggested a model of group formation in which animals avoided being alone but exercised no preference for joining groups of any particular size or composition; and from the observation that in red kangaroos (Johnson 1983) wallaroos (Taylor 1982a) and eastern grey kangaroos (Southwell 1984a, Taylor 1982a) average group sizes are positively correlated with density.

These observations and analyses are all consistent with Caughley's (1964) hypothesis that groups of these animals form in a random, or nearly random fashion, although they do not, of course, prove it. Given that associations between individuals in populations of *Macropus* kangaroos and wallabies may not be constant or exclusive, it is still possible that certain individuals may be found together significantly more often than expected from the frequency of chance encounters, and others not; we need detailed information on known individuals to decide this question and, if preferential associations do occur, to show how they are related to patterns of dispersal and distribution of kin within populations.

This chapter describes philopatry and dispersal in red-necked wallabies; analyses changes in the association between mothers and young as the young grow; identifies preferential associations between certain individuals and shows how these are correlated with kinship; and looks at other factors which influence frequencies of association between individuals.

7.2 Philopatry and dispersal

To show how the locations of the home ranges of young wallabies changed after they were weaned and as they matured, I found their centres of activity in successive two-month periods after their weaning, and measured the distances of these centres of activity from the centres of the ranges they had used as young-at-foot. Continuous records, spanning periods of up to 32 months post-weaning for animals who were weaned early in the study, were available for seven females and eleven males, and Figs. 7.1 and 7.2 plot the displacements of these wallabies from their infant centres of activity as they grew older. Trajectories of animals who disappeared during the study are terminated by question marks (data on individuals who disappeared within six months of being weaned are not included).

7.2.1 Females. Young females usually moved a small distance from their pre-weaning centres of activity during the first few months after their weaning, but thereafter most females' locations stabilised. This left them within the home ranges they had used as young-at-foot,

and well inside their mothers' home ranges (which have average radii of approximately 200 metres). However the displacements of some young females may have been sufficient to take them to the edges of, or just outside, their mothers' core areas (see Ch. 3) ; the inter-individual variation in Fig. 7.1 may therefore reflect relatively large differences in the degree of overlap between the core areas of mothers and daughters.

Five of the seven females included in Fig. 7.1 eventually gave birth within their mothers' home ranges, another four who were seen infrequently, and were therefore not included in the figure, also reached sexual maturity within the maternal home range. It may be significant that the two sub-adult females who vanished after surviving more than six months post-weaning had both had rather unstable home ranges during much of the time prior to their disappearance (see Fig. 7.1). I consider it likely that these two females died, as both were born in a central part of the study area and my chances of maintaining contact with them had they dispersed should therefore have been good. Stronger evidence of dispersal was provided by a female who was a weaned immature when I first identified her in 1981. She gave birth for the first time in 1982 (the infant subsequently died) but during that year she gradually shifted her home range and in 1983 settled in a new home range with a centre of activity 230 metres away from the centre of her 1981 range. I found her during each of several visits to the study area in 1984, and confirmed that she had made no further unusual movements. Of four other females who were weaned immatures when first identified in 1981, one disappeared before she had given birth, and the other three undertook no dispersive movements before starting to breed. Taken together, these results imply that the rate of dispersal of immature females may be as low as 6% ($n=16$) in this population; the one young female I consider to have dispersed moved a short distance only.

7.2.2 Males. Fig. 7.2 shows that the young males remained close to the places where they were weaned but at some time between twelve and eighteen months after leaving the pouch (i.e. at ages of 21 to 27 months) they all either disappeared or moved to other, distant parts of the study area. The four males who were observed to move to other

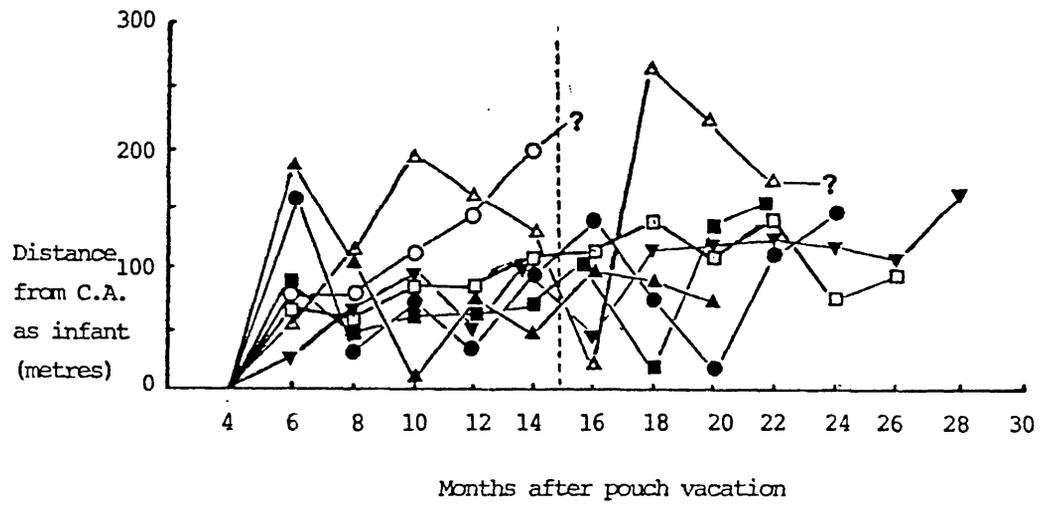


Fig. 7.1 Displacements of maturing females from the centres of activity they had used as young-at-foot. Dashed line equals mean date of first parturition.

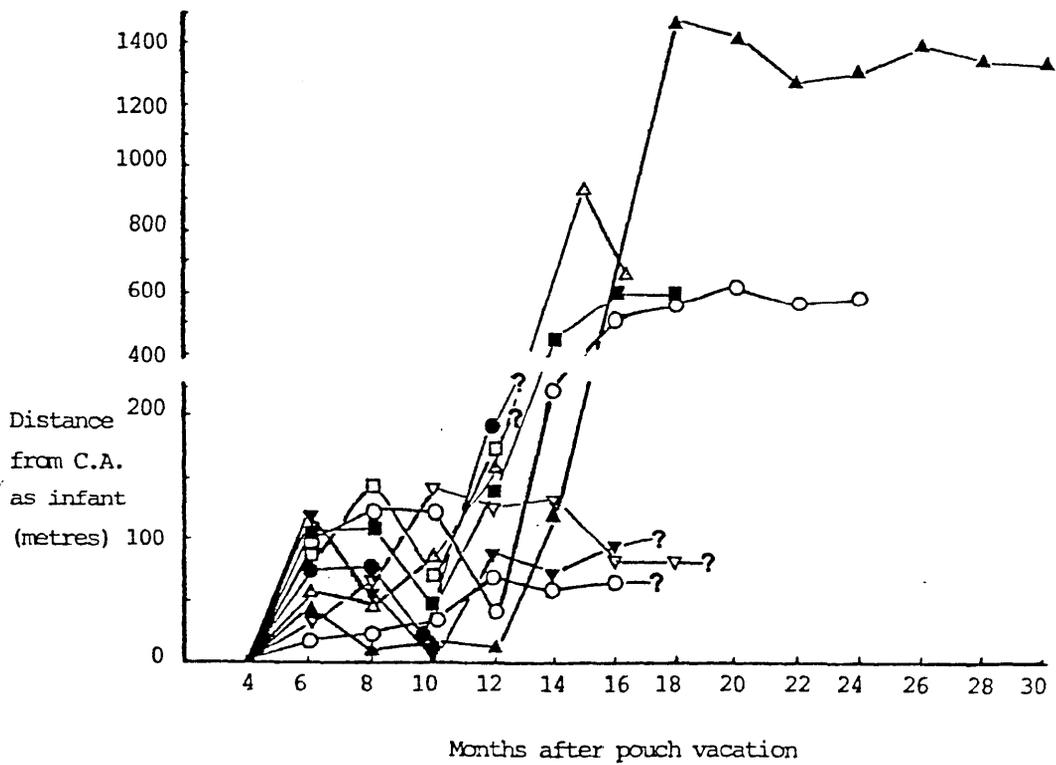


Fig. 7.2 Displacements of maturing males from the centres of activity they had used as young-at-foot.

parts of the study area did so at a mean age of 23.5 months, the six who disappeared completely did so at a mean age of 25.8 months; the similarity in the two mean ages suggests that the males who disappeared may also have dispersed, and either moved outside the study area, or dispersed within the study area but died very soon after moving, and before they could be resighted. The males who shifted home ranges within the study area moved a mean distance of 811 metres, if some of the males who disappeared actually left the study area, then this figure may be an underestimate of the true average dispersal distance. The known dispersers appeared to establish stable home ranges soon after dispersal.

Further evidence of dispersal by young males comes from observations of males who appeared abruptly in the study area after identification of all sedentary members of the study population had been completed - these males had apparently moved into the study area from outside. Seven such males entered the population and remained for periods of three months or more. They were all similar in size to the males discussed above, and were therefore probably also approximately two years old.

Although males eventually moved completely out of their maternal home ranges, they tended to move less during the first months after weaning than did young females. In the first six months after weaning, males maintained a median distance of 61.7 metres (n=11) from their juvenile centres of activity, compared with 90.0 metres (n=7) for females; this difference approaches significance ($U=19.0$, $P<0.10$, >0.05 , two-tailed).

7.3 Association between mothers and young

Fig. 7.3 shows how the proportion of time spent by mothers with those of their offspring who still remained within their mothers' home ranges varied with the age of the offspring. Association is defined according to the criterion used in Chapter 4, that is, two individuals were considered to be together if less than 30 metres apart when seen.

The most striking feature of the patterns shown in Fig. 7.3 is the differential association of mothers with sons and daughters after

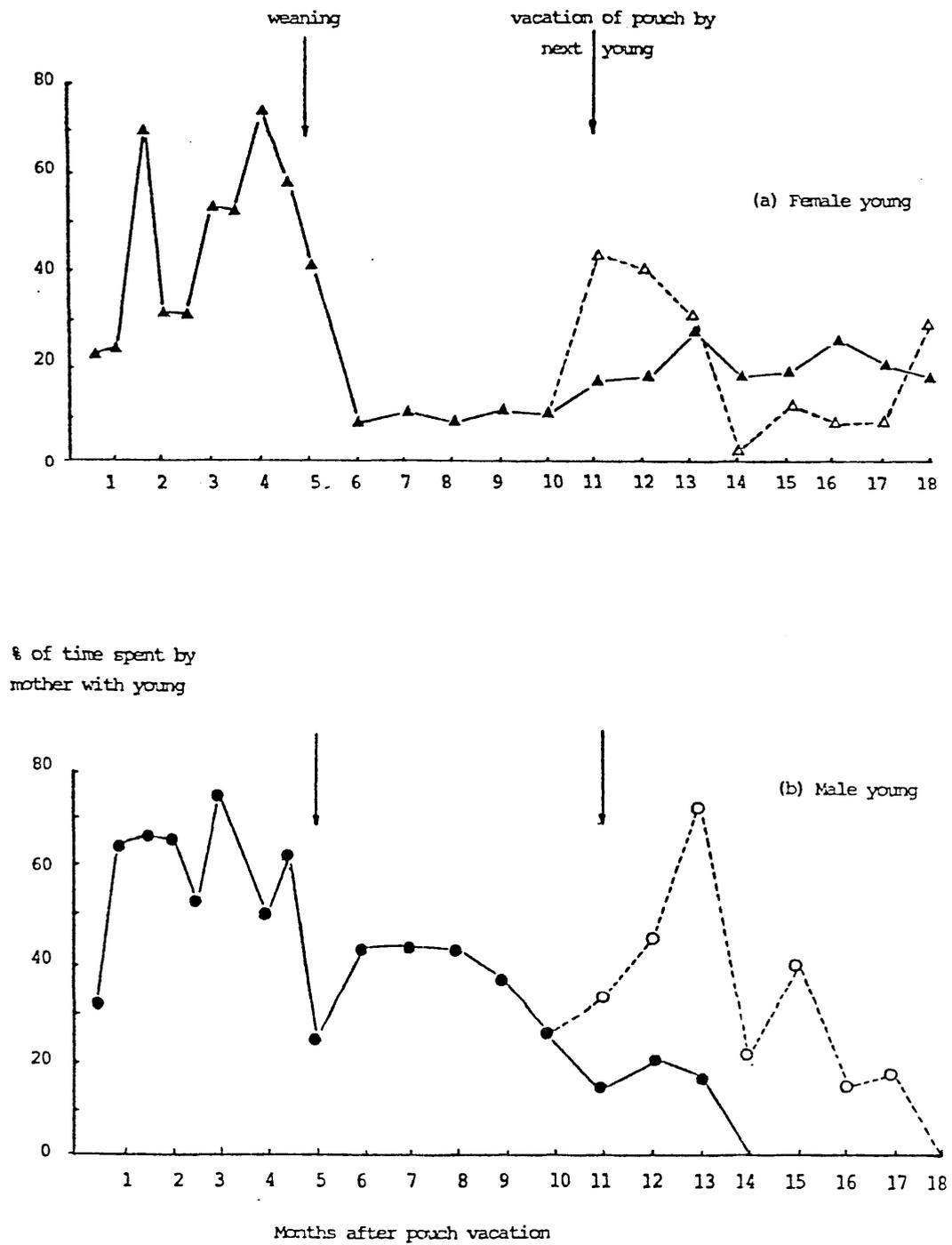


Fig. 7.3 Proportions of time spent by mothers with their maturing female and male offspring. Open symbols and dashed lines are for cases where the subsequent infant died soon after leaving the pouch.

weaning : mothers spent a median of 33% (n=11) of their time with sons and 8.5% (n=7) with daughters between their weaning and the emergence of the subsequent young from the pouch, a significant difference (U=4.5, P<0.01). In general terms, association between mothers and their sons declines from the time the subsequent young leaves the pouch and, of course, ceases altogether when the son disperses, whereas association between mothers and daughters increases somewhat, and continues into the adult life of the daughter. However, Fig. 7.3 shows that if that subsequent infant dies very soon after leaving its mother's pouch, association between the mother and yearling offspring of both sexes increases dramatically, then declines again after a few months.

7.4 Companion Preferences

7.4.1 Identification of social groups The extensive overlap of home ranges in the Wallaby Creek population made it possible for each individual to come into regular contact with a number of other wallabies of both sexes. An index of the frequency with which any two wallabies were seen together (where co-occurrence in groups is defined by the 30 m distance criterion, see ch. 4) is given by the formula :

$$\text{Association Index (A.I.)} = \frac{2n_{1j}}{n_1 + n_j} \times 100$$

where n_1 = the number of times wallaby 1 was seen
 n_j = the number of times wallaby j was seen
 n_{1j} = the number of times the two were seen together.

This index has been used by other workers (e.g. Penzhorn 1984); it approximates the percentage of each individual's time spent in groups with the other. A.I.s were calculated for all pairs of wallabies whose centres of activity were within 240 metres (for females) or 350 metres (for males) of one another (A.I.s for wallabies more distant

from one another than this were either very low, or were zero. A set of A.I.s was calculated for each year of the study; A.I.s were only calculated over periods during which both members of a pair had been resident in the study area.

Prima facie evidence of consistent associations between certain individuals is presented in Fig. 7.4. The curves of Fig. 7.4 were constructed by ranking each individual's known associates in descending order of A.I.; averaging the series of A.I.s obtained for different individuals; and plotting mean A.I. against companion rank. These calculations were made for four categories of dyad (male with male (n=32); female with female (n=55); adult female with adult male (n=20); and adult female with subadult male (n=10)). Fig. 7.4 shows that: the average subadult male spent much of his time with only one or two adult females, while spending relatively little time with a number of others; the average female likewise appeared to have one or two regular female companions; such regularities are less evident for associations among adult males, and scarcely appear at all in associations between males and females.

It is tempting to assume at once that the curves of Fig. 7.4 demonstrate that subadult males and females exercised quite clear preferences for the company of certain females, but a second interpretation is that the curves reflect some peculiarities in the extents to which the home ranges of such wallabies overlapped. There will naturally be some causal relationship between the degree to which any two individuals' home ranges overlap and the amount of time they spend together, and if this relationship is very strong it obscures the basis for any inference that these wallabies expressed preferences for one another's company.

Fig. 7.5 shows that the distances separating the centres of activity of pairs of wallabies were related to their A.I.s ($A.I. = 19.96 - 3.64 \ln D$, where D is the distance separating the centres of activity of two wallabies), although much of the variability in A.I.s remains unaccounted for by this correlation ($R=0.41$). At least some of the remaining variation could be due to preferences by certain wallabies for one another's company. The regression statistics calculated from the data of Fig. 7.5 can be used to derive the degree

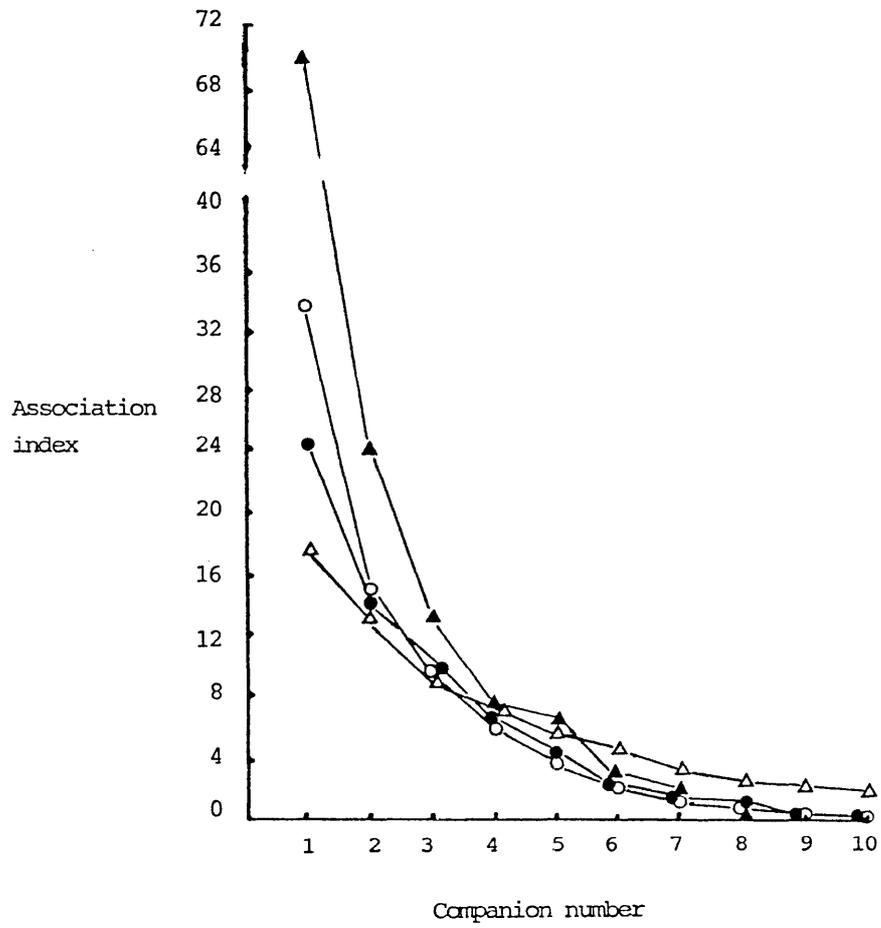


Fig. 7.4 Companion preference curves (see text) for female-subadult male (▲); female-female (○); male-male (●); and male-female (△) dyads.

to which the A.I. observed for any pair of wallabies differed from the A.I. expected simply from the closeness of their centres of activity, giving a measure of the strength of preferential associations between individuals which takes into account the degree to which their home ranges overlapped. Table 7.1 shows the average values of these deviations for several categories of dyad calculated from data gathered in 1982 and 1983. The table shows that the strongest preferential associations were between subadult males and their mothers, and the weakest were between subadult females and adult females other than their mothers. A Kruskal-Wallis test showed that there were significant differences between the median deviations of observed from expected A.I.s in the various categories of pairs ($T=28.35$, $P<0.001$). A multiple comparisons test (Conover 1980, see Table 7.1) showed also that preferential associations within pairs the members of which were known to be closely related were significantly stronger ($P<0.05$) than were associations between wallabies of unknown relatedness (many of whom were probably only distantly related, if at all).

It seems therefore that family relationships have an important proximate influence on the time spent by female and subadult male wallabies together, in addition to the effect of home range overlap. Strong preferential associations are maintained between mothers and their subadult offspring, especially their sons; as Table 7.1 shows, such associations are maintained into the adult lives of daughters (sons have by this time dispersed). These long-term relationships between kin should lead to the formation of clusters of matrilineally related wallabies. At present, not enough data are available to completely identify such clusters from knowledge of kinship; however groups of individuals linked together by high indices of association can be delineated by single-linkage cluster analysis (see Morgan et.al. 1974)

Dendrograms were constructed from the association indices of females and subadult males for each year of the study. Each dendrogram consists of a hierarchical arrangement of clusters, within which the closeness of any two wallabies is determined by the magnitude of their association index. The dendrogram grows from base to apex by first

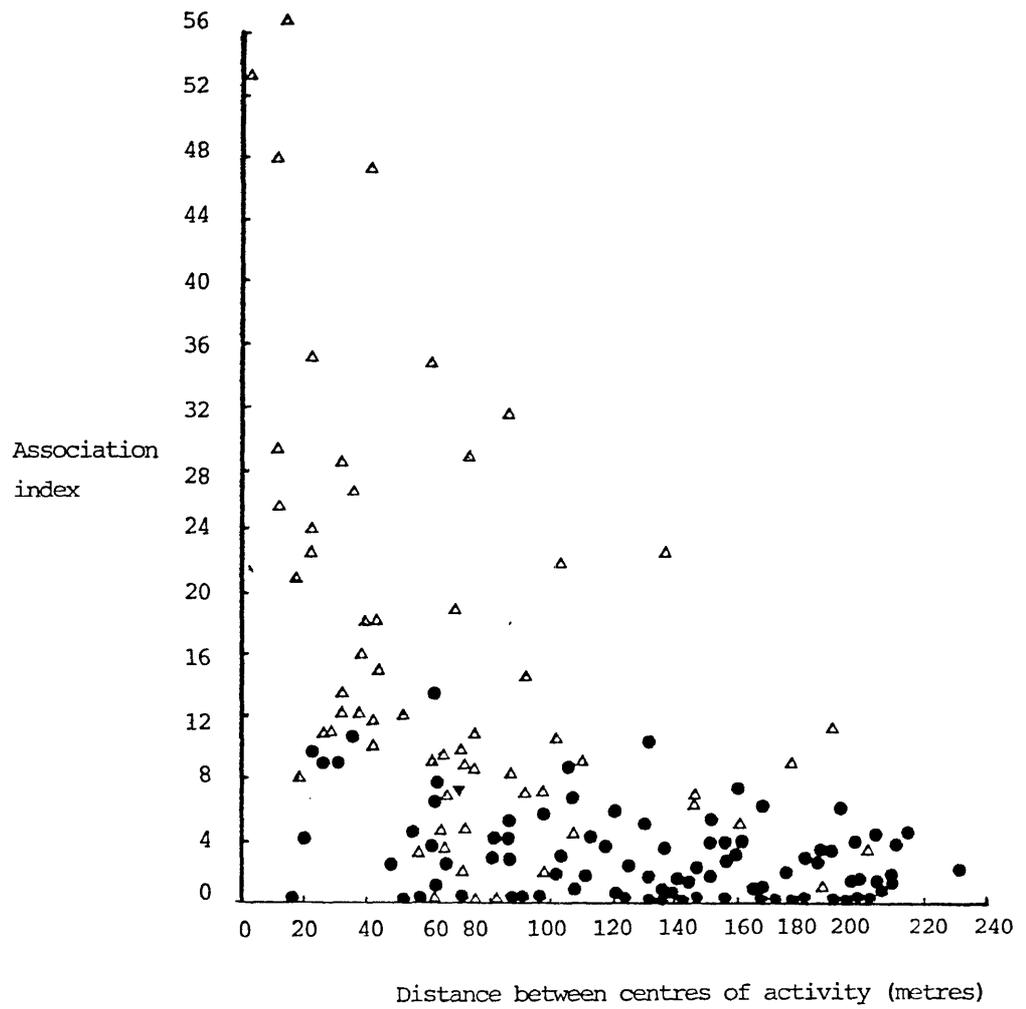


Fig. 7.5 Relationship between spatial proximity of centres of activity and association index for females (and subadult males) within (Δ) and between (\bullet) clusters (see text).

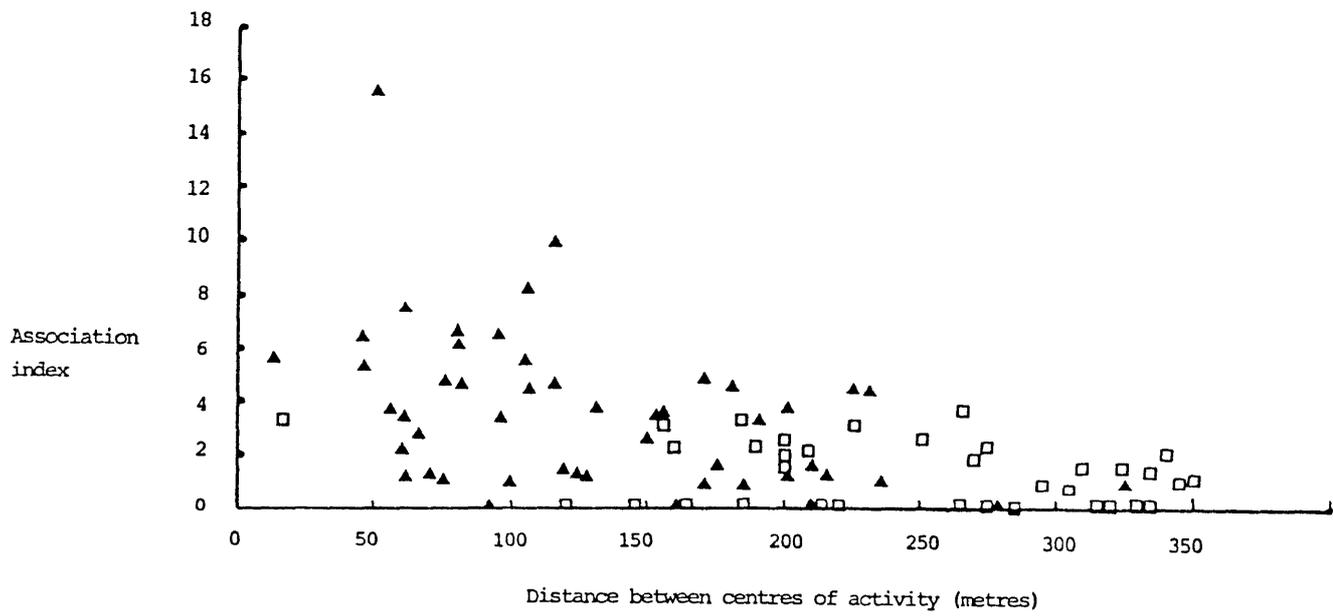


Fig. 7.6 Relationship between spatial proximity of centres of activity and association index for pairs of males within (▲) and between (□) clusters.

drawing single individuals together into 'simple' clusters, which are themselves then linked together to form larger and more heterogeneous 'complex' clusters. Simple clusters form through the connection of individuals with their closest associates, while complex clusters arise from less close associations between individuals belonging to different simple clusters. This distinction between simple and complex clusters provides a unique criterion for defining groups of wallabies using the dendrogram: each simple cluster was delineated at its maximal size (i.e. just before it was drawn into a complex cluster), and individuals whose association indices were all so low that they did not join any simple clusters, entering instead into complex clusters high in the dendrogram, were deemed to have been solitary. This method of defining groups is similar to the technique of drawing maximum spanning trees (Morgan et al 1974) except that it includes a criterion for defining some individuals with low A.I.s as solitary. Because one purpose of this analysis was to define clusters beyond the mother-subadult pair, such pairs were treated as single individuals when being assigned to groups.

This clustering technique arranged all of the adult females, subadult females and subadult males in the population into a series of solitary individuals and small groups. The small groups were probably primarily matrilineal in structure (because of the preferential associations they exercised, those females known to have adult daughters in the population were drawn into groups with them), and for convenience of discussion I shall hereafter refer to them as 'social groups', to distinguish them from temporary gatherings of wallabies, which I shall continue to refer to simply as 'groups'. These social groups are marked on the dendrogram of Appendix III, which was constructed from data collected in 1983.

Pairs of wallabies belonging to the same and to different social groups are distinguished in Fig 7.5, to show that wallabies who lived close together did not necessarily belong to the same social groups: individuals who had been assigned to the same social groups spent more time with one another than they did with others who also used home ranges overlapping their own (regression analyses showed that the relationship between spatial proximity and A.I. within social groups

had a significantly greater slope, higher intercept and stronger correlation than did the relationship between social groups, see Table 7.2). The clustering procedure described above was also applied to associations between adult males, to reveal a quite different result: degree of home range overlap was apparently the only factor determining the membership of clusters (see Fig. 7.6).

The association preferences of individuals in social groups tended to be stable from year to year. I demonstrated this by correlating the A.I.s for pairs of wallabies in 1982 and 1983; the correlation was significant ($r=0.639$, $n=26$, $P<0.01$). Unfortunately, this analysis could not be repeated for pairs who were present in 1981 through to 1983, because the relatively small number of individuals known in 1981 and the loss of some of those animals in the following years reduced the sample to an insufficient size and breadth. The strength of association between particular individuals did tend to decline over the years because females turned their attention from older animals to their most recently weaned offspring (see Table 7.1). The frequency with which mothers associated with their recently weaned (subadult) offspring did not vary significantly between or within years. I correlated the proportion of time spent by mothers with their young with mean monthly rainfall for the six months after weaning and mean minimum monthly temperature over the same period, and could find no significant correlation for males ($r=0.31$, $R=0.13$, $n=9$, n.s.) or females ($r=-0.40$, $r=-0.09$, $n=8$, n.s.).

The histograms of Fig. 7.7 show that wallabies who were regularly seen together tended to stay closer to one another within groups than did wallabies who associated rarely: mothers and their subadult offspring (histogram I) spent much more time in association less than four metres apart than did other wallabies belonging to the same social groups (histogram II), while wallabies from different social groups were, on the occasions when they were seen together, more likely to be separated by greater than 20 metres (histogram III). Distributions I and III both differ significantly from distribution II ($\chi^2 = 19.6$, d.f. = 2, $P<0.001$, $\chi^2 = 6.47$, d.f. = 2, $P<0.05$ respectively); to meet the requirements of minimum expected frequencies for χ^2 the distance classes in the histograms were

combined into three classes of equal breadth).

7.4.2 Breeding synchrony and social grouping. Females who associated often and closely with one another tended also to breed in synchrony. The degree of synchrony in the breeding cycles of any two females was measured as the number of months, from zero to five, separating their parturition dates : females giving birth in the same month were considered to be breeding perfectly in phase, while, given that the average inter-birth interval for females was ten months, females giving birth five months apart were completely out of phase. This measure of synchrony was calculated for each pair of wallabies whose centres of activity were less than 240 metres apart, and the frequency distributions of these measures were then compared for wallabies who had been assigned to the same and to different social groups. The comparison (see Fig. 7.8) shows that wallabies belonging to the same social groups tended to give birth within less than three months of one another, whereas wallabies living close together yet belonging to different social groups were more likely to breed out of phase with one another. The two distributions differ significantly ($\chi^2=11.26$, $P<0.05$). (Breeding synchrony for each pair of females was measured only once for the whole study, not once each year. Where two females had both bred in more than one year, I calculated their difference in phase for the latest year in which both were present; this was usually 1983). Females of the same social group bred, on average, 2.3 months out of phase, while mothers and daughters bred 1.9 months out of phase. This trend was examined further by testing for a correlation between breeding synchrony and association index of pairs within social groups. For this analysis the measures of breeding synchrony were subdivided to show the number of half-months separating the dates at which females gave birth to give a wider range of values in this variable. The correlation between the two variables was rather weak, but significant ($r = 0.334$, $n=36$, $P<0.05$) : individuals who associated frequently tended to give birth at the same time of the year.

7.5 Home range overlap between social groups

Although the members of different social groups often used home

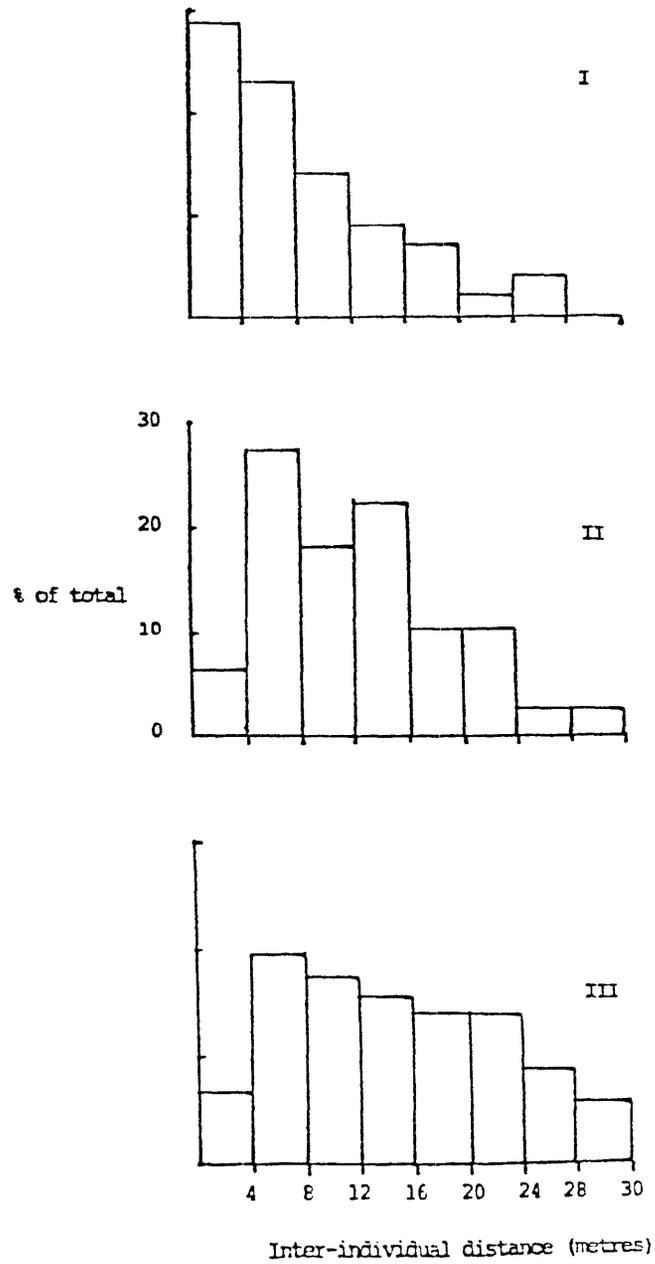


Fig. 7.7 Inter-individual distances for mothers and subadult offspring (I), other members of the same social groups (II), and members of different social groups (III), when in association. (n=88, 77 and 58 respectively).

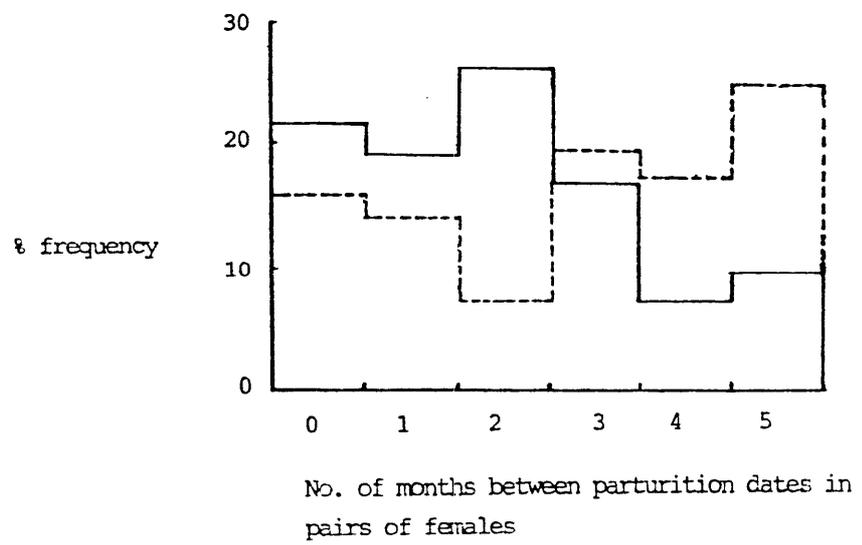


Fig. 7.8 Synchrony of breeding of pairs of females belonging to the same (solid lines) and to different (dashed lines) social groups (n= 39 and 59 pairs respectively).

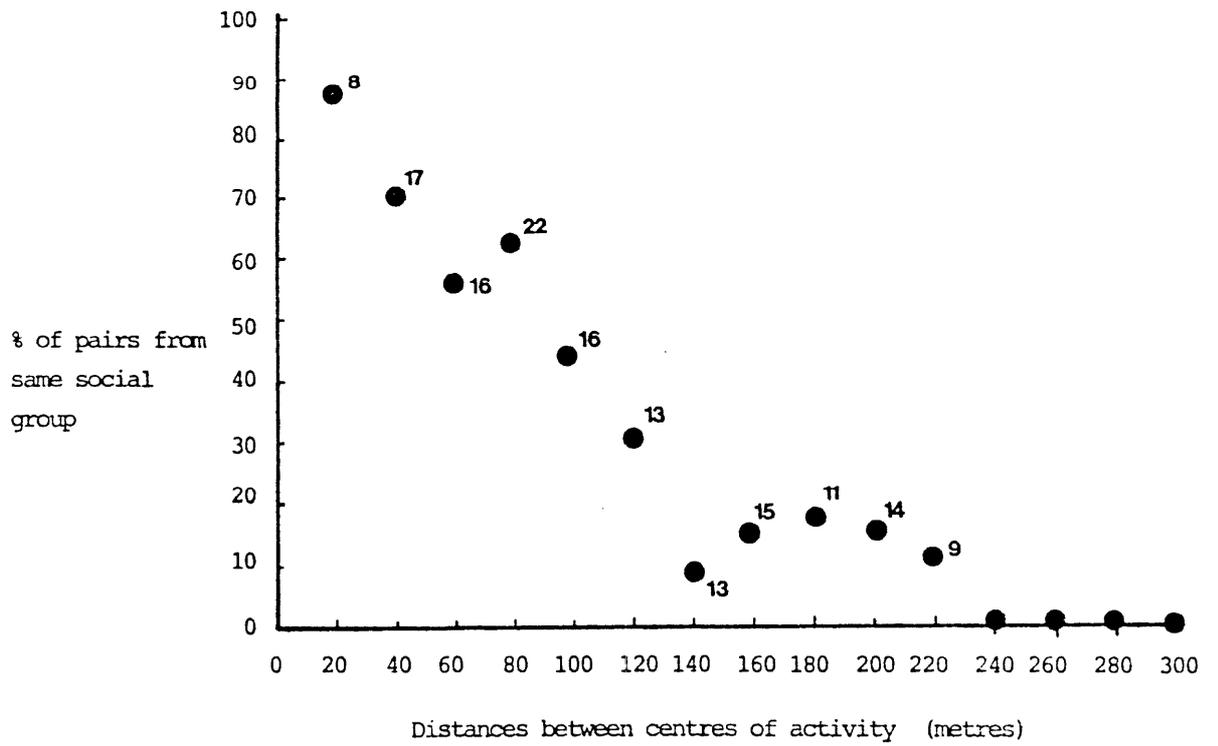


Fig. 7.9 Relationship between proximity of centres of activity and probability of membership of the same social group, females and subadult males. Sample sizes are numbers of pairs.

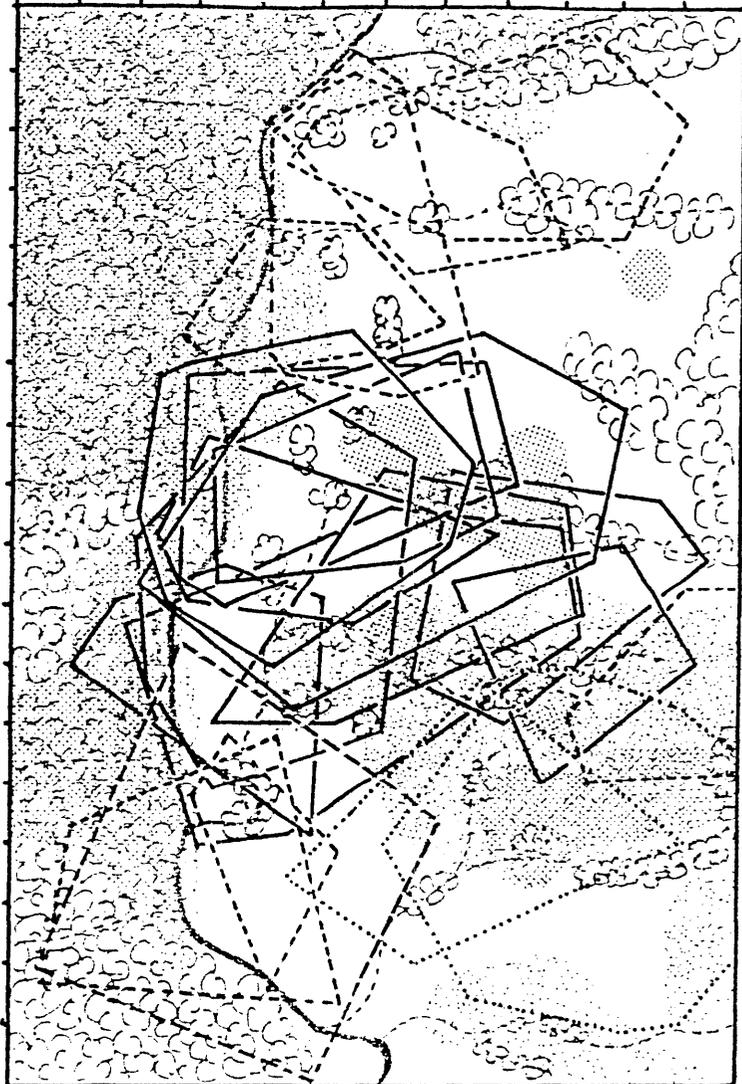


Fig. 7.10 Home ranges of social groups, 1983. Solid, dashed and dotted lines are used to distinguish apparent aggregations of home ranges.

ranges which overlapped, the degree of home range overlap within social groups was much greater. Fig. 7.9 shows how the probability that two females or subadult males would belong to the same social group declined with increasing separation of their centres of activity. Viewed from the standpoint of an individual female this means that females or subadult males who habitually use large sections of her home range, including its core, will mostly be members of her own social group, while at the periphery of her range will be other wallabies of different social groups. I am unsure of the meaning of the disjunction in the curve of Fig. 7.9; it may simply reflect some weakness in the method of assigning individuals to social groups. There are only a small number of individuals from the same social group in the tail of the curve.

The home ranges of whole social groups are mapped in Fig. 7.10 where I have also distinguished what appear to me to be large aggregations of these group ranges. The boundaries of these aggregations appear to be purely ecological in nature : there is one aggregation associated with each of the major gully systems of the study area, and one resting on the creek flats in the south eastern part of the study area. This pattern of distribution reflects the distribution of the centres of activity of individuals (see Ch. 3).

7.6 Effects of Season and Reproductive State on Sociality of Females

The proportion of her time that a female wallaby spent in the company of other females varied with both her reproductive state and the time of year. Because the wallabies breed in a partly seasonal pattern, the two effects can easily interact with one another in analysis, and some care must be taken in separating them. I dealt with this problem by restricting my analysis to one ten-month reproductive cycle from each of twelve female wallabies. Each of these twelve reproductive cycles began in a different month of the year, so that the data on association for each month of the year are averages of ten wallabies each in a different phase of a ten-month cycle; and the data on association in each month of the ten-month cycle are averages for twelve wallabies, the data on each having been

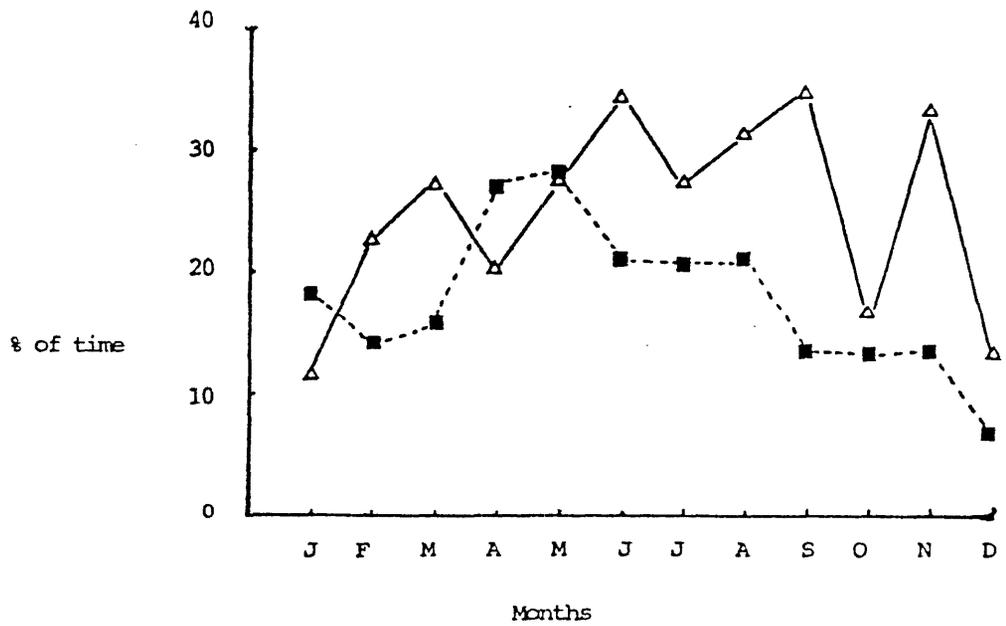


Fig. 7.11 Seasonal variations in proportions of time spent by females with other females (Δ) and with males (■).

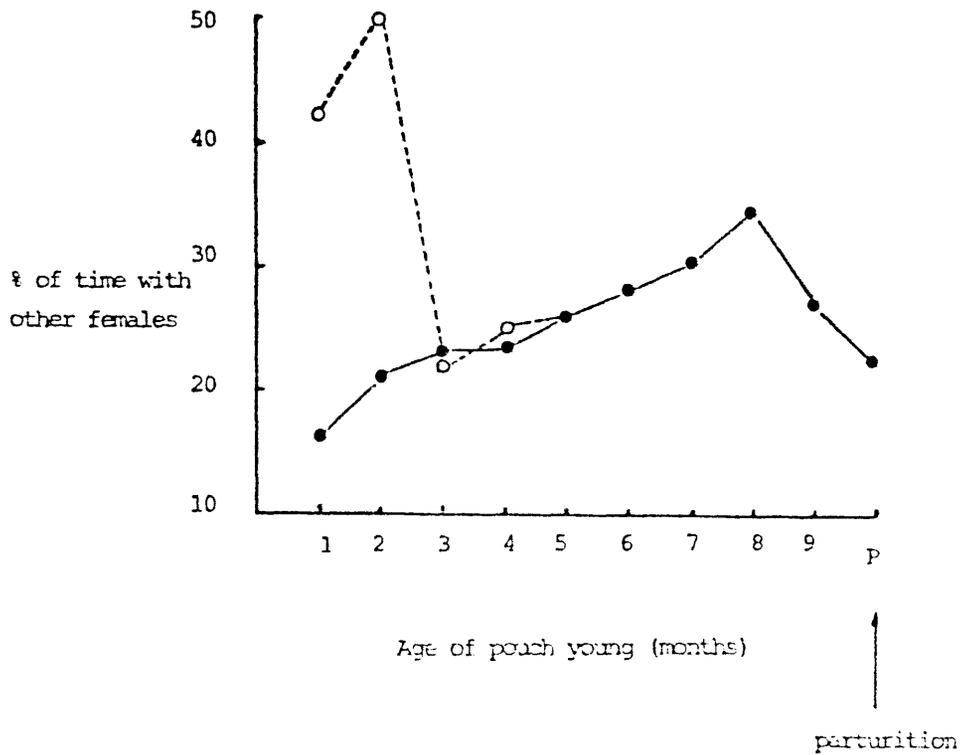


Fig. 7.12 Relationship between females' reproductive states and the time they spend with other females (open circles and dashed line: females with small pouch young but no young-at-foot).

collected in a different calendar month. The trends plotted in Figs. 7.11 and 7.12 are therefore calculated from perfectly balanced data, and do not confound one another.

Fig. 7.11 shows that females spent more time in the company of other females in winter and spring than in summer and autumn; a pattern of this form is to be expected from the data on seasonal variation in group size presented in Ch. 4. There was a similar, though less pronounced, seasonal pattern in the association of females with males. Fig. 7.12 shows that females were least likely to be in the company of other females when they had a small pouch young and small young-at-foot, but those females whose previous young had died before reaching the young-at-foot stage, so that they had small pouch young and no young-at-foot, were relatively social (there were four such females in this sample, and they were distributed evenly throughout the calendar year). Females tended to associate more with other females as their pouch young grew, but again became less social during the last two months of pouch life. The pattern of association between females and males through the female's reproductive cycle will be described below.

7.7 Association between males

Although males apparently do not live in discrete or partially discrete clusters of preferentially associating individuals, the suggestion remains from Fig. 7.4 that they do exercise some preference for other male companions. This section analyses the degree to which such preferences were determined by differences in the body sizes of individual males. All of the males in the study area were ranked according to differences in body size; these rankings are good predictors of dominance orders and, more approximately, age (see Ch. 8), and are thus useful as a starting point for discerning patterns in other behavioural differences between males.

As Fig. 7.13 makes clear, males generally prefer to associate with other males similar to themselves in body size : in 1983, the body size ranks of males were positively correlated with the body size ranks of their most frequent male companions ($r_s=0.70$, $n=26$, $P<0.01$). This correlation was most precise among small and medium-sized males,

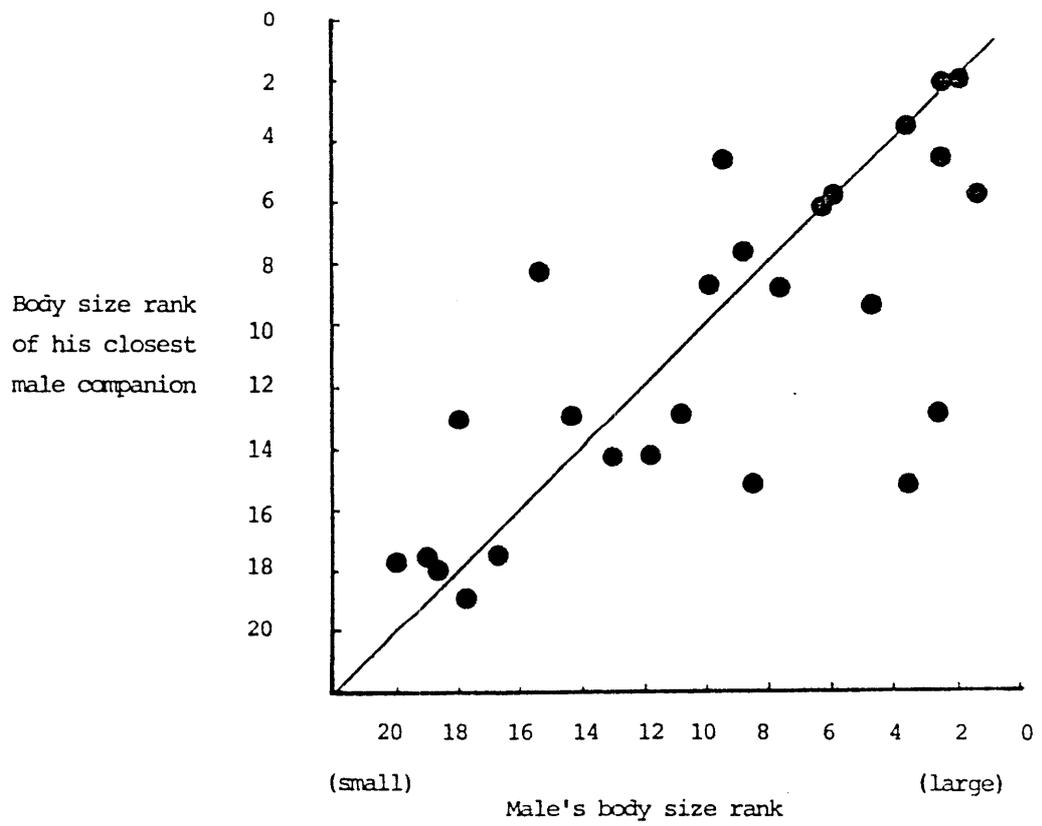


Fig. 7.13 Relationship between the body size ranks of males and the size ranks of their closest male companions, 1983.

but large males tended to have as their most frequent companions males somewhat smaller than themselves.

The proportions of time spent by males with other males are plotted against body size in Fig. 7.14. These data suggest that medium-sized males spend more time with other males than do smaller or larger males, although the difference between medium and other males in this respect in 1983 was not significant ($U=22$, $P<0.20, >0.10$). There was, however, a very clear pattern in the proportions of time spent by males completely alone: large males spent significantly more time not accompanied by any other wallaby, male or female, than did other males (see Fig. 7.15; $U=1.5$, $P<0.001$). Note that, as in earlier analyses, I have excluded instances of males accompanying oestrous females from this, and from the following, analysis; associations between males and oestrous females are discussed in Ch. 9.

7.8 Associations between males and females

The proportion of time spent by males with females declined slightly with increasing body size (Fig. 7.16). This was mainly due to the fact that young males who had not yet dispersed from their natal home ranges spent a relatively high proportion of time with females (mostly their mothers); if these young males are excluded from the analysis, the relationship does not reach significance ($r_s = -0.21$). However, the way in which males distributed their time among the females with whom they associated did change significantly with body size. I measured this by calculating, for each male, the standard error of the mean value of his association indices with his known female associates. A low value of this standard error indicates uniform association with each of a number of females, a high value indicates preference for one, or a small number of females over the others. The relationship between body size and this statistic is shown in Fig. 7.17; the correlation is significant, regardless of whether young males not yet dispersed are ($r_s = -0.71$, $P<0.0201$) or are not ($r_s = -0.70$, $P<0.001$) included in the analysis. Large males were less likely to express a sustained preference for certain individual females than were small males.

There is, however, clear evidence that males concentrated their

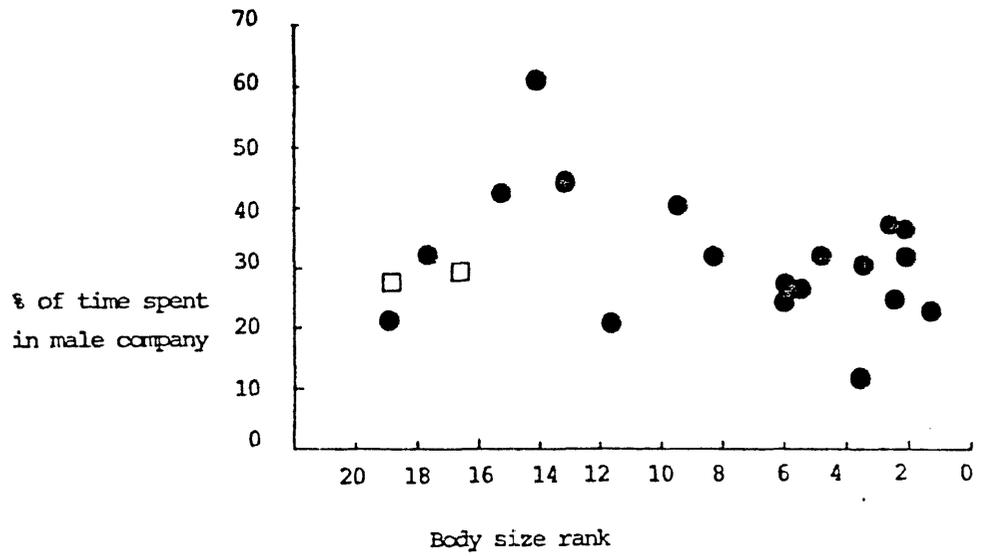


Fig. 7.14 Relationship between the body size ranks of males and the proportions of their time spent with other males, 1983 (open squares represent subadult males).

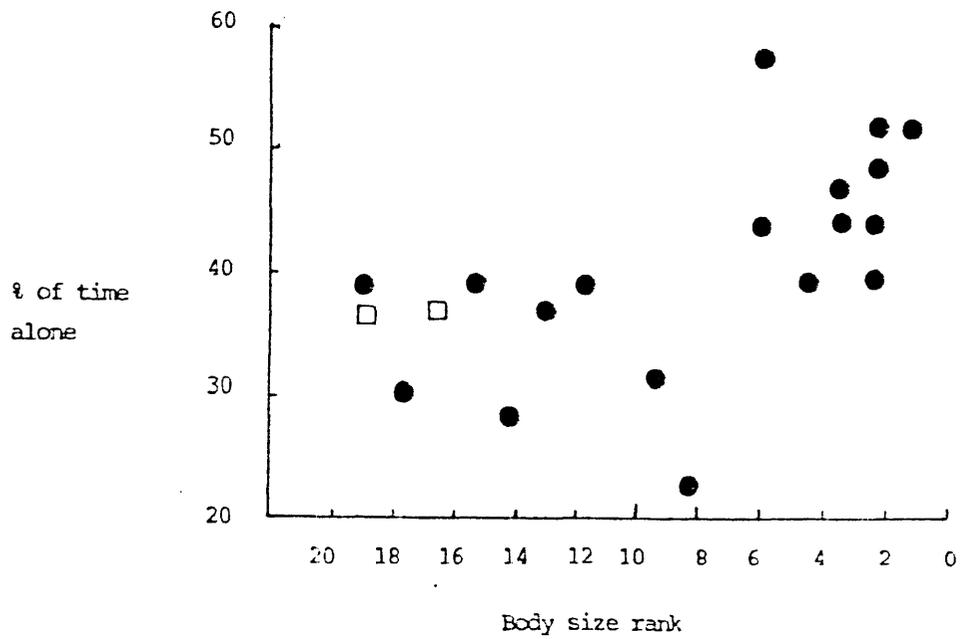


Fig. 7.15 Relationship between the body size ranks of males and the time they spend completely alone, 1983.

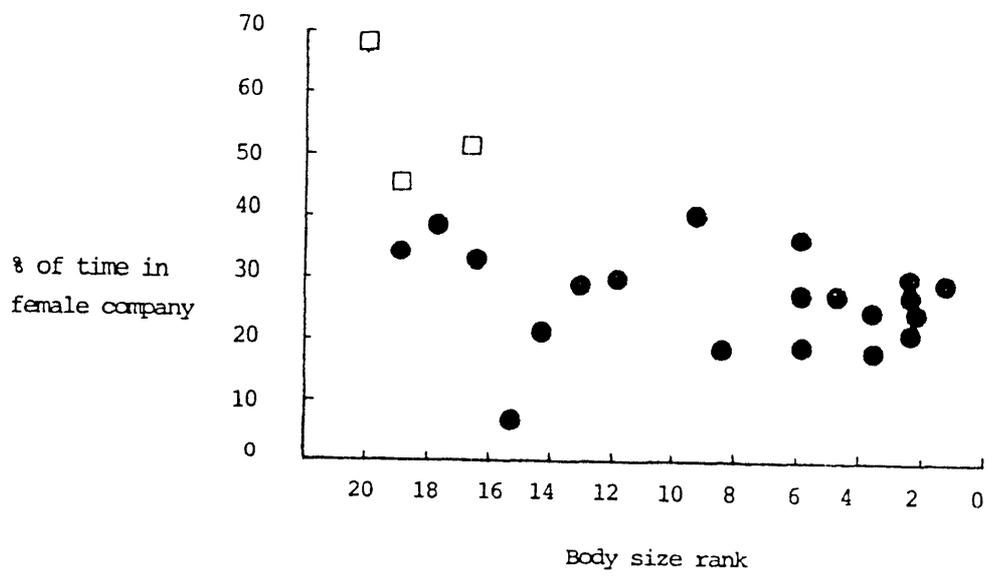


Fig. 7.16 Relationship between the body size ranks of males and the proportions of their time spent with females, 1983 (open squares represent subadult males).

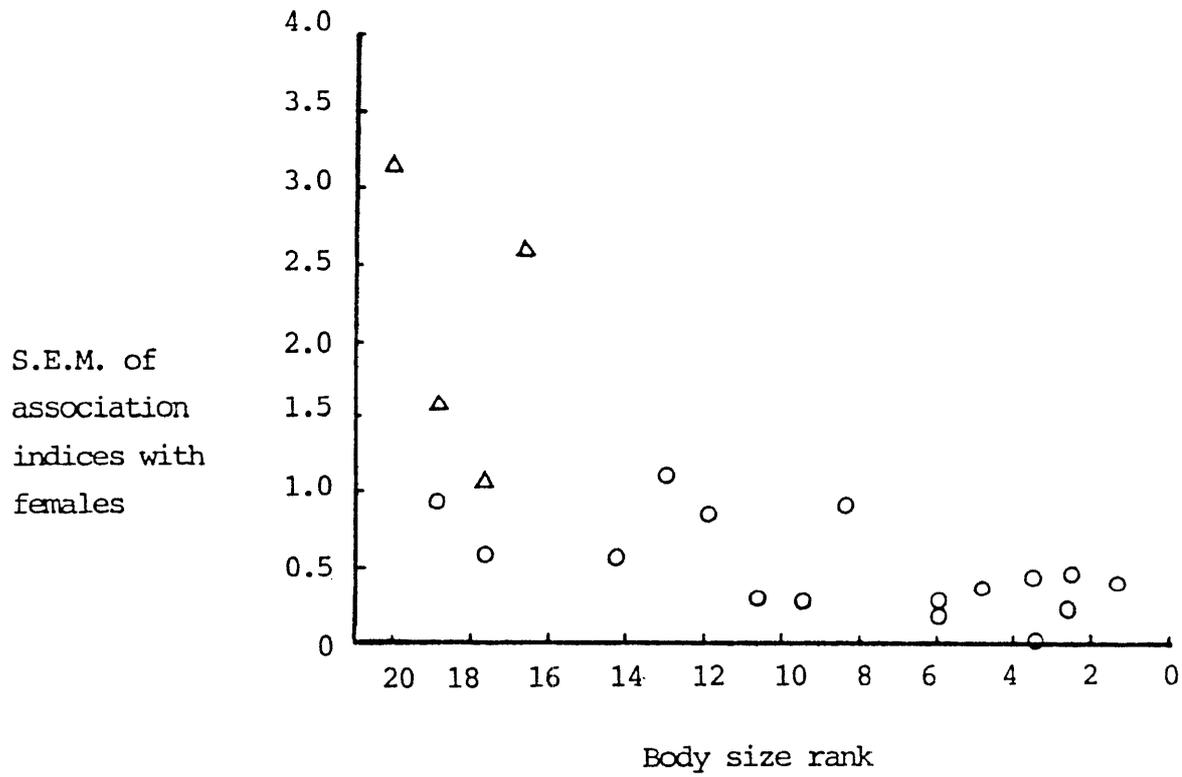


Fig. 7.17 Relationship between the body size ranks of males and the distribution of their association preferences among females (open triangles represent subadult males).

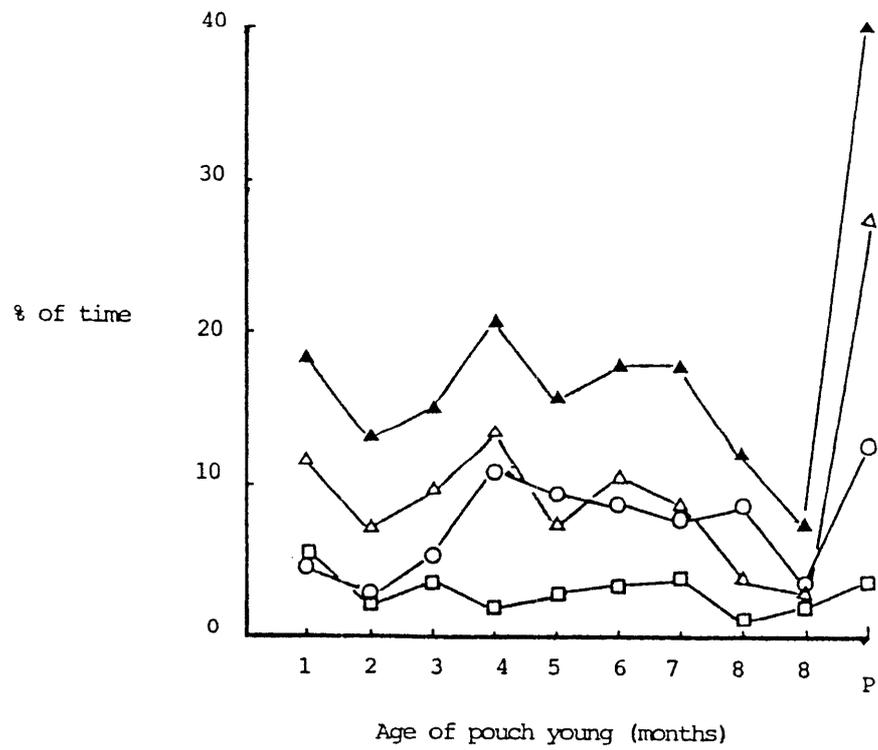


Fig. 7.16 Relationship between females' reproductive states and the proportion of their time spent with large (Δ), medium (\circ) and small (\square) males, and any males (\blacktriangle).

attention on females in certain reproductive states (Fig. 7.18). Females were most often accompanied by males during the month in which they gave birth and mated. Accompaniment by males was also quite high during the early months of pouch life but thereafter declined and reached its lowest level in the month immediately preceding the month of parturition, when the female had a very large young in her pouch. This pattern of association between males and females was followed by large and medium males, but not by small males, who were apparently uninfluenced by the females's reproductive state. The data in Table 7.3 show that males of each of the three major size classes spent similar proportions of their time with females of three broad reproductive classes (in the table Fpt denotes females in the month in which they gave birth and mate; Fsy denotes females with pouch young less than or equal to three months of age; and Fmy and Fly denote females with pouch young from four to ten months old). There was a slight tendency for large males to devote more of their time to Fpt females at the expense of the other females than did medium or small males, but the difference is a small one.

This general sketch does not show whether or not the members of any particular class of males were able to have exclusive access to any particular class of females; data on this point are presented in Table 7.4. Table 7.4 records, for each of several classes of males, the proportions of the time they spent with females of several reproductive classes when they were the only male in attendance. The absolute values of these proportions are not important, but the differences in values between classes of males are. I have considered five classes of males: the three major size classes (small, medium and large males, as defined in Ch.2) and two sub-classes of the large male class - those known from observations on their social interactions to have dominant social status, and those known to be subordinate in status (see following chapter). The dominant males were those who were able to dominate all other males in all or a large part of their home ranges; subordinate males were the remaining large males. Table 7.4 shows that large males were most likely to be the only males with females who were within a month of coming into oestrus (Fpt females), and dominant large males were more likely than

subordinate large males to be the only males in the company of such females. Again, however, the differences are not large. However, dominant large males were much more likely than subordinate large males to be the only *large* males with these females, they were also considerably more likely to be the only large males with females with small pouch young (Table 7.5). It seems, then, that dominant large males may prevent males immediately inferior to them in status from joining them with certain females (particularly those likely to be near oestrus) while allowing smaller males to attend these females.

7.9 Social interactions

Interactions between males and between males and females, will be described in detail in succeeding chapters. As my data on interactions between females are not extensive I shall briefly review them here. In 32 hours of systematic observations of groups containing more than one adult female wallaby, interactions between the females occurred at a rate of 0.19 per hour. I saw a total of 15 interactions between females, these were all displacements, in which one female moved towards another, who moved aside. In some cases the approach was a rapid dash, accompanied by growls and raised forearms by the aggressor, but none resulted in actual contact or fighting between females. In six of these interactions the relative ages of the two participants were known. In each of these cases it was the older wallaby who dominated the younger.

I saw only three interactions between mothers and their subadult sons, and in each case the mother dominated the son.

The immediate function of many of these interactions appeared to be the maintenance of an unoccupied space around dominant females - females would actively supplant others who had come close to them. At other times females who had not been provoked in this way would deliver threats, as if they were simply emphasising the inferior social status of the other wallaby.

This sample of interactions, though inadequate for most purposes, suggests that there may be a dominance hierarchy among females, with older females dominant to younger females and to subadult males.

7.10 Discussion

Red-necked wallabies are among the least social members of their genus, in the sense that individuals are often alone, and large groups form only rarely. However, behind this apparent asociality lies a stable social organisation, which rests on regular preferential associations between certain individuals. This social organisation is discernible only through a probabilistic analysis of companion preferences : certain individuals associate with one another more frequently than one would expect from chance, even though group compositions change repeatedly in the short term and home ranges overlap extensively, so that each individual may have transient contacts with a relatively large number of others.

Sons remain within their mother's home range for almost a year after weaning, and daughters usually do so for life. This inheritance of the mother's home range by daughters tends to produce clusters of related females sharing common home ranges, which in low density populations might perhaps be wholly or partly separate from one another. In the dense Wallaby Creek population, home ranges of many wallabies overlap, but individuals known to be closely related express positive association preferences, and spend a disproportionately large amount of time together. Such preferences have, in this study, been demonstrated between females and their subadult and adult daughters and their subadult sons.

The relatively long dispersal distances and lack of coordination of the dispersal of related males must reduce the probability that any male will spend his life among close relatives. Males associate non-preferentially with females, and only small and medium males show any clear preferences for certain other males, that is, those similar to themselves in size. Large males are mostly solitary except for the time they spend with oestrous or near-oestrous females.

In this chapter, I have used cluster analysis to draw abstract boundaries around sets of preferentially associating females and subadult males, and I refer to these sets as social groups, but because of the fluidity with which gatherings of wallabies form and change composition there is, at present, a degree of arbitrariness in this drawing of limits. However, the assignation of animals to social

groups provides a very useful basis for other analyses and comparisons, and confirms the matrilineal nature of wallaby social organisation - individuals known to be related almost invariably belonged to the same social group. In addition to this, females of the same social group tend to stay closer to one another when associating than do females of different social groups, and are also more likely to breed in synchrony.

Greater synchrony of breeding within than between social groups has also been observed in Soay sheep *Ovis aegris* (Grubb 1974), lions *Panthera leo* (Bertram 1975, Packer and Pusey 1983) and sperm whales *Physeter macrocephalus* (Best and Butterworth 1980), among other species (see McClintock 1981). Female lions are brought into synchrony when incoming males kill the cubs of a pride (Packer and Pusey 1983); Best and Butterworth suggested that synchrony is greater within than between groups of sperm whales because of small differences in the environments inhabited by different groups. My analysis of synchrony in red-necked wallabies compared the closeness of parturition dates in pairs of wallabies of the same group with pairs belonging to different groups but having overlapping home ranges, and thereby controls for differences across groups in the environmental control of breeding. Young female red-necked wallabies tend to breed in phase with their mothers, and the synchrony within whole groups probably reflects their matrilineal structure. This synchrony between relatives may perhaps be mediated by air-borne chemical signals (McClintock 1981).

The inheritance of maternal home ranges ('natal philopatry') by daughters and the dispersal from them by sons is a common pattern in mammals (Greenwood 1980, Dobson 1982, Waser and Jones 1983, Packer 1979) and coherent social groups, where they occur, are usually composed of female relatives, often with unrelated male attendants. Natal philopatry by daughters is widespread amongst solitary as well as social mammals, and it seems that the lifetime proximity of female kin has been an important precursor to the evolution of sociality and cooperative behaviour in mammals (Waser and Jones 1983, Michener 1983). Perhaps the most common outward form that mammalian sociality takes is for matrilineal groups to occupy discrete home ranges or

territories, which may also be defended by males. This is a widespread mode of organisation in populations of, for example, ground squirrels (Michener 1983) and terrestrial social carnivores (Bertram 1979, MacDonald 1983). Females may also live in stable, closed-membership matrilineal groups which use overlapping home ranges, as in African elephants *Loxodonta africana* (Douglas-Hamilton 1972) and gelada baboons *Theropithecus gelada* (Kawai et al. 1983, Dunbar 1983). Open-membership matrilineal groups with overlapping group home ranges, such as I have described for red-necked wallabies, occur in some ungulates, such as red deer *Cervus elaphus* (Clutton-Brock et al. 1982) white tailed deer *Odocoileus virginianus* (Hawkins and Klimstra 1970, Nelson and Mech 1981, Ozoga et al. 1982) mountain sheep *Ovis canadensis* and *O. dalli* (Geist 1971) and probably in roe deer *Capreolus capreolus* (Strandgaard 1972, Bromley 1970) and others as well.

Previous discussions of macropodid social organisation have paid special attention to the subdivision of populations into large assemblages of animals using common home ranges (Kaufmann's 'mobs'). This kind of organisation may occur in red-necked pademelons (K.A. Johnson 1977) and tamar wallabies (Inns 1980) as well as in quokkas (Holsworth 1964, 1967, Nicholls 1971), eastern grey kangaroos and whiptail wallabies (see section 7.1). For quokkas, Holsworth (1964, 1967) initially suggested that these assemblages were stable social groupings, and referred to their home ranges as 'group territories', but Nicholls (1971) argued that their boundaries were set by ecological rather than social barriers, and that the group home ranges simply reflected aggregations of animals on patches of suitable habitat. The boundaries of the mobs mapped by Kaufmann (1974a) for whiptail wallabies also coincided, where they were distinct, with abrupt discontinuities in habitat. Although Kaufmann's data suggested that young males disperse from their mother's mob while daughters remain within it, there is apparently little movement between aggregations by young quokkas of either sex (Holsworth 1964). These mobs or assemblages are comparable in area and numbers of animals present to the aggregations of home ranges of social groups of female red-necked wallabies on gully systems and creek flats at Wallaby Creek

(see Fig. 7.10); they are probably superimpositions on the important social structuring of the population, not the units of that social structure. Statistical analysis of association frequencies between individuals should yield useful and interesting results in other species of macropodids, particularly quokkas, where it has already been suggested that enduring pair-bonds form between males and females (Kitchener 1972), and in the more gregarious *Macropus* species, which could be compared with red-necked wallabies to illuminate the pathway by which sociality has evolved in macropods and to indicate the selective pressures responsible for its evolution.

One of the most striking variations on the theme of preferential association between related red-necked wallabies is the sex differences in association between subadult offspring and their mothers. During the six months after their weaning, sons are seen with their mothers over three times more often than are daughters. The analyses of this chapter show that this strong association is partly due to the very high degree of overlap between the home ranges of subadult sons and their mothers, and an unusually high association preference given that degree of home range overlap. This difference is an exaggeration of a disparity that was already clear in infancy (see Ch. 6) : male young-at-foot spent more time with their mothers than did females. That difference was due to the males' greater eagerness to follow their mothers. The sex difference in association of subadults with their mothers may have similar origins, but for the differing preferences of male and female subadults to be realised, their mothers must be tolerant of persistent accompaniment by sons, and may even encourage it in some ways. Unfortunately, I do not have the detailed data on interactions between mothers and subadults of both sexes which would allow me to disentangle the influences contributing to the expression of differences.

Although kinship is apparently the most important factor determining long-term levels of association between female red-necked wallabies, the proportion of time spent by a female with other females, and with males, varies according to her current reproductive state. Females are most solitary during the time that they have small young-at-foot, but as their pouch young grow and their association

with their young-at-foot wanes, they spend more time with other females, until the last two months of pouch life, when they again become more solitary. The solitariness of females with young-at-foot is impressive, and has also been observed in red kangaroos (Croft 1981a, Johnson 1983), western grey kangaroos (Johnson 1983), euros and wallaroos (Croft 1981b, Taylor 1983) and eastern grey kangaroos (Southwell 1981, Jarman, Southwell and Stuart-Dick, pers. comm.). Two explanations for this have been offered. Croft (1981a) suggested that it might be that the relatively weak locomotor abilities of the young-at-foot constrains the ranging of the mother, so that she finds it difficult to maintain contact with other females while also staying near to her infant; or, alternatively, that young-at-foot in multi-female groups might become confused and follow the wrong female in moments of alarm and flight, and that females with young-at-foot therefore avoid other females because of the risk of becoming inadvertently separated from their offspring. Support for this second hypothesis comes from Croft's observations of such confusion in infant red kangaroos, and from Taylor's (1983) data on wallaroos, which show that when females with young-at-foot were found in groups, they were more often than expected the only female in the group. I noticed that large red-necked wallaby pouch young may easily become confused between their mothers and other females during their brief excursions from the pouch (see Ch. 6), and I suggest that this is the reason why females apparently began to avoid contact with other females during the last two months of pouch life, but I saw no indications that young-at-foot have any such difficulty in recognising and following their mothers. It may be that females with young-at-foot become asocial because they spend much of their time in those small, densely-vegetated parts of their home ranges in which their young-at-foot live and because, after temporary separations from their infants, mothers return to the places where they are most likely to relocate them. Both these constraints must make the maintenance of contact with other females difficult.

Males prefer to associate with females who are within a month of giving birth, and to a lesser extent, with females who have small young in the pouch, but spend very little time with females who have

large pouch young. Females mate within a few hours of giving birth, and for about a week prior to the time that she mates a female will be followed by an entourage of up to seven males, with a large dominant male staying closest to her (see Ch. 9). This accounts for the high level of accompaniment by males of parturient females, but it is not so easy to explain why females should more often be accompanied by males when with small rather than large pouch young. I suggest that this may be because males use the size of a female's pouch young as a first approximation of the probability that she is near-oestrous. Recall that females give birth and mate about three weeks after their infant vacates the pouch. The presence of a large young in the pouch alters a female's shape very dramatically, and a casual glance at such a female should be sufficient to show a male that she will not be in oestrus for at least three weeks. However, males may need to make closer visual and olfactory inspections of females with small, less easily discernible pouch young, and as a result spend more time with them. In other species of macropods, males, particularly large males, spend more of their time than expected with females who are in that stage of their breeding cycle at which they are most likely to be in or near oestrus. In red kangaroos and wallaroos this is when the female have young-at-foot and no discernible pouch young (Johnson 1983, Taylor 1983); in eastern grey kangaroos at Wallaby Creek, it is when the females have small pouch young (Jarman and Southwell, in press).

It is typical of kangaroos that large males are more solitary than small males, and in particular that small males spend more time with others of their own class than do large males. This latter tendency is especially evident in the data on red kangaroos and wallaroos collected by Croft (1981a) and Taylor (1983). Large male red-necked wallabies also tend to be solitary (when not actively courting oestrous females) and although the total amount of time spent with other males did not decline significantly with body size, small and medium-sized males were more likely than large males to have as their closest companion a male of similar size. Most of the studies of kangaroos and wallabies cited above have found no indication that some males are able to maintain exclusive access to

any class of females, except in the sense that a large male will try to prevent smaller males from actually interacting with any female he is courting. However, Jarman and Southwell's (in press) study on associations between eastern grey kangaroos, and my data on red-necked wallabies, show that dominant large males are more likely than subordinate large males to be the only large males with females likely to be in or near oestrus. Apparently, although there is a fairly free mixing of males and females in wallaby society, fine differences in social rank have a significant influence on the frequency and manner of association by males with particularly attractive females.



Plate 4. Adult male red-necked wallabies fighting.

Table 7.1 Strengths of preferential association (see text for explanation) between individual wallabies. Vertical lines to the left of the table join dyads which do not differ significantly.

Dyad	Median deviation of observed A.I. from expected	n (number of dyads)
S.A. ♂ - mother	+20.8	9
S.A. ♀ - mother	+12.8	6
Adult ♀ - mother	+8.2	6
Adult ♀ - adult ♀	-1.0	129
Adult ♀ - S.A. ♂	-1.4	29
Adult ♀ - S.A. ♀	-1.8	18

TABLE 7.2: Regressions of association indices (A.I.) on distances separating centres of activity (D) for females and sub-adult males belonging to the same and to different clusters

Associations within clusters:

$$\text{A.I.} = 22.58 - 3.82 \ln D \quad n = 65$$

Regⁿ coefficient significant, $P < 0.0001$

$$r = -0.60, \quad P < 0.001$$

Associations between clusters:

$$\text{A.I.} = 5.79 - 0.90 \ln D \quad n = 107$$

Regⁿ coefficient significant, $P < 0.0001$

$$r = -0.30, \quad P < 0.001$$

Comparison of regression lines:

Slopes differ, $P < 0.0001$

Intercepts differ, $P < 0.0001$

Correlation coefficients differ, $P < 0.05$

TABLE 7.3: Percentages of time spent by males of the three major size classes with females in three reproductive states (see text for details)

	Classes of females:			n (sightings)
	Fpt	Fsy	Fmy + Fly	
Small males	19.46	9.9	16.8	483
Medium males	18.48	9.0	13.1	1526
Large males	22.28	7.5	14.7	1472

TABLE 7.4: Percentages of time spent with females in which males of various classes were the only male present (sample sizes in parentheses)

	Classes of females:		
	Fpt	Fsy	Fmy + Fly
Small males	21.30 (94)	64.60 (48)	53.10 (81)
Medium males	24.50 (282)	47.50 (137)	63.00 (200)
Large males	28.35 (328)	51.80 (110)	55.10 (216)
Subordinate large males	23.76 (101)	45.60 (46)	55.90 (93)
Dominant large males	30.40 (227)	56.20 (64)	54.50 (123)

TABLE 7.5: Percentages of time spent with females where dominant and subordinate large males were the only *large* male present (sample sizes in parentheses)

	Classes of females:		
	Fpt	Fsy	Fmy + Fly
Dominant large male	77.50 (227)	87.50 (64)	83.70 (123)
Subordinate large male	37.60 (101)	67.40 (46)	71.00 (93)