

Chapter 4

Reproduction in the social organisation

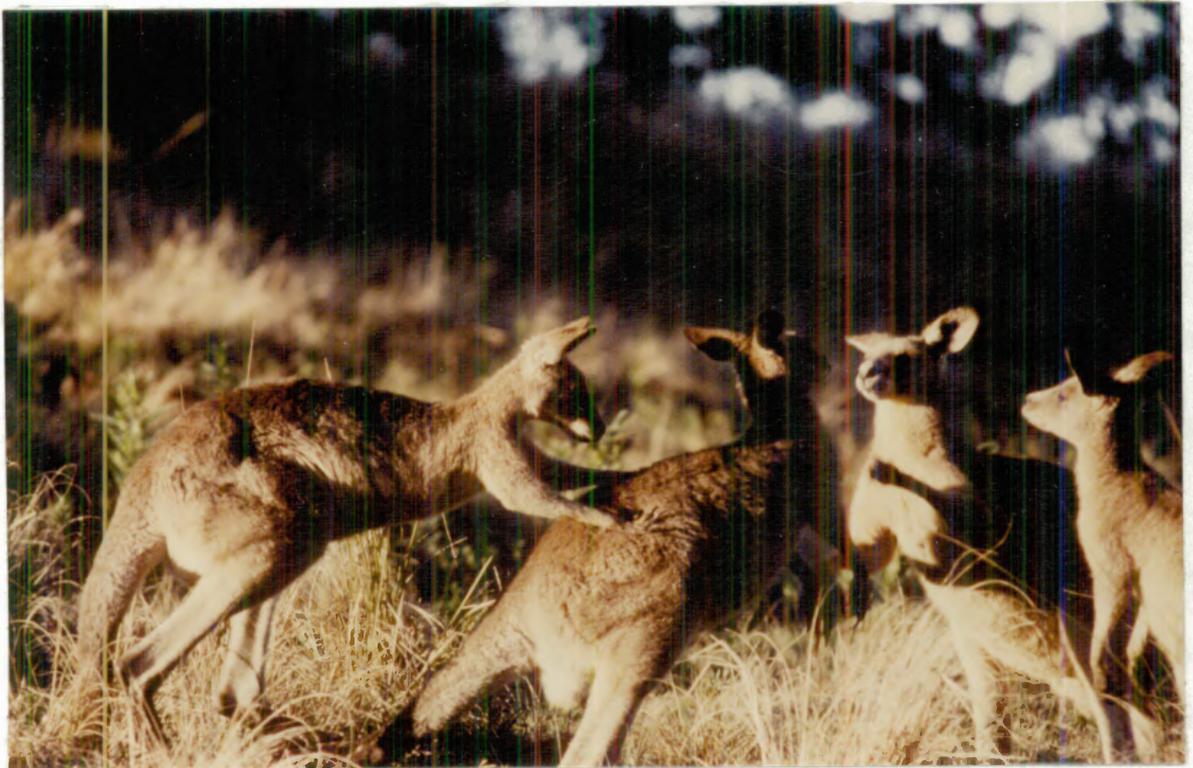


Figure 36: *The boys, ... what they do when they have left mum.*
Four subadult males play-fighting.

4.1 Introduction

The behaviour of the mother eastern grey kangaroo and her young occurs within a social organisation which is in part defined by the mother-young pairs themselves. However, the relative position of mother and young within this social organisation may change as the young develops. Rearing a young to an adaptive schedule may involve periods when there is an increased risk of predation, or an increased demand on the mother's metabolism (Altmann, 1980, 1983). A mother may have a very different activity schedule from that of her peers who do not have young of a similar age. The young too may exhibit a changing activity schedule as it develops, and be particularly vulnerable to separation from the mother during some stages of its ontogeny. Overall the changes in the mother and young's activities, risk of predation, and physical condition may affect their ranging behaviour and social relations with others.

Since males and females have quite different life-histories as adults, they may behave differently as young or be reared differently (see chapter 1). Consequently, mothers of sons and mothers of daughters may vary their social behaviour to a different schedule through the young's ontogeny. The types of differences in the social behaviour of mothers of young of different sexes may provide further insight into whether sons and daughters gain different forms of 'benefit' from the manner they are reared and whether the mother in turn invests in the sexes to different schedules.

As I have previously mentioned mothers may differ in their 'social relationships' with others or their access to the local resources (Wasser, 1983; Silk and Boyd, 1983; Dunbar, 1984). Consequently, mothers might differ in the manner they rear young.

In this chapter I discuss the ranging behaviour of the mother and young and their level of gregariousness in relation to the sex and age of the young, as well as in relation to characteristics of the mother such as her 'age'. I also discuss whether females relate to each other in a manner which differentiates them; in particular, whether they are organised into matriline, and whether some females are 'harassed' by others to a greater than average extent.

4.2 Home ranges

4.2.1 Female home ranges: size, location, and centres of activity

For a given habitat, the size of an herbivore's home range is a function of the animal's metabolic requirements, which scale to the animal's size and the way in which the local population exploits the available resources (Damuth, 1981a and b; Jarman, 1974; Clutton-Brock and Harvey, 1977). If it is advantageous for individuals of a species to aggregate in groups, or if a variety of resources are required by an individual, and these resources are scattered over a large area, then the individual's home range should increase above the area assigned per individual according to the density of the local population (*ibid.*), resulting in range overlap.

Eastern grey kangaroos are known to gather in transitory aggregations, which may be related to predator detection; individuals survey less frequently when in large aggregations than in small aggregations (Jarman, 1987; Southwell, 1981). However, feeding in groups may be costly to individuals (van Schaik *et al.*, 1983b; Jarman, 1974). Consequently when the advantages of predator detection are small or the probability of being predated when in a group is no less than when solitary, individuals may become less gregarious.

Female kangaroos with YAF are often reported as being more solitary than other classes (Croft, 1981a and b; Southwell, 1981; Kaufmann, 1974). Females, especially when rearing a YAF, may be using core areas within their home range which are separate from the core areas of other females. Alternatively, females may share a home range with a particular set of other females, and range over that area in a relatively even manner. In this latter case, a female's social relationships with the other females (e.g. her relative rank, or relatedness) may affect her access to the local resources or, more broadly, her rate of rearing young and reproductive tactics (Dunbar, 1984; Clutton-Brock *et al.*, 1986).

Since I concluded from data presented in chapter 3 that a female eastern grey kangaroo's age probably had a strong influence on her reproductive tactics, I have specifically investigated the relationship between females' 'ages' and their ranging behaviour.

I have used the minimum convex polygon method for calculating home range areas. This method can result in including areas in the estimate of a female's home-range size which are not used by the female (Anderson, 1982). However, I believed that this problem was unlikely to occur in this case since the female eastern grey kangaroos studied by Jaremovic (1984) had home ranges defined by a set of sightings that were normally

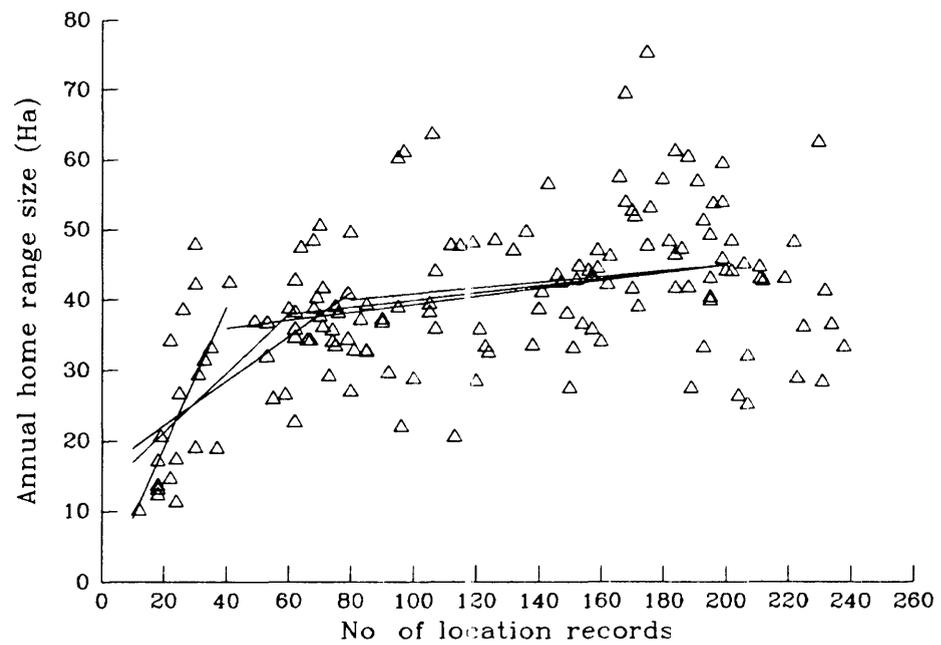


Figure 37: Relationship between the number of location record (NLR) for a female and her annual home-range size (AHRs). The following equations were the best-fit results for data between particular X-co-ordinate values and are depicted by the linear curves in the figure:

$$40 \geq x \leq 10, (AHRs) = -0.51 + 0.97(NLR), R^2 = 0.3, p = 0.009;$$

$$60 \geq x \leq 10, (AHRs) = 12.84 + 0.42(NLR), R^2 = 0.257, p = 0.010;$$

$$80 \geq x \leq 10, (AHRs) = 15.82 + 0.32(NLR), R^2 = 0.423, p < 0.001;$$

$$200 \geq x \leq 40, (AHRs) = 34.20 + 0.05(NLR), R^2 = 0.088, p < 0.001;$$

$$200 \geq x \leq 60, (AHRs) = 35.09 + 0.05(NLR), R^2 = 0.067, p = 0.004;$$

$$200 \geq x \leq 80, (AHRs) = 36.41 + 0.04(NLR), R^2 = 0.030, p = 0.084.$$

distributed in space. Further, the females at Wallaby Creek did not appear to use local areas which were connected by travelling routes only.

The other disadvantage of the convex polygon method, according to Anderson (1982), is that the variance of the estimate of home range size does not decrease readily as the sample size increases. However, Anderson compared estimates based on 10, 30, and 100 points only. On average, I used 145 points to calculate a female's annual home range, and I discarded all estimates of females' home range areas which comprised less than 60 locations. This appeared to be the point (fig. 37) below which the number of locations (used to plot a female's home range) was strongly correlated, but above which was less strongly correlated, to the estimated annual home-range size.

However, as I was particularly concerned with investigating the changes in a female's ranging behaviour as her young developed, I have also calculated an estimate of the size of the area a female ranged over each field trip (trip-home-range). This was done only for the females in the South. I was typically able to locate these females every day of a field trip.

The average adult female's home range was 41 and 44 hectares in 1983 and 1984, respectively. Females were typically sharing their home range with about 25 others and ranged over approximately 30% of their annual home-range per 10 days (the average field-trip duration). The average size of the females' trip-home-range did not vary significantly with the month of the year (see table 34 for home-range information).

Mature females tended to range over a larger area than older females, and females with small annual home-ranges tended to rear young to weaning at a faster rate than the females with large annual home-ranges (table 34 and figs. 38 and 39). The young females tended to have larger annual home-ranges but smaller trip-home-ranges than the mature females.

According to single and average linkage cluster analyses of the females' annual home-range centres (geometric centre of their home range), the females were divided into two distinct 'sets' (Appendix D). These two sets of females were also apparent to an observer in the field, as the 'Northern set' were rarely located in areas south of the centre of the study site and vice versa for the 'Southern' females. Nor did adult females shift their home range from either of these areas to the other.

The geometric centres of the females' trip-home-ranges changed from month to month by an average 131m (table 34). Fig. 40 depicts the month by month changes in the trip-home-range centres of a typical female, 'Fawn' (one trip per month). In general, the area which bounded the month by month changes in the location of a typical southern female's

Table 34 Home-range statistics for females. Units are hectares and metres. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *. RWY refers to a females rate of weaning young (see section 3.3).

	sample size	mean	SE	range		
size of annual home range:						
1983	52	42.0	1.1	28.4-63.6		
1984	51	43.8	1.5	22.0-69.4		
mean trip-home-range size (approximately 10 days):						
	34	12.7	0.42	6.9-16.5		
mean distance between consecutive trip-home-range centres:						
	20	131.1	5.4			
mean number of conspecifics in females' home range:						
1983		27				
1984		23				
annual home range						
	R^2	1983 p	R^2	1984 p	mean trip-home-range	
					R^2	p
age	0.081	0.072†	0.229	0.002*	0.425	0.020*
equation:		46.6 - 1.3(age)		57.4 - 3.0(age)	11.1 + 2.1(age)	-0.4(age) ²
RWY	0.147	0.028*	0.076	0.074†	0.051	0.469ns
equation:		0.225 - 0.828 × 10 ⁻² (HRS)		0.058 - 0.059 × 10 ⁻² (HRS)		
		+0.009 × 10 ⁻² (HRS) ²				
month of the year:					0.104	0.145ns
					quadratic	

Table 35: Areas of minimum convex polygons enclosing trip-home-range centres. Units are hectares.

mean area which includes all South females' THRC/trip		
sample size	mean	SE
34	7.8	0.54
mean area of all THRC		
female	area	number of trips
Caarn	13.5	32
Inga	20.5	34
Kinktail	10.2	34
Vera	12.8	28
Fawn	9.9	33

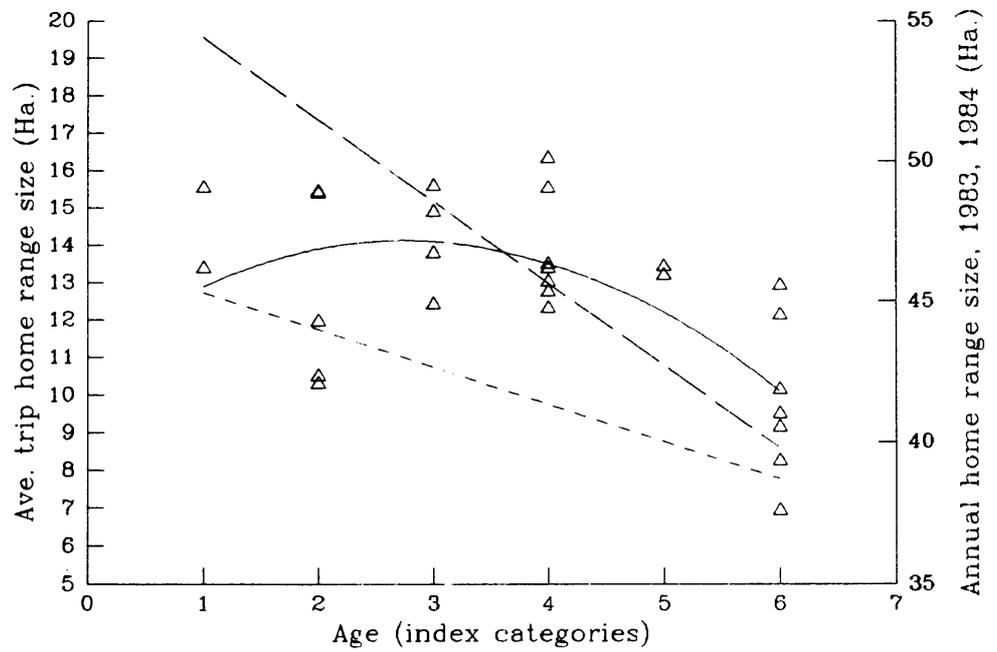


Figure 38: Relationship between females' 'ages' and size of annual home-range and trip-home-range. The continuous line represents the best-fit equation for trip-home-range size. The short and long dashed lines represent the best-fit equations for the females' annual home-range sizes in 1983 and 1984, respectively.

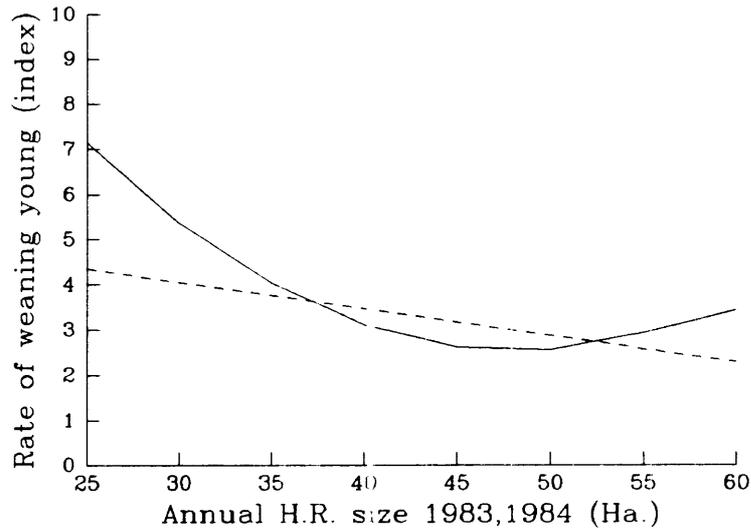


Figure 39: Relationships between females' rates of weaning young and their annual home-range sizes. The continuous and broken lines represent best-fit curves for data from 1983 and 1984 respectively.

trip-home-range centres included the area that bounded the southern females' annual home-range centres (figs. 41 and 42). In table 35 I have noted the average area per month which bounded all south females' trip-home-range centres, and the average size of the area which bounded all of the trip-home-range centres for a few typical females. The trip-home-range centres of the females of a 'set' tended to cluster together to a greater extent than did all the trip-home-range centres of a typical female. Hence, females within a 'set' probably tended to utilise the same sites within a 'set' home-range in a temporally co-ordinated manner.

However, this conclusion awaits substantiation by further research; it is enough for the purposes of this thesis to know that females within 'sets' were not utilising unique core areas (unless on a very fine scale). If females are differentiated in their access to the local resources within a 'set', a social factor other than those which determine the females' spatial separation, probably acts as a mediator.

Figure 40: *The trip-home-range centres for the female Fawn. Fawn was present in the study area throughout the 4 study years. Her consecutive centres are connected by lines.*

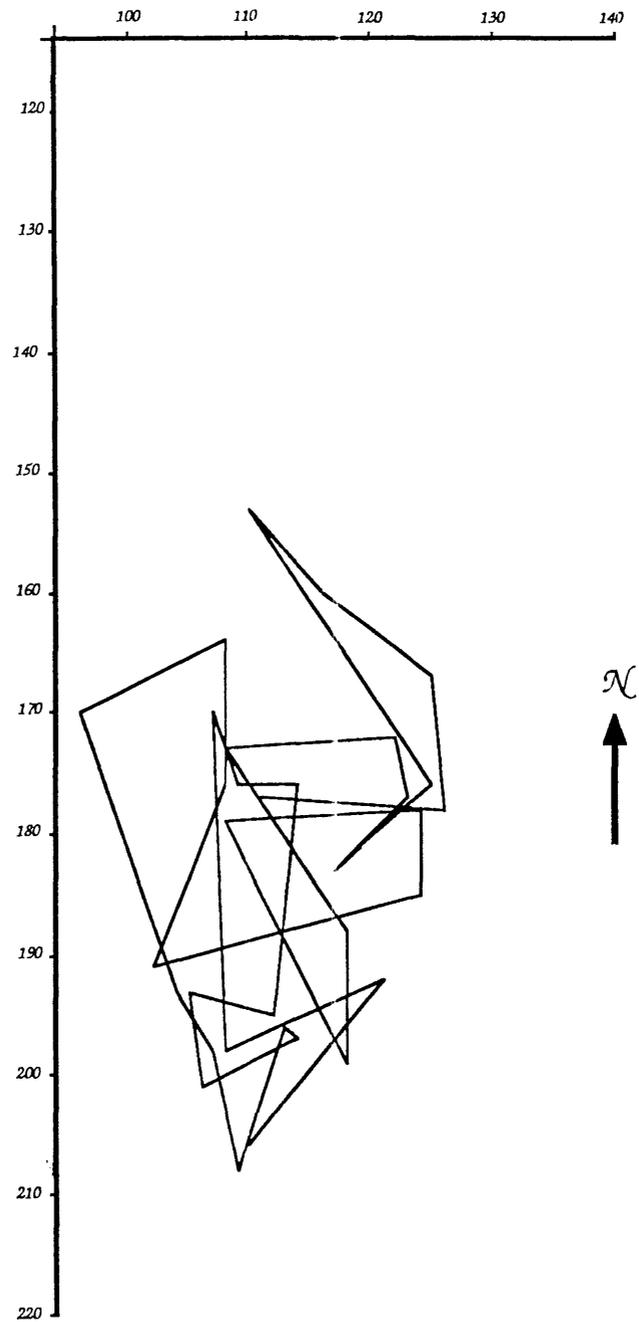


Figure 41: The grid locations of all females' annual home-range centres for 1983. Note that there are two distinct clusters. See also Appendix D.

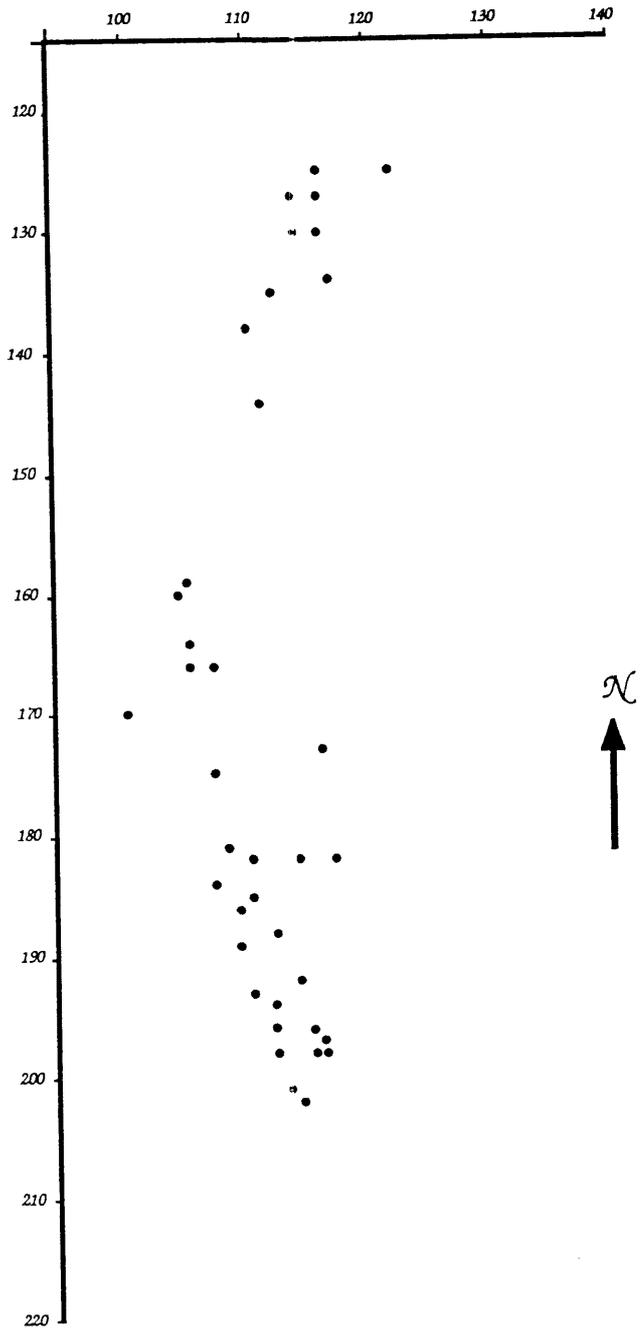
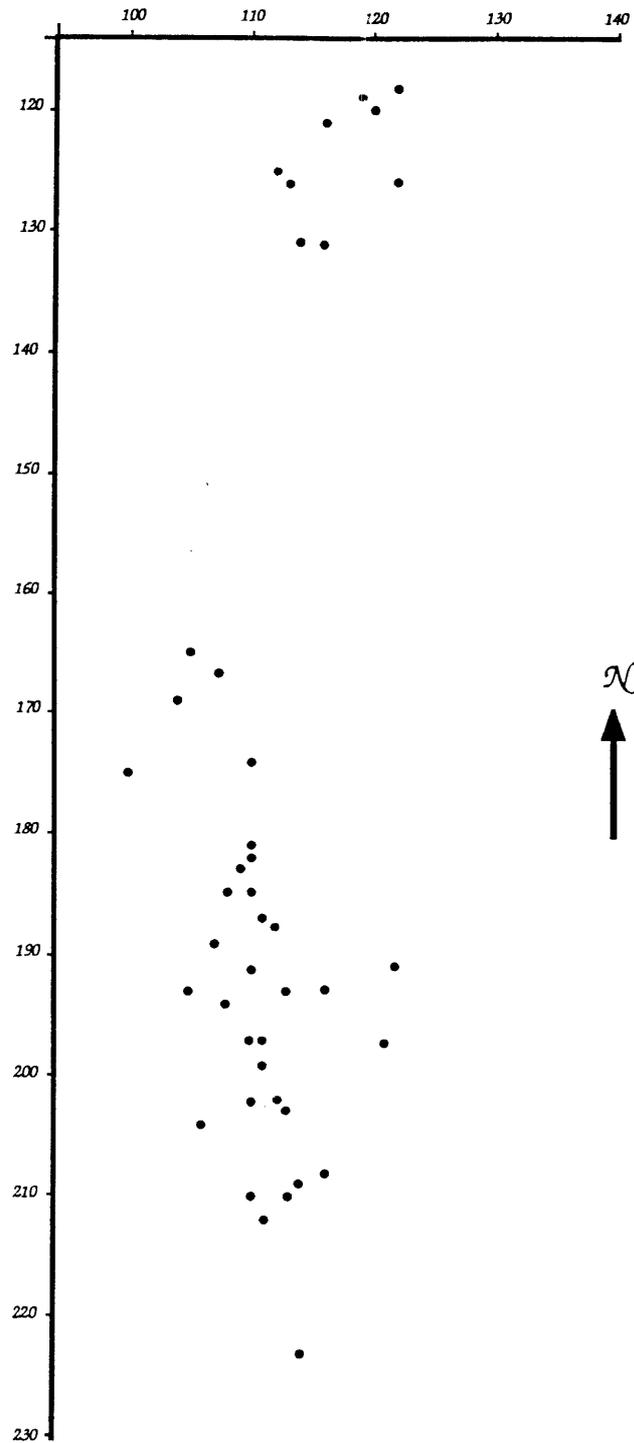


Figure 42: *The grid locations of all females' annual home-range centres for 1984. Note the two distinct clusters. See also Appendix D.*



4.2.2 The ranging behaviour of females around the time of their young's permanent emergence

The ranging behaviour of female ungulates can be restricted around the time of parturition, and may remain so from less than a day following birth, for example as in pronghorn (Kitchen, 1974), goats (Rudge, 1970; Lickliter, 1984), moose (Stringham, 1974), defassa waterbuck (Spinage, 1969) and reindeer (Espmark, 1971), to several weeks or more following birth, for example white-tailed deer (Ozoga *et al.*, 1982) and impala (Jarman, 1976, and Jarman and Jarman, 1979) (see also Lent, 1974; Leuthold, 1977; and DeVos *et al.*, 1967). Mothers may even move to areas where the quality of the food is obviously poorer (Edwards, 1983).

At the end of this period of voluntary isolation by a mother ungulate, she may either resume her social life and typical ranging behaviour with her young at heel, or she may leave the young behind in relative seclusion within a small area (see Lent 1974; Leutlold, 1977). A young who spends time separated from its mother and conspecifics is known as a 'hider' while a young who remains with its mother is known as a 'follower'. There are variations in the behaviour of ungulate mother-young pairs that fall between these extremes (Ralls *et al.*, 1986). Probably the type of behaviour found in individual pairs is related to minimising the young's risk of predation (Lent, 1974; Estes, 1976). Generally, if the adults typically use crypsis to avoid detection by a predator, their young are most likely to hide. If the adults use early detection of and flight from a predator to avoid predation, the young are more likely to be followers.

To date little information has been published on the ranging behaviour of mother-young pairs of macropods. Some authors have noted that kangaroo mothers with their YAF are found more often than expected in a small ranging area e.g. Croft (1981a and b) for red kangaroos and euros, and Kaufmann (1974) for whiptail wallabies. Individuals of these 3 species grow to a relatively large size for a macropod, inhabit lightly wooded to open grazing country, and probably use detection and flight to avoid predation.

Johnson (1985) reported that on permanent emergence red-necked wallaby young exhibit a type of behaviour similar to the 'hiding' behaviour of some ungulate young. This hiding behaviour of young following permanent emergence may be a common phenomenon in the small- to medium-sized macropods. I have seen a captive parma wallaby young 'hide' upon emerging permanently, and seen young rufous bettongs, in the field and in captivity, remain or return to 'hide' in a nest while their mother forages at night. Clancy (1982) mentions

that young red-bellied pademelons may 'hide' during the day while their mother forages; at night the mother and young rest together. Jarman (pers. comm.) has observed young of the brush-tailed rock-wallaby, red-necked and red-legged pademelons, swamp wallaby, rufous bettong, and long-nosed potoroo 'hiding'. Johnson (1985) reported circumstantial evidence of 'hiding young' for a variety of macropod species. All of these species, that appear to have young which hide, are characterised by being small to medium macropods that spend much of their time in habitats which offer cover in which to hide from predators.

Since the eastern grey kangaroo is one of the largest species of the Macropodoidea, and inhabits lightly wooded grazing country, I would expect that the young would be 'followers' rather than 'hiders'. In addition, I would expect that, in a manner similar to ungulate mothers at parturition, during the permanent emergence of their young, the mother kangaroos at Wallaby Creek would tend to reduce their ranging area to sites which offer cover and separation from conspecifics. There is a high probability of a young dying during the two months from permanent emergence (section 3.5), which is comparable to the increased vulnerability of ungulate neonates.

The mother and her young at Wallaby Creek were almost invariably found together (section 6.9).

Many females did appear to be preferentially ranging in areas separated from the other females when they had small YAF. In order to test this hypothesis, I plotted the south females' trip-home-range centres for a number of randomly selected trips, and used the relative locations of these centres to categorise each female's centre as being:

1. more than 50m from any other females' centres,
2. within 50m of other females' centres, but only from one 180 degree side (i.e. the female's trip-home-range centre was on the boundary of the cluster of female home-range centres), or
3. within 50m of other centres for more than 180 degrees around the centre (i.e. the female's trip-home-range centre was inside the cluster of home-range centres).

The females' home-range centres were significantly (table 36) more likely to be on the boundary of or at a distance of more than 50m from the main cluster of centres, if they had a YAF or a young who was permanently emerging, as compared to the home range centres of females with no young or a pouch-young. These latter females were more likely to be

Table 36: The relative location of females' home-range centres (HRC) for females of different classes. Statistical tests comparing frequencies of HRC locations between classes are included. Probabilities of less than 0.05 are presented with an *.

class of mother:	a within the general cluster of HRC i.e. within 50m of other HRC on $\geq 180^0$	b on the boundary of the general cluster of HRC i.e. within 50m of HRC from 1 side only, $< 180^0$	c > 50m from any other female's HRC	total
with no young or pouch-young	131 (47%)	116 (42%)	32 (11%)	279 (100%)
with PEP young	6 (19%)	19 (61%)	6 (20%)	31 (100%)
with YAF	11 (16%)	48 (72%)	8 (12%)	67 (100%)
total	148	183	46	377

chi-squared tests

PEP young & YAF with a & (b+c), $df = 1, \chi^2 = 0.118, ns$
 PEP young & YAF with b & c, $df = 1, \chi^2 = 1.169, ns$
 no/PY & PEP young & YAF with a & b, $df = 2, \chi^2 = 100.34, p < 0.001*$
 PEP young & YAF with a & c, $df = 2, \chi^2 = 9.816, p < 0.01*$

Table 37: The number of females who had a smaller than average or larger than average trip-home-range (THR) while they had a permanently emerging young. Tests comparing frequencies for 'types' of females, females with sons and daughters, females with peak and offpeak young, and females who lost or weaned their previous young are included. Probabilities of less than 0.05 are presented with an *.

PEP home-range:	<100% of mean THR	≥100% of mean THR	total	χ^2	probability
all females	47 (67%)	23 (33%)	70	13.747	< 0.001*
'peak-only'	19 (54%)	16 (46%)	35		
'offpeak also'	28 (80%)	7 (20%)	35	5.245	< 0.05*
with sons	21 (66%)	11 (34%)	32		
with daughters	25 (71%)	10 (29%)	35	0.626	ns
peak season	33 (67%)	16 (33%)	49		
offpeak season	12 (71%)	5 (29%)	17	0.062	ns
previous lost	16 (53%)	14 (47%)	30		
previous weaned	14 (70%)	6 (30%)	20	1.388	ns

the mean size of a THR on PEP was 81% (SE 42.8%)
of the average THR

the mean size of a THR on PEP for females who
reduced their ranging area was 55% (SE 21.4%)

Table 38: The size of a female's home-range while her young was permanently emerging (PEP HR size) related to the following variables: the proportion of daughters produced (FSR), rate of weaning young (RWY), mean subgroup size (SGPN), 'age', and sex and season of PEP of the young.

variable related to PEP HR size	equation	R^2	probability	
			linear	quadratic
FSR	$37.15 - 34.46(FSR + 1) + 10.71(FSR + 1)^2$	0.039	0.220	0.249ns
RWY	$7.96 + 1.23(100RWY) - 0.10(100RWY)^2$	0.020	0.352	0.444ns
SGPN	$-21.17 + 7.46(SGPN) - 0.41(SGPN)^2$	0.053	0.650	0.740ns
age	$2.04 + 39.85(\text{age}) - 4.38(\text{age})^2$	0.049	0.119	0.149ns
		% variation	F test	probability
PEP HR size variance explained by:				
	<i>sex of young</i>	0.3	0.15	0.700ns
	<i>season of PEP</i>	0.1	0.07	0.787ns
	<i>sex X season</i>	1.7	0.84	0.364ns

Table 39: The mean trip-home-range sizes for females in the months before and after a permanent emergence. Units are hectares.

	months from PEP										
	-5	-4	-3	-2	-1	PEP	1	2	3	4	5
sample size	66	70	76	77	78	74	42	38	34	32	26
mean	13.4	14.4	15.4	14.4	15.2	9.9	10.2	11.8	11.7	11.0	12.8
SE	0.92	0.82	0.91	0.81	0.84	0.76	0.91	1.07	1.20	1.04	1.58

found in the middle of the females' cluster of home-range centres. There was a tendency, although it was not significant, for females with permanently emerging young to be at a distance from the others, while females with YAF were likely to be on the boundary of the cluster of centres.

Significantly more females than expected had a trip-home-range size, smaller than their average when they had a young permanently emerging from the pouch (table 37). The relative size of this area, for females who reduced their range, was 55% (SE 3.1%, N=47) of the female's average trip-home-range size.

An analysis of variance of the relative reduction of a female's trip-home-range during permanent emergence did not attribute a significant proportion of the variation to the sex of the young, or the season of permanent emergence. Nor was the mother's rate of rearing young to weaning, her offspring sex ratio, whether or not she lost the previous young, her 'age', or the average size of the subgroup she was found in, significantly related to her relative reduction in her ranging area (see table 38 for tests). But mothers were significantly more likely to reduce their ranging area while their young was emerging if the mother was an 'offpeak also' female as compared to a 'peak only' female (table 37).

In table 39 I show the average trip-home-range sizes in the months prior and subsequent to a permanent emergence. The reduction in a mother's home range appears to occur rather suddenly with the onset of the permanent emergence of her young; the mother's trip-home-range gradually increases in size following her young's permanent emergence in a significant relationship to the age of the young; ($R^2 = 0.022$, $T-H-Rsize = 9.52 + 0.472(YAFage)$, $p=0.037$).

4.2.3 Dispersal

In the majority of mammalian species the males rather than the females disperse or at least move further away from their natal site (Greenwood, 1980; Dobson, 1982; Wasser and Jones, 1983). Dispersal typically occurs prior to the time when the male commences reproduction (Morris, 1982; Gaines and McClenaghan, 1980).

The class of eastern grey kangaroos which had the highest rate of disappearance from the study site was the small male class (section 2.3). At the end of the study in March 1986, only 4 of 29 males reared to weaning during the study were still present in the study site. The average age of the small adult males that disappeared was 31 months (SE 1.6, N=19, range 22-45 months). Seven of these males were sighted at later dates. Some were observed

Table 40: Age of disappearance for sons related to the following variables: the son's association level with his mother (M-SA assoc), the son's association level with other male subadults (SA-SA assoc), the mother's 'age' (M age), the duration of the son's YAF phase (YAFL), and the season of the son's PEP, and his 'type' of mother. A 'pp' son is one who emerged in the peak season from a 'peak only' mother. An 'op' son is one who emerged in the peak season from an 'offpeak also' mother. An 'oo' son is one who emerged in the offpeak season from an 'offpeak also' mother.

variable related to dispersal age	equation	R^2	probability	
			linear	quadratic
M-SA assoc	$35.06 - 0.18(M - SA) + 0.002(M - SA)^2$	0.023	0.647	0.605ns
SA-SA assoc	$33.28 + 2.54(SA - SA) - 1.97(SA - SA)^2$	0.083	0.814	0.580ns
M age	$21.50 + 2.41(Mage)$	0.210	0.074†	
YAFL	$16.76 + 0.98(YAFL) - 0.02(YAFL)^2$	0.002	0.863	0.860ns
dispersal age: \bar{x} , SE, (N)		MWU test probability		
'peak only', peak sons: 28.8, 3.29, (6)		pp vs op, $U=38$		< 0.1†
'offpeak also', peak sons: 35.9, 2.33, (8)		op vs oo, $U=42$		< 0.05*
'offpeak also', offpeak sons: 27.3, 2.52, (6)				

making a temporary return to the study site; others were observed with other kangaroos outside the main study population's home range.

All immigrants to the study site were male, and most belonged to the small adult class (see section 2.3).

Although there was a relatively high disappearance of subadult females 42% (11/26), it seems likely that most died rather than dispersed. Five of the 26 female young reared to weaning during the 4 study years had commenced reproduction in their mother's home range by April 1986. Overall, females are probably preferentially philopatric.

The variation in the small males' age of disappearance was not related to the duration of their YAF phase, to the degree of association they had as a subadult with their mother, or to the degree of association they had as a subadult, with other subadult males (table 40). It was positively correlated with their mother's 'age' (table 40). Also, the sons, of 'offpeak also' mothers, who emerged during the peak season, tended to disperse at an older age than the sons who emerged during the offpeak season (MWU test $U = 42$ $N = 6$, $N = 8$, $p < 0.05$), and were also later than the sons of 'peak only' mothers (MWU test $U = 38$ $N = 6$, $N = 8$, $p < 0.1$).

Table 41: Home-range statistics for subadult sons and daughters. THR refers to trip-home-range. Units are hectares and metres. Probabilities of F tests and t tests between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

	sons:			daughters:			mothers:		
	sample size	mean	SE	sample size	mean	SE	sample size	mean	SE
size of trip-home-range:									
1st month	14	13.5	1.98	11	10.9	2.36			
average	13	12.5	1.13	11	13.2	0.95	34	12.7	0.42
mean distance between consecutive THR centres:									
	14	153.8	10.79	10	134.1	7.57	20	131.1	5.37
<i>sons vs daughters F test F=2.923, ns, t test t=1.372, ns</i>									
distance between mothers' and SA THR centres:									
							<i>test</i>	<i>probability</i>	
1st month	12	84.7	1.66	9	46.6	1.45	$F=1.820$	ns	
							$t_p=1.981$	< 0.1†	
average	12	96.8	1.87	9	54.8	0.78	$F=8.210$	< 0.05*	
							$t_{up}=2.077$	< 0.1†	
mother's PEP	10	98.9	30.0	7	93.4	27.2	$F=9.459$	< 0.05*	
							$t_{up}=1.368$	ns	

4.2.4 Subadult ranging behaviour

Parental investment in subadults may arise either by allowing subadults to share the local resources (e.g. mute and Bewick's swans (Scott, 1980, 1984), red deer (Clutton-Brock *et al.*, 1982b), guanaco (Franklin, 1983) and red-necked wallabies (Johnson, 1986a)), or may include protecting the subadults from harassment by others (e.g. swans (Scott, 1984, 1980) and chimpanzees (Pusey, 1983)).

Although the male eastern grey kangaroos tended to disperse from their natal site, they typically remained in the local population for at least 4 more months after they were weaned (at approximately 16 months of age). Daughters were typically philopatric. Consequently, mothers may continue to invest in both male and female young post-weaning. However, maternal investment may not be evenly distributed between subadult sons and daughters. Since sons eventually disperse as young adults, their ranging behaviour as subadults may be different to that of the female subadults.

The average trip-home-ranges of subadult sons and daughters were both not significantly different in size from the average adult female's trip-home-range size (see table 41 for all home-range results for subadults).

The mean distance between consecutive trip-home-range centres of the typical subadult was not significantly different for sons and daughters. Also, the mean distance between

the consecutive trip-home-range centres of the average subadult was similar to the mean distance obtained between their mothers' consecutive trip-home-range centres. These movements of trip-home-ranges placed the geometric centres approximately on the boundary of the previous trip-home-range (see fig. 43 for schematic diagram).

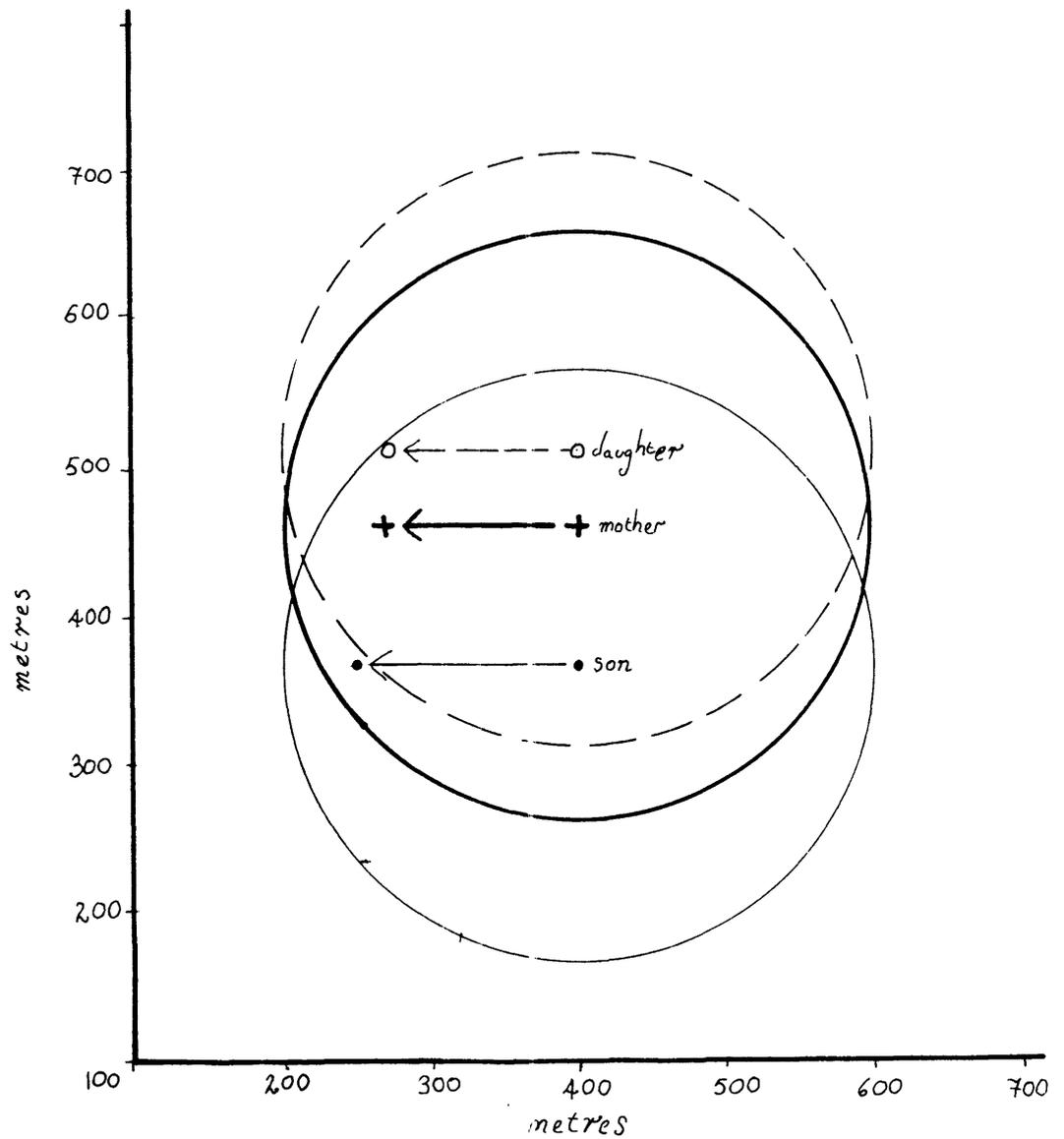
The distance between a subadult's trip-home-range centre and its mother's centre was significantly related to the sex of the subadult (see also fig. 44). A son's centre tended to be twice as far from his mother's centre as a daughter's centre. The difference was apparent right from the first month after weaning. A mother's daughter was typically one of the mother's three closest female neighbours ('neighbouring' peers have been ranked according to the distances between home-range centres). A son's home-range centre was on average just closer to his mother's home-range centre than her ninth closest female neighbour.

Thus, a mother and her subadult daughter appear to maintain a much higher degree of overlap of their ranging areas, temporally as well as spatially, than do a mother and subadult son.

The birth of a mother's next young in eutherian species is often reported as being associated with a further separation between a mother and her subadult offspring (e.g. Leuthold, 1977; Hirth, 1977). Since permanent emergence in macropodoids may be likened to birth in ungulates (see chapter 3 and section 4.2.2), the degree of overlap in the ranging area of kangaroo mothers and subadults may decrease when the mother's next young permanently emerges.

Daughters were observed to have home-range centres which tended to be further from their mothers' centres while the next young was permanently emerging compared to the distance between their centres prior to this time (table 41). There was no similar increase between the trip-home-range centres of sons and mothers. However, the distance between the centres of daughters and mothers while the next young was permanently emerging was still less than the average distance between the centres of sons and mothers. If the permanently emerging young is lost, then the distance between the subadult's and mother's centres may decrease (table 42).

Figure 43: Schematic diagram of the relative sizes and movements of consecutive trip-home-ranges for subadult sons and daughters, and their mothers. The mother's range is depicted by the thickly outlined circle and her centres by crosses. The son's range is depicted by the finely outlined circle and his centres by solid circles. The daughter's range is depicted by the circle outlined by dashes and her centres by open circles.



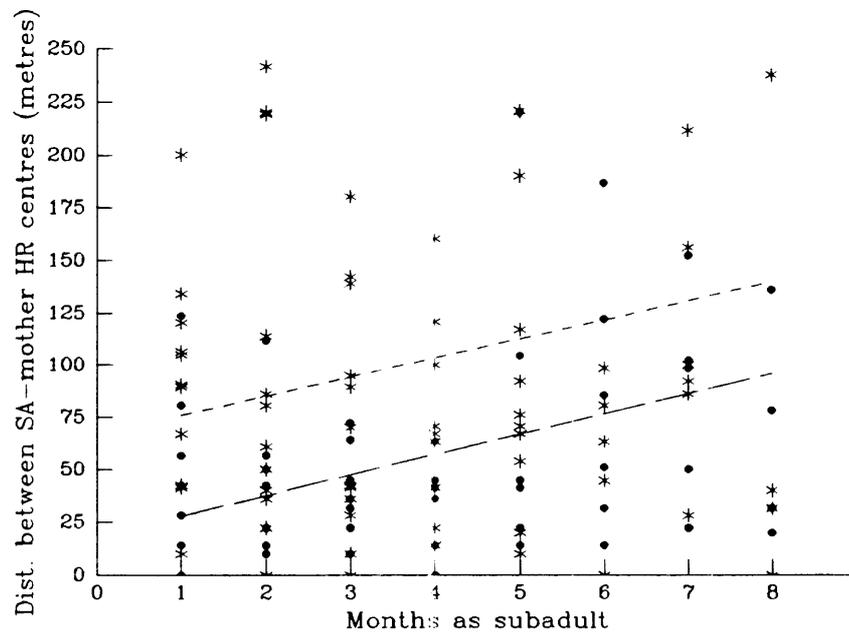


Figure 44: Relationship between the time from weaning for a subadult and the distance between the subadult's and mother's trip-home-range centres. Sons are represented by stars and the short-dashed line ($R^2 = 0.050$, $(\text{dist THRC}) = 6.73 + 0.91(\text{months})$, $p = 0.05$). Daughters are represented by solid circles and the long-dashed line ($R^2 = 0.133$, $(\text{dist THRC}) = 1.80 + 0.97(\text{months})$, $p = 0.005$).

Table 42: *The difference between the before and after PEP distances between a subadult's and mother's trip-home-range centres. Whether the next young (whose PEP is referred to) was lost or weaned is included. THRC refers to trip-home-range centre. Units are metres. A positive value means that the post-PEP distance was greater than the pre-PEP distance.*

subadult	previous young	difference between post-PEP and pre-PEP mother-subadult THRC
male:	<i>weaned</i>	+103
	<i>lost</i>	+140
	<i>lost</i>	-42
	<i>lost</i>	-6
	<i>lost</i>	+34
	<i>lost</i>	+55
	<i>lost</i>	+1
	<i>lost</i>	+40
	<i>lost</i>	0
female:	<i>weaned</i>	+157
	<i>lost</i>	-14
	<i>lost</i>	+30
	<i>lost</i>	+56
	<i>lost</i>	+36
	<i>lost</i>	+33

4.3 Subgroup sizes

4.3.1 The size of subgroups females were found in

Individuals sharing the same home range may tend to aggregate together. The reasons and factors involved have been discussed by many authors (Hamilton, 1971; Pulliam, 1973; Wrangham, 1980; Alexander, 1974; Jarman, 1974; van Schaik *et al.*, 1983a and b, Treisman, 1975; Bertram, 1978; Gosling and Petrie, 1981; Clutton-Brock and Harvey, 1977; Crook *et al.*, 1976). Most authors agree that an individual's chances of detecting a predator in time to escape may be increased by aggregating into groups. Consequently, congregating with conspecifics may be an important means to avoid predation for individuals of species which do not use crypsis. This is providing the individual is not an outstanding or vulnerable member of the group (Jarman, 1974).

There is some contention in the literature as to whether group formation enhances or reduces an individual's exploitation of the local resources (Wrangham, 1980; van Schaik, 1983; van Schaik *et al.*, 1983a; Gosling and Petrie, 1981). But since the argument for increased efficiency of feeding in groups usually depends upon the individuals belonging to a social group of closed membership occupying an exclusive and defended territory, it is unlikely to be applicable to eastern grey kangaroos.

Eastern grey kangaroos aggregate in spatial groups of open membership. The individuals enter and exit from a group at will; an individual typically moves between groups several times during the course of a day. These spatially defined groups have been reported to consist of from one to more than one hundred individuals (Jaremovic, 1984; Southwell, 1981; Taylor, 1982; Caughley, 1964; Kirkpatrick, 1966; Kaufmann, 1975). There does not appear to be any form of a spatially defended territory, either at individual level or at the 'mob' level. The latter is the largest predicted 'social group' of kangaroos (Kaufmann, 1974 and 1975) (see section 2.3).

Since individuals compete for the local resources, there are likely to be some disadvantages to individuals in feeding in a group. Others may actively inhibit the individual's efficiency in obtaining those resources necessary to breed when spatially aggregated (Jarman, 1974; Janson, 1985; Dittus, 1979; Wasser, 1983; Silk and Boyd, 1983; Stacey, 1986). Further, when feeding in a group, an individual may come across a greater proportion of patches which already have been exploited (Jarman, 1974). Conversely there can also be

advantages to individuals feeding in a group comprising more than a few individuals. Individuals of such groups may spend less time alert for predators and more time feeding than an individual in a smaller group (Alados, 1985; Bertram, 1978 and 1980; Berger, 1978).

Eastern grey kangaroos are known to spend less time alert when feeding in large groups as compared to small groups (Jarnian, 1987; Southwell, 1981). As yet there has not been a study investigating whether search time for food increases with group size. But, since individual kangaroos move between groups readily, an individual presumably has the opportunity to move to groups which provide a close to optimum balance between the costs and gains of aggregating in a group.

This optimum group size may vary between individuals. The diet of eastern grey kangaroos consists principally of low fibre grass leaf (Southwell, 1981; Taylor, 1983). Some localities in the study area may have had a higher component of the pasture consisting of low fibre grass. But as the females, at least within 'sets', were ranging over the same pasture, the size of group that a female was found in at Wallaby Creek should reflect her vulnerability to predation, or social relations, or class-specific food demands, rather than any local differences in food dispersion (see Jarman, 1974; van Schaik and van Hooff, 1983).

The above discussion refers to spatially defined 'groups'. The 'group' of eastern grey kangaroos is not always an obvious entity to define in practice. Individuals may be dispersed over several hectares in what initially may appear to be a random manner. In this study I employed Southwell's definition of a group (see section 2.2); at Wallaby Creek, the maximum group size was 40 and the minimum 1, when using this definition. However, individuals within groups were often neither randomly nor evenly dispersed, but aggregated into 'subgroups' (see section 2.2). I have chosen to analyse the variation in the females' gregariousness at the level of the subgroup.

I expected that if there were social factors which differentiated females in their gregariousness, these factors would be more apparent from an analysis of subgroups rather than groups. Females may still vary their preferred size of subgroup in relation to their vulnerability to predation, or class-specific food demands, in a manner similar to that predicted for groups. If they do not, I will not be able to conclude that they do not vary their preferred size of group in relation to predation or grazing demands. However, it may mean that the average size of the subgroup which a female is found in may be less flexibly varied by the female.

If females do vary their gregariousness according to inherent differences or their reproductive state, there are a number of predictions from previous research (on mammals) against which my results can be interpreted:

1. females who are outstanding or particularly vulnerable individuals are expected to prefer small groups, which may be less easily located by a predator, or bypassed (Jarman, 1974). This may apply for subgroups. The females who are likely to be particularly vulnerable are those with large pouch-young, permanently emerging young, or small YAF; and old females.
2. the females who may have a relatively high metabolic requirement for food are likely to be those with large pouch-young or permanently emerging young (Dove *et al.*, 1987; Clarke and Loudon, 1985). Therefore, these females may prefer larger subgroups, where they may concentrate upon feeding. This is providing that the females are not individuals particularly susceptible to feeding interference from others and that search time for food items does not significantly increase with increasing subgroup size.
3. females particularly susceptible to feeding interference from others may tend to feed in small subgroups. Young females are often smaller or lower-ranking individuals who may be threatened or displaced frequently by others, and who consequently may be less gregarious than other females (for red deer: Thouless and Guinness, 1986; Clutton-Brock *et al.*, 1982a and b, 1986).
4. females may tend to aggregate in kin-based subgroups and consequently those with many relatives may be found on average in larger subgroups (Clutton-Brock *et al.*, 1982b; Johnson, 1985).
5. females who belong to large matrilineal groups may suffer a depressed rate of rearing young to weaning (Clutton-Brock *et al.*, 1982a and b, Johnson, 1985 and 1986a).

There are conflicting predictions in the above paragraph. However, the types of relationships found between the females' average subgroup size and their age, rate of rearing young to weaning, size of home range, and type of breeding (peak only versus offpeak also) may show consistent patterns, which may be interpreted according to one or a few of these predictions. If the obtained relationships are spurious, I would not expect to find consistent patterns in the relationships between these variables.

Table 43: Tests relating the following variables to a female's mean size of subgroup (SGPN): breeding 'type', annual home-range sizes in 1983 and 1984 (HRS1983 and HRS1984, respectively), trip-home-range size (THR), rate of weaning young (RWY), and 'age'. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

	sample size	mean	SE	range		
the average female's mean subgroup size:						
	63	7.0	0.79	4.4-8.3		
type of mother:						
'peak only'	25	7.0	0.19			
'offpeak also'	31	7.0	0.13			

variable related to SGPN	equation	R^2	probability		
			linear	quadratic	
HRS1983	$21.9 + 2.8(SGPN)$	0.077	0.052†		
HRS1984	$-10.6 + 15.1(SGPN) - 1.0(SGPN)^2$	0.027	0.465	0.510ns	
THR	$4.06 + 0.24(THR)$	0.527	0.000	0.000*	
RWY	$7.23 - 0.24(100RWY) + 0.03(100RWY)^2$	0.079	0.056	0.077†	
	<i>classes related to RWY separately</i>				
	<i>the following only were significantly related</i>				
MPY	$7.68 - 0.53(100RWY) - 0.07(100RWY)^2$	0.091	0.053	0.035*	
LPY	$7.39 - 0.96(100RWY) + 0.11(100RWY)^2$	0.169	0.004	0.043*	
age	$7.62 - 0.17(age)$	0.088	0.059†		
	<i>classes related to age separately</i>				
	<i>the following only were significantly related</i>				
SPY	$2.25 + 3.15(age) - 0.43(age)^2$	0.306	0.001	0.000*	
MPY	$2.59 + 2.34(age) - 0.27(age)^2$	0.159	0.157	0.042*	
LYAF	$-2.89 + 5.95(age) - 0.731(age)^2$	0.318	0.005	0.004*	

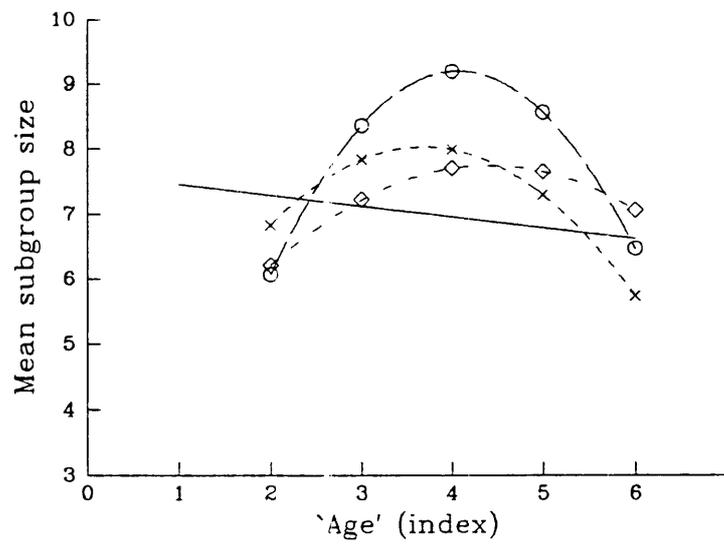


Figure 45: Relationships between 'age' and mean subgroup size. The continuous line is for all females. The short-dash close-space line with crosses is for females with small pouch-infants. The short-dash wide-space line with diamonds is for females with medium pouch-young. The long-dash line with circles is for females with large YAF.

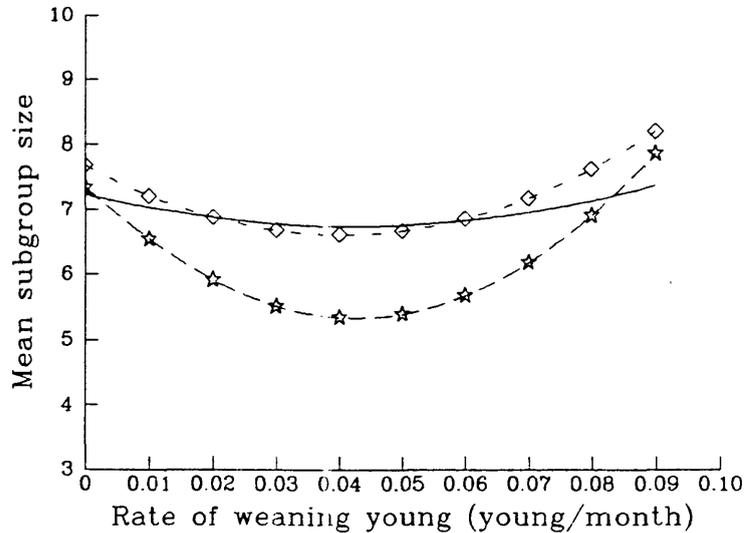


Figure 46: Relationships between rate of weaning young and mean subgroup size. The continuous line is for all females. The short-dash line with diamonds is for females with medium pouch young. The long-dash line with stars is for females with large pouch young.

The average size of subgroup in which the typical female (Jarman, 1974) was found was 7.0 individuals (SE 0.79, N=63, includes the female). I have presented the results of the tests for relationships between the females' average subgroup size and their age, rate of rearing young to weaning, size of home range, reproductive class, and type of seasonal breeder in table 43 (see also figs. 45, 46, and 47). The tests were conducted using the individual females' average subgroup size and also using the class-related subgroup sizes for individual females.

In general, females were found in small subgroups when they had a large pouch-young, a young who was permanently emerging from the pouch, or a small YAF (table 44). Their relatively small average subgroup size was probably a function of tending to be more solitary; females with permanently emerging young were found in subgroups of 1 more frequently than expected (table 45).

The average subgroup sizes of the females in these classes was not significantly related to the females' ages, rates of rearing young to weaning, or average trip-home-range sizes. Probably females of these classes tended to prefer small subgroups regardless of their preferences

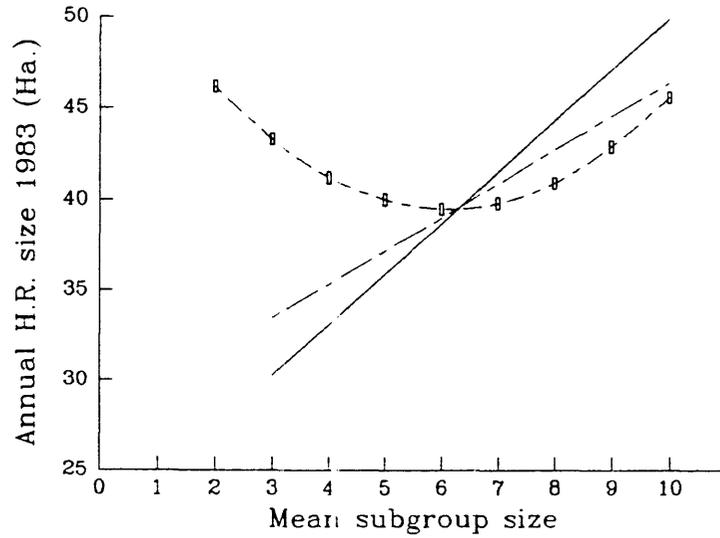


Figure 47: Relationships between mean subgroup size and annual home-range size in 1983. The continuous line is for all females. The short-long dashed line is for females with no or small pouch young. The medium dashed line with rectangles is for females with small YAF.

Table 44: The mean subgroup size for females of the different classes. \bar{x} refers to mean. N refers to sample size. SE refers to standard error.

	female classes:							
	NPY	SPY	dim PI	very small PI	small PI	medium PI	large PI	very large PI
(N)	57	52	47	46	49	49	41	46
\bar{x}	7.0	7.4	7.0	7.0	7.3	7.0	5.9	6.2
SE	0.19	0.18	0.29	0.40	0.32	0.38	0.28	0.43
	PEP young		small YAF		large YAF			
(N)	35		49		29		38	
\bar{x}	5.5-YAF=4.5		5.8-YAF=4.8		6.6-YAF=5.6		7.6-YAF=6.6	
SE	0.43		0.29		0.40		0.35	

Table 45: The frequencies of females found in different subgroup sizes for the general population of females and for when the females have a PEP young. Results from a G test comparing the frequencies is included.

	subgroup size:							
	1	2	3-6	7-10	11-14	15-18	≥ 19	total
<i>for females with PEP young:</i>								
frequency	169	70	175	90	29	21	22	576
(%)	(29)	(12)	(30)	(16)	(5)	(4)	(4)	
<i>for the females in the population in general:</i>								
frequency	2074	2597	3469	968	299	145	99	9651
(%)	(21)	(27)	(36)	(10)	(3)	(2)	(1)	
G test: subgroup size (1 or > 1) vs PEP or typically								
df=1. G=18.310, p < 0.001*								

Table 46: The mean subgroup size, trip-home-range size, and rate of weaning young, for females of the 6 'age' classes.

	age classes:					
	very-young	young	young-mature	old-mature	old	very-old
subgroup size						
sample size	11	5	6	13	6	12
mean	7.3	6.5	7.3	7.4	6.9	6.4
SE	0.22	0.40	0.17	0.22	0.29	0.30
trip-home-range size (ha)						
sample size	2	5	5	7	2	7
mean	14.5	12.7	15.2	13.8	13.3	9.9
SE	1.53	1.27	0.49	0.61	0.17	0.86
rate of weaning young (young/month)						
sample size	-	5	6	13	6	10
mean	-	0.043	0.031	0.037	0.014	0.039
SE	-	0.0070	0.0055	0.0074	0.0077	0.0053

when in other reproductive classes.

As predicted older females were found on average in smaller subgroups. They also ranged less widely than the others. This was consistent with the finding that females who were found on average in small subgroups tended to range less widely. 'Very Young' females, that is the nulliparae, were found on average in large-sized subgroups. 'Young-Mature' and 'Old-Mature' females also tended to be found in large subgroups. All three age classes tended to have large home ranges. However, the 'Young' females, which included the two females who commenced reproduction midway through the study, were found in small subgroups and ranged less widely per trip, just as did the 'Old' and 'Very Old' females (see table 46).

Females who had a high or very low rate of weaning young were found on average in large subgroups. To be consistent with the above results, females at the extremes in the rate of weaning young should have a large home range. But, in section 4.2, I found that females who weaned young at a high rate tended to have small annual home-ranges, although the relationship was weak and there was no significant relationship with the average trip-home-range size. Further, the 'Young' females had the highest average rate of weaning young, and they averaged a small subgroup size, as well as a small average trip-home-range size (table 46). Thus, a female's rate of weaning young was not related to her other characteristics in a consistent manner. It is possible that if females belonged to matrilineal groups the effect of the size of the matriline on a female's rate of rearing young to weaning may have added a compounding effect.

Overall, 'Young' 'Old' and 'Very Old' females were most likely to be found in small subgroups at all times, while other females were likely to be found in small subgroups on average only when with large pouch-infants, permanently emerging young, or small YAF. Except for the 'Young' females, who were supposedly in good condition (section 3.3), this selection of females preferring small subgroups is most consistent with the hypothesis that a female's vulnerability to predation may reduce her gregariousness. 'Very young' and 'Young' females were particularly susceptible to aggression from the other females (section 4.5). Since the 'Young' females were reproducing, their metabolic demands were possibly greater than those of the 'Very Young' females. Consequently, the 'Young' females may seek small subgroups to allow them to feed without harassment. This requires further study, especially to determine whether small or large subgroups increase an individual's efficiency when feeding.

Since there was much variation in the females' average subgroup size that was not

explained by 'age' (the correlations were all quite low), females may have been organised in social aggregations. I explore this topic further in section 4.4.

4.3.2 The average subgroup size of females around the time of permanent emergence

Just prior to giving birth many ungulate mothers (Lent, 1974; Leuthold, 1977, see section 4.2.2) seek a secluded spot, and remain isolated from their conspecifics for a period varying from a day to a month or more.

Eastern grey kangaroo mothers tend to be found solitary more often around the time when their young permanently emerge (section 4.3.1). Permanent emergence is a period in the mother-young relationship which I have likened to birth in ungulates, as there is a high rate of mortality of young and the mother may reduce her ranging area to sites away from the main cluster of female home-range centres. However, not all mothers were found to reduce their ranging area. Mothers who produced only peak-season-emerging young were less likely to reduce the area they ranged over during this stage of their young's life. The same might hold true for whether mothers reduce their level of gregariousness, i.e. not all mothers may be found, on average, in smaller subgroups during this period. However, the factors, which influence whether or not a mother reduces her ranging area, may not necessarily effect her level of gregariousness.

Other factors may apply. For example, mothers with daughters may be harassed by others to a greater extent than mothers with sons (Silk *et al.*, 1981; Simpson and Simpson, 1985) and as a result may become less gregarious. The season in which a young permanently emerges from the pouch might also influence the mother's average subgroup size. If many of the mother's peers have concurrently produced young, then mother and young may no longer appear as outstanding members of a group (Jarman, 1976; Jarman and Jarman, 1979) and be consequently vulnerable to predation. In this case, it might be to the advantage of both mother and young to aggregate with their similarly classed peers (Jarman and Jarman, 1979; Clutton-Brock and Guinness, 1975).

I conducted several analyses-of-variance tests on the mothers' average subgroup size during permanent emergence using the following independent variables: sex of young, season of emergence, type of mother ('peak only' vs 'offpeak also'), and home-range site (North vs. South) (table 47). The former three factors significantly explained variation in the mothers' average subgroup size during permanent emergence. However, the type of mother is

Table 47: *The variance in females' home-range size during PEP explained by sex of the young, season of PEP, 'type' of mother, mean size of subgroup, and home-range site. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.*

variation explained by:	% variation	df	F test	probability	R ²
<i>home range site</i>	0.03	2	0.02	0.984ns	
<i>PEP season</i>	9.08	1	11.48	0.001*	
<i>interaction</i>	1.22	2	0.77	0.466ns	
<i>mean subgroup size</i>	13.00	1	16.45	0.000*	1.244
<i>error</i>	76.68	97			
<i>sex of young</i>	5.28	1	5.83	0.018*	
<i>PEP season</i>	10.33	1	11.40	0.001*	
<i>interaction</i>	0.72	1	0.80	0.375ns	
<i>error</i>	53.66	76			
<i>home range site</i>	0.17	2	0.09	0.910ns	
<i>type of mother</i>	3.22	1	3.64	0.059†	
<i>interaction</i>	1.79	2	1.01	0.368ns	
<i>error</i>	54.82	98			

Table 48: *The mean size of subgroup which females with PEP young were found in according to the sex of the young, season of PEP, and 'type' of mother.*

type of mother:	sons:			daughters:		
	<i>peak only</i>	<i>offpeak</i>	<i>also</i>	<i>peak only</i>	<i>offpeak</i>	<i>also</i>
type of young:	<i>peak</i>	<i>peak</i>	<i>offpeak</i>	<i>peak</i>	<i>peak</i>	<i>offpeak</i>
<i>sample size</i>	33	15	21	17	15	15
<i>mean</i>	5.3	5.7	3.7	6.1	5.7	5.2
<i>SE</i>	0.39	0.66	0.30	0.58	0.67	0.58

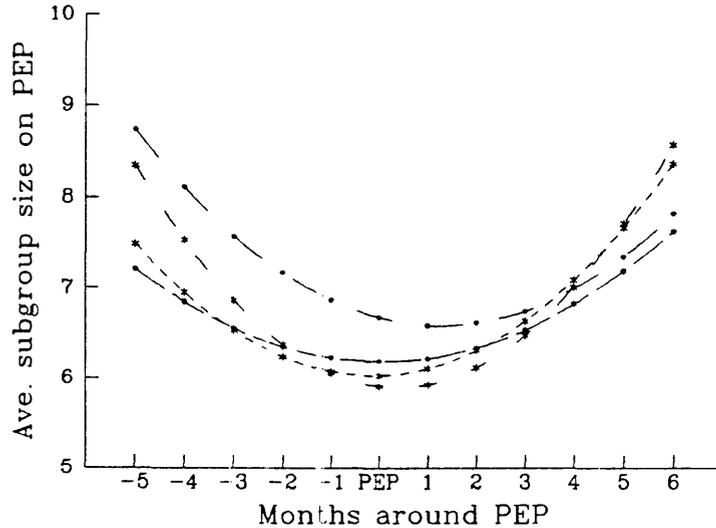


Figure 48: Relationships between the mother's mean subgroup size ($SGPN$) and the time span before and after PEP . The relationship for mothers with offpeak sons (short-dash wide-gap) is: $(SGPN) = 0.09(\text{month})^2 - 1.08(\text{month}) + 9.35$, $R^2 = 0.076$, quadratic probability = 0.002. The relationship for mothers with peak sons (short-dash short-gap) is: $(SGPN) = 0.06(\text{month})^2 - 0.73(\text{month}) + 8.15$, $R^2 = 0.051$, quadratic probability < 0.001. The relationship for mothers with offpeak daughters (long-dash wide-gap) is: $(SGPN) = 0.05(\text{month})^2 - 0.80(\text{month}) + 9.48$, $R^2 = 0.093$, quadratic probability = 0.038. The relationship for mothers with peak daughters (long-dash short-gap) is: $(SGPN) = 0.04(\text{month})^2 - 0.490(\text{month}) + 7.66$, $R^2 = 0.029$, quadratic probability = 0.007.

probably not important in explaining the variation when the season of a young's permanent emergence is also taken into account. In general, mothers who produced a son who permanently emerged in the offpeak season tended to be found on average in significantly smaller subgroups (table 48) than mothers of daughters or mothers of peak-season-emerging sons.

In contrast, it would appear that mothers with daughters tend to be found in small subgroups for a longer period after their daughters' emergence than mothers of peak or offpeak sons (figs. 49 and 48).

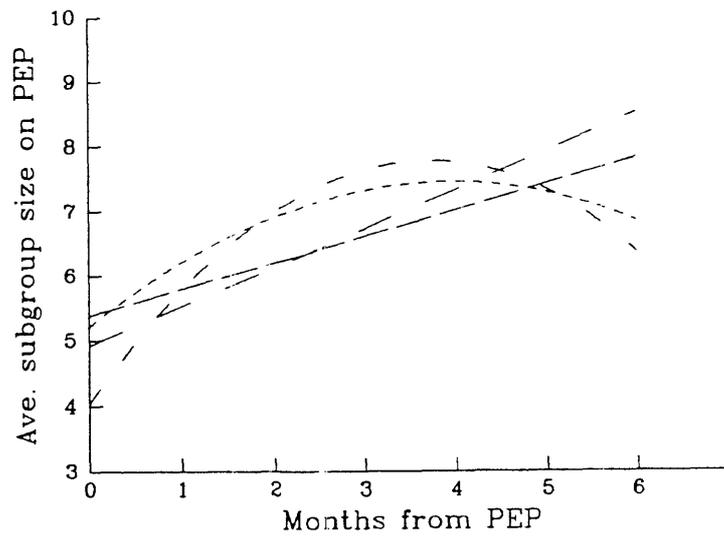


Figure 49: Relationships between the mother's mean subgroup size (SGPN) and the time elapsed since PEP. The relationship for mothers with offpeak sons (short-dash wide-gap) is:
 $(SGPN) = -0.27(\text{month})^2 + 5.26(\text{month}) - 17.79$, $R^2 = 0.234$, quadratic probability = 0.04.
 The relationship for mothers with peak sons (short-dash short-gap) is:
 $(SGPN) = -0.14(\text{month})^2 + 2.84(\text{month}) - 6.68$, $R^2 = 0.106$, quadratic probability = 0.039.
 The relationship for mothers with offpeak daughters (long-dash wide-gap) is:
 $(SGPN) = 0.60(\text{month}) + 1.33$, $R^2 = 0.241$, linear probability = 0.004.
 The relationship for mothers with peak daughters (long-dash short-gap) is:
 $(SGPN) = 0.407(\text{month}) + 2.95$, $R^2 = 0.107$, linear probability < 0.001.

4.3.3 The size of subgroups subadults were found in

According to much of the ungulate literature, there is often a close association between mothers and their subadult offspring (e.g. Lent, 1974; Altmann, 1958; Franklin, 1983; David, 1975; Langman, 1977; Ozoga *et al.*, 1982). However, while the attraction ungulate young have for their mother may survive weaning, it may be markedly lessened with the birth of the mother's next young (Espmark, 1971; Hirth, 1977; Lent, 1974; Stringham, 1974). Around this time, the ungulate mother may be very aggressive toward all conspecifics, including her previous offspring. The subadult may resume a positive association with its mothers once she is no longer avoiding conspecifics, and especially if she loses her new young (Hirth, 1977; Rudge, 1970; Pratt and Anderson, 1979).

Alternatively, in some particularly gregarious ungulate species, such as wildebeest, young aggregate to form creches, rather than continuously following their mother. Estes and Estes (1979) have suggested that the association of young with each other may supplant the mother-young 'bond' early in the young's life. In these species, the mother-young 'bond' may be rather weak prior to weaning, and the relationship between mother and subadult may be nonexistent, or no greater than that which the mother has with others of her social group.

In general, information about the dissolution of the mother-young relationship in ungulates is rather sparse, especially concerning any differential in the behaviour of mothers and subadult sons as opposed to daughters.

Information about the dissolution of the mother-young relationship in macropods is virtually nonexistent. The exception is a study by Johnson (1985 & 1986a), who found that in red-necked wallabies subadult sons maintain a higher association with their mothers following weaning than do daughters. This occurred despite daughters remaining in their natal home-range to breed and sons dispersing when small adults.

Since eastern grey kangaroos are larger and more gregarious than red-necked wallabies, a quite different pattern in the relationship of mothers and subadults may occur. For example, peer association may be important to subadult eastern grey kangaroos, especially sons whose ranging area drifts further from their mothers' ranging area than daughters. Since daughters and mothers were maintaining a ranging area which considerably overlapped temporally in spite of the changing location of their consecutive trip-home-ranges, I would expect that mothers and their subadult daughters might maintain a stronger association level than mothers and sons.

Table 49: Tests relating mother-subadult (SA) association levels to the sex of the subadult. Tests comparing the mother and subadult association levels when the mother's next young was at PEP and their average association levels are included. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

% of subgroups SA with mother	sons:			daughters:		
	sample size	mean	SE	sample size	mean	SE
<i>1st month as SA</i>	13	52	8.2	7	65	11.8
<i>mother's next PEP</i>	12	19	7.0	9	35	6.8
<i>SA average</i>	19	39	5.7	11	51	5.5
<i>as small adult</i>	10	17	3.5	6	26	5.5
tests comparing sexes:						
<i>1st month following weaning</i>						
<i>F test</i>	$F=2.074, p > 0.05ns$					
<i>t test</i>	$t_p=0.973, df=18, p > 0.05ns$					
<i>MWU test</i>	$U=5^9, p > 0.1ns$					
<i>during mother's next PEP</i>						
<i>F test</i>	$F=1.470, p > 0.05ns$					
<i>t test</i>	$t_p=1.498, df=19, p < 0.1†$					
<i>on average as a subadult</i>						
<i>F test</i>	$F=1.375, p > 0.1ns$					
<i>t test</i>	$t_p=1.389, df=27, p < 0.1†$					
<i>as adults</i>						
<i>F test</i>	$F=1.377, p > 0.1ns$					
<i>t test</i>	$t_p=1.658, df=13, p < 0.1†$					
tests comparing PEP and on average:						
<i>for sons</i>						
<i>F test</i>	$F=1.127, p > 0.05ns$					
<i>t test</i>	$t_p=2.236, df=29, p < 0.025*$					
<i>for daughters</i>						
<i>F test</i>	$F=1.196, p > 0.05ns$					
<i>t test</i>	$t_p=1.903, df=15, p < 0.05*$					

Table 50: Relationships between mother and subadult association levels (*M-SA assoc*) with the mother's 'age' (*M age*) and the subadult's association level with same-sex peers (*SA-SA assoc*). Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

variable related to M-SA assoc	equation	R^2	probability	
			linear	quadratic
<i>for sons:</i>				
<i>SA-SA assoc</i>	$73.81 - 20.04(SA - SA)$	0.203	0.061†	
<i>M age</i>	$110.57 - 41.94(Mage) + 5.41(Mage)^2$	0.194	0.316	0.252ns
<i>for daughters:</i>				
<i>SA-SA assoc</i>	$1.99 - 0.02(M - SA) + 0.0003(M - SA)^2$	0.042	0.761	0.696ns
<i>M age</i>	$4.841 - 0.02(Mage) + 0.0002(Mage)^2$	0.004	0.896	0.907ns

Mothers and their YAF were almost always found in the same subgroup (see sections 6.4 and 6.5). This close association dropped considerably upon weaning (table 49). In the month following weaning sons and daughters were seen with their mothers on an average of 52% and 65% of sightings respectively. This difference between the sexes was not significant (see tables 49 and 50 for tests on mother subadult association). However, during the month when the mother's next young emerged permanently, not only was the level of association between mothers and subadults significantly lower than the level observed in the first month of subadult life, but also it was significantly lower for sons (19%) than daughters (35%). This was probably a reflection of a consistent difference in the relationship between mothers and subadult sons as opposed to mothers and subadult daughters. Over the whole of the subadult phase, sons averaged a 39% association level with their mothers, significantly lower than the average association level of 51% for daughters.

The level at which subadults associated with their mother was not significantly related to her 'age'.

Subadult daughters were probably positively associating with their mother, even while her next young emerged from the pouch, as females were found with their closest non-daughter female associate on only 22% and 25% of their sightings in 1983 and 1984 respectively (see next section); these association levels are lower than those found for mothers and subadult or known adult daughters (table 49). Adult sons prior to their dispersal were found in the same subgroup as their mothers much less often (see same table); their average association level was comparable to the mother's average association with her fourth closest female-associate (including daughters) (section 4.3.4).

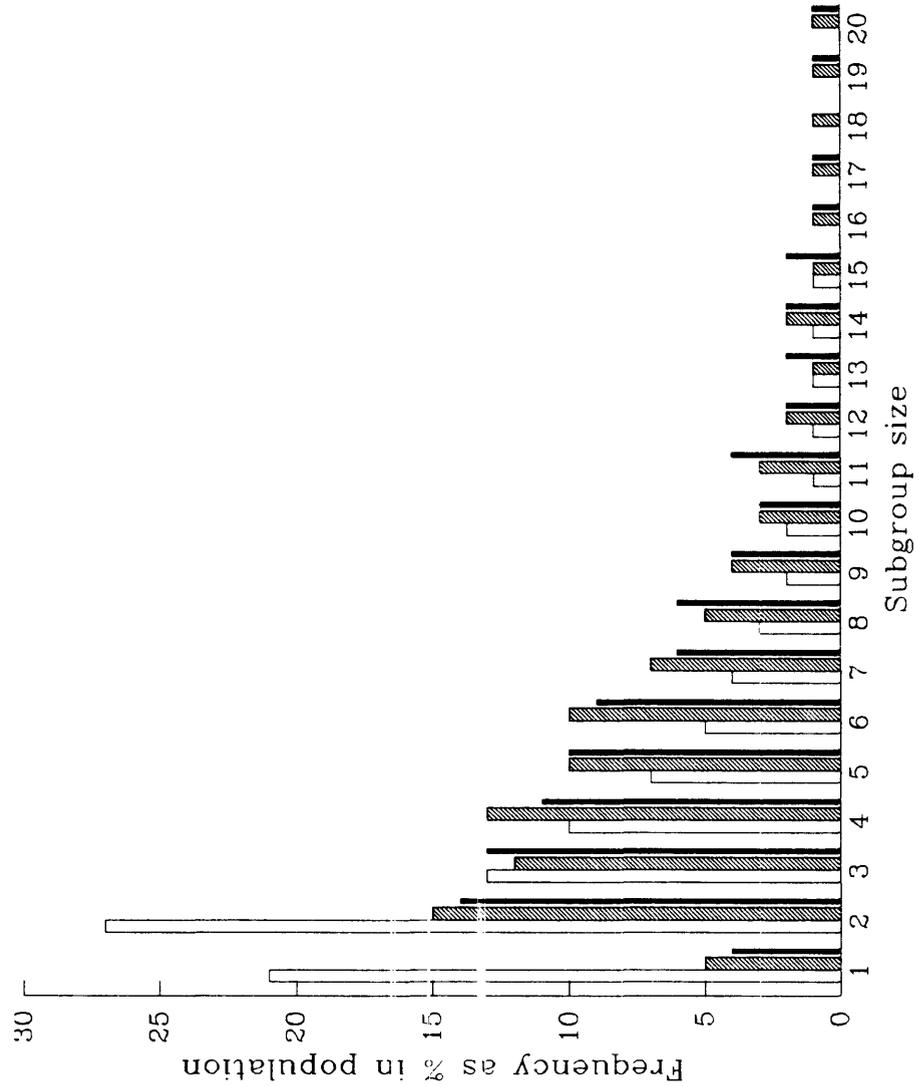


Figure 50: The percentage of different sized subgroups in the population, in total, and for those containing male and those female subadults. The unshaded bars represent the percent for the population in general. The lightly shaded bars represent the percent for subgroups with male subadults. The densely shaded and narrower bars represent the percent for subgroups with female subadults.

Table 51: χ^2 tests comparing the frequencies of subgroups of either comprising 1 or 2 individuals, or greater than 2, for subgroups with male and those with female subadults, against all subgroups. Probabilities less than 0.05 are presented with an *.

subgroup size:	1-2	≥ 3	total	χ^2 test
<i>total frequency in population</i>	4571	4980	9651	
(%)	(48)	(52)		
<i>frequency of subgroups with subadult males</i>	293	1126	1419	<i>males vs pop.=454</i>
(%)	(21)	(79)		$p < 0.01^*$
<i>frequency of subgroups with subadult females</i>	231	1075	1306	<i>females vs pop.=423</i>
(%)	(18)	(82)		$p < 0.01^*$

Table 52: χ^2 tests comparing the frequencies of subadults observed in total, more often or less often than expected in subgroups with other subadults.

	sighted		χ^2	probability
	more often than expected	less often than expected		
with male subadults				
<i>male subadults (expected)</i>	17 (10)	3 (10)	9.8	$< 0.01^*$
<i>female subadults (expected)</i>	17 (6.5)	2 (6.5)	6.2	$< 0.02^*$
with female subadults				
<i>male subadults (expected)</i>	10 (10.5)	5 (10.5)	5.8	$< 0.02^*$
<i>female subadults (expected)</i>	17 (6.5)	2 (6.5)	6.2	$< 0.02^*$

Subadults were attracted to larger subgroups than expected from the frequency of different-sized subgroups present in the population (fig. 50 and table 51). This behaviour occurred for subadults of both sexes, and was probably related to a general attraction of subadults for other subadults.

For each subadult I calculated the percentage of subgroups it was found in that included at least one other subadult, and the percentage of subgroups in the population during the same period which included male subadults or female subadults other than that individual subadult (table 52). Significantly more of the individual subadults than expected were found in more subgroups than expected which included subadults other than the individual itself. The expected frequency for the individual subadults (i.e. the frequency each would be found in subgroups which included other subadults by chance alone) was calculated by determining the frequency of subgroups in the population which included subadults [other than the individual the expected was calculated for] during the period the individual was a subadult. The sexes were analysed separately.

However, the degree to which subadult sons tended to be found with other subadult males was negatively correlated to their association level with their mother (table 50). There was no similar correlation for subadult daughters.

Overall, the association between mothers and subadults drops significantly upon weaning, especially between mothers and sons. The association between mother and subadult was typically further reduced while the mother's next young permanently emerged from the pouch. In general, the less often a son associated with his mother the more likely it was that he associated with other subadult males. Daughters typically maintained a stronger association with their mothers, even into adulthood. As for sons, the daughters were seen with other subadults more often than expected; but unlike sons, this preference appeared to be irrespective of the daughter's level of association with her mother.

4.4 Association preferences of adult females

Researchers have accepted for some time that in many primate and ungulate societies the females in social groups are related (for red deer see Clutton-Brock *et al.*, 1982b; for white-tailed deer see Hirth, 1977; for elephants see Dublin, 1983; for Japanese macaques see Kurland, 1977; for baboons see Ransom and Rowell, 1972; and for sheep see Hunter and Milne, 1963). In these species males are more likely to disperse from their natal home

range, while daughters are philopatric. However, only recently has research focussed on investigating the effect of the relatedness of individuals on the types and rates of their social interactions. For example, macaque females remain in their natal home range and inherit ranks close to their mothers' ranks (Kurland, 1977; Silk *et al.*, 1981; Dittus, 1979; Horrocks and Hunte, 1983). A female macaque's rank influences the amount of harassment she receives and gives to others, which in turn appears to influence her reproductive success (Drickammer, 1974; Fairbanks and McGuire, 1986). Female gelada baboons (Dunbar, 1984) have been found to maintain stable affiliations with others in their group who are usually close female relatives. Red deer (Clutton-Brock *et al.*, 1982b) and impala (Murray, 1981) live in open-membership societies, but the females preferentially associate with their female kin. The close association of baboon and red deer young-females with their close relatives appears to reduce the amount or the intensity of harassment they receive from others (Dunbar, 1984; Clutton-Brock *et al.*, 1982b). Not only may the existence of matrilineal societies affect the types of inter-female interactions, but the females' reproductive strategies may be affected. For example, one consequence may be that daughters exact a post-weaning investment from the mothers (Dittus, 1979; Clark, 1978; Clutton-Brock *et al.*, 1982a; Johnson, 1986a).

Not all primate or ungulate societies are based on matrilineal societies (Harcourt, 1978; Pusey, 1980; Klingel, 1969). However, the social organisation of the eastern grey kangaroo is a likely candidate for a matrilineal society, as sons disperse while daughters tend to be philopatric (section 4.2). This potential in itself does not permit the assumption that females' preferential associates within a social group will be their closest female kin, or that interactions between individuals will be influenced by their relatedness. Some authors (Underwood, 1981; Seyfarth, 1976; Jarman and Jarman, 1979; Jarman, 1974; Wasser, 1983) have found that individuals may preferentially associate with others of similar age, reproductive class or rank. These types of associate preferences may arise because individuals with similar fates aggregate to reduce their conspicuousness in a group (Jarman, 1974), or may be related to intrasexual competitive tactics (Wasser, 1983) or reciprocal altruism (Russell, 1983).

In this section, I discuss the association preferences of the eastern grey kangaroo females at Wallaby Creek. My principal aim is to explore whether matrilineal relationships might exist between the females and whether as a consequence there is likely to be greater maternal investment in adult daughters than adult sons.

I calculated annual association index values for all female pairs using Sorenson's index (Pielou, 1977) (see Appendix E). I then analysed the resulting matrices from the 1983 and

Table 53: *The mean level of association between females and their 1st to 20th ranked associate. Association levels are as a percentage of sightings that the two relevant females were found in the same subgroup (Pielou's index, see appendix 1').*

rank of associate	1983:		1984:	
	mean (sample size = 61 females)	SE	mean (sample size = 54 females)	SE
1	30	2.3	28	1.6
2	20	0.6	22	6.4
3	18	0.5	20	0.8
4	17	0.5	19	0.8
5	16	0.4	18	0.7
6	15	0.4	17	0.6
7	14	0.4	16	0.6
8	14	0.4	15	0.5
9	13	0.4	14	0.5
10	12	0.3	13	0.5
11	12	0.3	12	0.5
12	11	0.4	11	0.5
13	11	0.4	10	0.5
14	10	0.4	10	0.6
15	10	0.4	9	0.6
16	9	0.5	8	0.6
17	9	0.5	8	0.6
18	8	0.5	8	0.6
19	8	0.5	7	0.6
20	8	0.5	7	0.6

1984 data via single and average linkage cluster analysis (Sokal, 1977). The dendrograms linking females into clusters of 'associates' are presented in Appendix E. The mean percentage of association of the first 20 closest associates of females are presented in table 53.

Basically, in all four analyses the females were segregated into two main clusters; these same two clusters were previously found from cluster analyses of the distance between females' home-range-centres (section 4.2, Appendix, D). The chaining of females as single units to the main sets (which occurred in the single-linkage analyses) was reduced in the average-linkage analyses. However, the various within-set clusters were still defined at a wide variety of association values. Apart from clusters of pairs, there were few consistently defined within-set clusters between the two years 1983 and 1984.

Known mother-daughter pairs were typically closely linked, especially in 1983 (Appendix E). Some pairs of older adult females associated relatively strongly too. Unfortunately I do not know whether these females were related. These latter pairs did not necessarily associate strongly with each other in both years.

As a daughter ages she is found less frequently in the same subgroup as her mother (section 4.3). It could be that the association between mother and daughter falls to a random level, and the temporary strong associations between some adult females were the result of chance. If this is so, and the females within sets are randomly associating with each other, I would expect that the closer two females' home-range centres are, the more frequently they would associate.

However, this relationship was not found to be very strong. The distance between two Southern females' annual home-range centres was significantly related to their level of association in both 1983 and 1984; but the relationship explained only 37% and 55% of the variance in females' association levels (table 54). Further, for each South female the variance in the ranks of association of the ten closest neighbours was very weakly explained by their rank as a neighbour (table 54). Thus, though it is obvious that a close associate is likely also to be a close neighbour, a close neighbour need not be a particularly close associate.

Female association preferences changed from year to year. If they were choosing to change associates from year to year, it probably would be in response to a characteristic of the females which also changes over time. The females' reproductive class fits this requirement. The inter-PEP interval is highly variable between females (chapter 3). Hence,

Table 54: Relationships between association levels or rank of associate and distance between annual home-range centres (HRC) or rank as a neighbour. The frequency distribution of the first associates' rank as a neighbour are included for 1983 and 1984 separately.

		rank of 1st associate as a neighbour:										total
		1	2	3	4	5	6	7	8	9	≥ 10	
1983:												
frequency		12	13	8	0	2	3	4	1	5	13	61
(%)												(30)
1984:												
frequency		16	6	5	5	4	6	2	4	3	3	54
(%)												(20)

variable	equation	R^2	probability	
			lin.	quad.
<i>for South females:</i>				
1983 % assoc	$= 16.527 - 0.059(\text{distbetwHRC}) + 0.53 \times 10^{-4}(\text{distbetwHRC})^2$	0.371	< 0.001	< 0.001
1984 % assoc	$= 20.324 - 0.089(\text{distbetwHRC}) + 1.07 \times 10^{-4}(\text{distbetwHRC})^2$	0.553	< 0.001	< 0.001
<i>for 1st 10 closest neighbours:</i>				
1984 assoc rank	$= 6.36 + 0.32(\text{neighbour rank})$	0.025	0.0002	

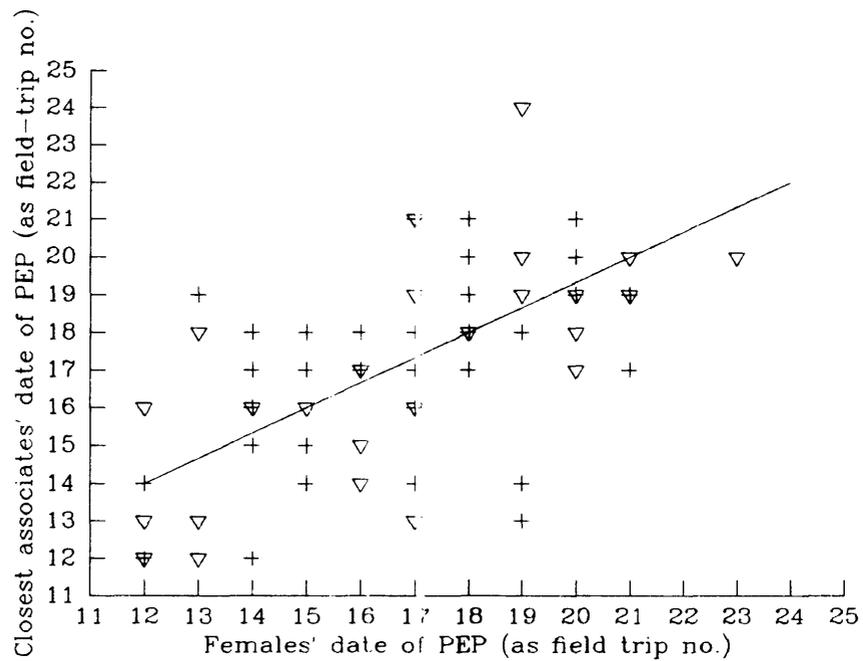


Figure 51: *The relationships between the date of a female's PEP and her closest associate's date of PEP. The crosses and continuous line refer to data from 1983. The triangles and broken line (underneath continuous line) refer to data from 1984. The best-fit relationship for 1983 is: (1st assoc PEP month) = 0.69(female's PEP month) + 5.43, $R^2 = 0.367$, probability < 0.001. The best-fit relationship for 1984 is: (1st assoc PEP month) = 0.71(female's PEP month) + 8.83, $R^2 = 0.588$, probability < 0.001. The slopes are significantly different from 1:1. 1983 - $t_s = 2.346$, $df = 46$, $p < 0.05^*$. 1984 - $t_s = 3.102$, $df = 40$, $p < 0.05$. The slopes are obviously not significantly different from each other. Note that the field trip numbers for the 1984 data are +12 of the numbers on the axes.*

females who were reproductively synchronised one year may not be the next.

The dates (by month) of permanent emergence for closest-associates were significantly correlated in both years (fig. 51). The slopes were significantly different from the expected 1:1 gradient (i.e. expected if females tended to associate with others of similar class regardless of the seasonal timing of their reproductive attempt). This significant difference probably arose because the seasonal peak in permanent emergence is likely to have limited the offpeak females' choice of associates. These females might be more likely to associate with females whose date of permanent emergence is one or two months closer to the peak season than their own date. Consequently, as was found, the best-fitted equation would

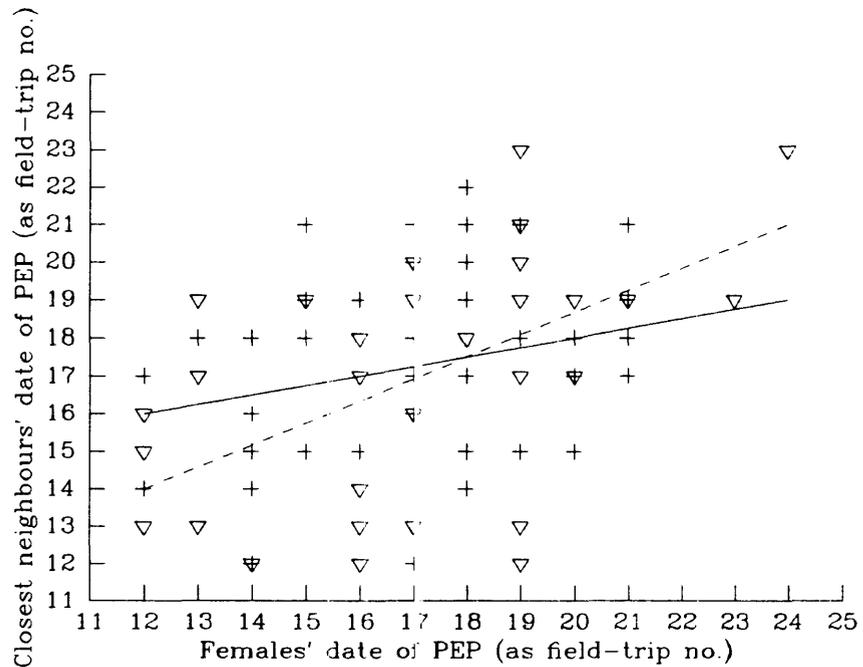


Figure 52: The relationship between the date of a female's PEP and her closest neighbour's date of PEP. The crosses and continuous line refer to data from 1983. The triangles and broken line refer to data from 1984. The best-fit relationship for 1983 is: (1st neighbour PEP month) = 0.29 (female's PEP month) + 12.12 . $R^2 = 0.094$, probability = 0.03 . The best-fit relationship for 1984 is: (1st neighbour PEP month) = 0.62 (female's PEP month) + 10.82 . $R^2 = 0.418$, probability < 0.001 . The slopes are significantly different from 1:1. $1983 - t_s = 18.518$, $df = 46$, $p < 0.001^*$. $1984 - t_s = 69.874$, $df = 40$, $p < 0.001$. The slopes are significantly different from each other: $t_s = 11.563$, $df = 84$, $p < 0.001^*$. Note that the field trip numbers for the 1984 data are +12 of the numbers on the axes.

Table 55: *G* tests comparing frequencies of the difference between the dates of PEP for females and their closest-associate's with their closest-neighbour's dates of PEP. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

months between PEP dates:	0-1	2-3	4-5	G test	probability
1983:					
<i>associates</i>	25	17	7	5.462	< 0.1†
<i>neighbours</i>	15	17	15		
1984:					
<i>associates</i>	25	10	4	7.915	< 0.02*
<i>neighbours</i>	15	16	12		

have a slope of less than one, since the peak season months were assigned central dates.

Therefore in order to check that the close correlation between the dates of permanent emergence of a female and her closest associate was not an artefact of chance, arising from a the general seasonal peak in reproduction. I compared the slopes obtained from the above-mentioned relationship, to those obtained by regressing the date (by month) of permanent emergence of the female's closest neighbour (female with closest home-range-centre) with the female's own date of permanent emergence. This simultaneously checked whether association preferences were significantly more correlated to reproductive class than geographical position.

The correlations between the dates of permanent emergence for a female and that of her closest neighbour were significant, but weaker than for closest associates (fig. 52). Most importantly, the slopes were significantly less steep than the slopes obtained for the closest associates (neighbour vs associates slopes: 1983, $t_s = 4.033$, $df = 90$, $p < 0.01$ *, and 1984, $t_s = 9.568$, $df = 78$, $p < 0.01$). From these results it would seem that a female's closest associate was more likely to have a date of permanent emergence which was 0 to 1 month away from her own, but her closest neighbour was comparably more likely to have a date of permanent emergence which was several months away. This interpretation was supported by a *G* test comparing the frequencies of the differences in the dates of permanent-emergence between closest associates and closest neighbours (see table 55).

Females and their closest associates could be synchronised because they did preferentially associate with each other, or they could be preferentially associating because they were synchronised. If the latter is true, then a female should have changed her 1983 closest associate to one whose date of permanent emergence in 1984 was closer to her own.

Basically, most of the females (57%) did change their closest associate, to a female

whose date of permanent emergence in 1984 was closer than their 1983 closest associate's date of permanent emergence was in 1984. However, 29% of the females changed their closest associate to one whose permanent-emergence date was no closer than the 1984 date of their previous closest-associate. Fourteen percent of females did not change their closest associate.

In 1983 30% (18/61) and in 1984 22% (12/54) of females had at least one closer neighbour whose date of permanent emergence was as close as or closer than their closest associate's month of permanent emergence. In general, if the date of permanent emergence and the distance between home-range centres were the sole factors which explained a female's association preferences, I would expect that there would be a strong relationship between the difference in the dates of permanent emergence and the levels of association for pairs of females which comprise females and their neighbours who had home-range centres nearer than were closest associates' home-range centres (for each female). However, only 3.5% of the variance of the rank of an associate having a home-range centre closer than that of a female's first associate was explained by the difference between the dates of permanent emergence of the females and their associates ($R^2 = 0.035$, Associate rank = $5.351 + 0.686(\text{PEP date difference})$, $df = 171$, $p = 0.013$).

Hence, I suggest that there may be some other factor involved, especially as a female's choice of closest associate was not based on the female who was the closest neighbour with a permanent-emergence date within two months of their own permanent-emergence date.

The age of a female's closest associate was not correlated to the female's own age (fig. 53).

As the known mother and adult-daughter pairs generally associated with each other at a relatively high level, I suggest that females might be associating preferentially with kin whose reproductive state is synchronised with theirs. This possibility is given further credence from the division of the females into North versus South sets, which appears to be a socially derived phenomenon, rather than one arising from geographic barriers. These sets may be likened to impala 'clans' (Murray, 1981) or red deer matriline (Clutton-Brock *et al.*, 1982b). Much more work is required to substantiate the existence of matriline; but it is at least quite probable that mothers invest in daughters at least during their early adult life to a greater extent than they do in sons.

Lastly, this section found that females show a preference for associating with others with whom they are reproductively synchronised.

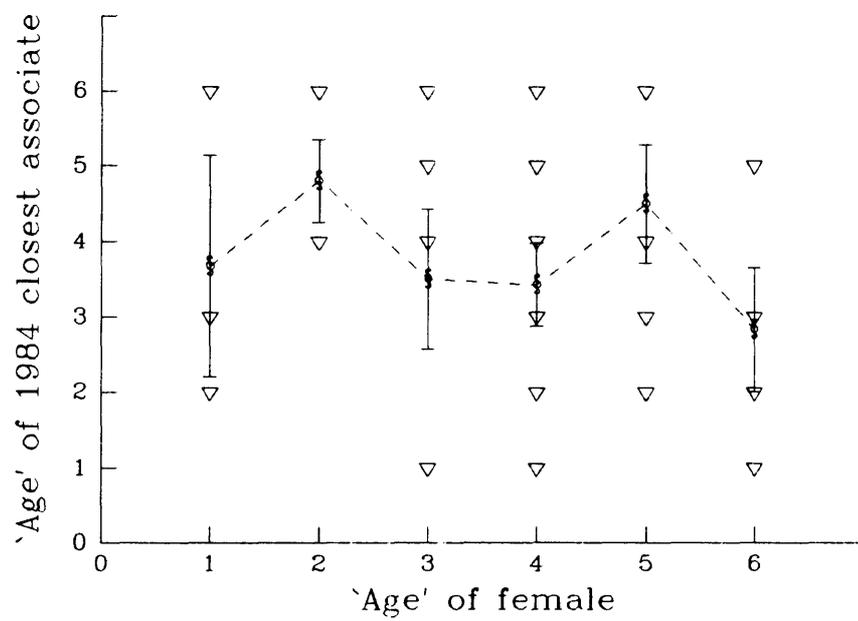


Figure 53: *The means and standard errors for the 'age' of a female's closest associate according to the female's 'age'. These are results from the 1984 data. However no significant relationship could be fitted to either the 1983 or 1984 data.*

Table 56: *The categories into which I divided the female-female interactions.*

-
1. *one female pursues another. The former female is typically growling and attempting to cuff or jump at the latter.*
 2. *one female jumps at or cuffs at another, while growling. No chase develops.*
 3. *one female growls at another.*
 4. *one female cuffs or paw-waves at another.*
 5. *one female displaces another from her position without a growl, cuff, or paw-wave.*
 6. *one female stretches toward another with her nose the closest point between her and the other; the second female may do likewise.*
-

4.5 Interactions between females

Female eastern grey kangaroos have been reported to interact with each other on a rank-related basis (Grant 1973), as do the females in species such as horses, cows, red deer, reindeer, american bison, macaques, capuchin monkeys, baboons and vervets (Wells and von Goldschmidt-Rothschild, 1979; Clutton-Brock *et al.*, 1976; Thoules and Guinness, 1986; Espmark, 1964; Reinhardt, 1985; Rutberg, 1985; Horrocks and Hunte, 1983, Dittus, 1979, Drickammer, 1974; Janson, 1985, Seyfarth, 1976; Tyler, 1972). In general, low ranking females are harassed by others of their social group to a greater extent than are high ranking females. A female's rank may be correlated to her success in rearing young and her access to the local resources (see above references). This in turn may mean that the females of different ranks may follow different strategies in rearing young (Silk *et al.*, 1981; Altmann, 1980).

I was not able to rank the female kangaroos of the study site, as I observed too few interactions. In some species of ungulates, the females' ranks have been found to be highly correlated to their age (e.g. red deer, reindeer, American bison, horses, and cows; see Thoules and Guinness, 1987; Clutton-Brock *et al.*, 1976; Espmark, 1964; Reinhardt, 1985; Rutberg, 1986). Furthermore, from my previous analyses it appears that the females at Wallaby Creek follow different rearing strategies according to their 'age'. It is possible that this might be related to social rather than physical factors.

Table 57: Relationships between females' interactions and their 'age' and rate of weaning young. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

variables	equation	R^2	probability
age:			
proportion of interactions won:	$32.25 + 8.51(\text{age})$	0.293	0.0006*
number of interactions:	$11.64 - 1.12(\text{age})$	0.129	0.031*
type of interaction:	$2.81 + 0.30(\text{age})$	0.136	<0.001*
proportion initiated:	$0.51 + 0.03(\text{age})$	0.032	0.299ns
number initiated:	$6.71 - 0.57(\text{age})$	0.076	0.103ns
rate of weaning young:			
proportion of interactions won:	$4.23 - 1.0(\text{proportion won})$	0.012	0.500ns
number of interactions won:	$3.19 - 0.06(\text{number won})$	0.009	0.564ns
number of interactions:	$2.92 + 0.08(\text{total number})$	0.032	0.271ns
number initiated:	$3.04 - 0.10(\text{number initiated})$	0.022	0.358ns

Table 58: The frequency distributions of interaction intensity for 'very young' and 'young' females and for the females of the 'older' 'age' categories. A G test comparing the frequency distributions is included.

	interaction categorisation:						total
	1	2	3	4	5	6	
	high	intensity...				low	
<i>'very young' and 'young' females:</i>							
frequency	6	19	47	13	3	3	91
(%)	(7)	(21)	(52)	(14)	(3)	(3)	
<i>the 'mature' and 'old' females:</i>							
frequency	0	11	18	14	4	20	67
(%)	(0)	(16)	(27)	(21)	(6)	(30)	
G test: interaction categories combined into 3 pairs							
$G=22.154, df=2, p < 0.01$							

Consequently, in order to determine whether the females differed in their social behaviour, I correlated the type of interactions, the number and proportion of interactions won, the number and proportion of interactions initiated, and the total number of interactions of each female with the female's 'age' and their rate of weaning young (table 57). The categories into which I divided the interactions into are presented in table 56. I considered a female to have 'won' an interaction, if she made the last cuff or threat. It was rare for an interaction between females to escalate above one female threatening another.

The 'Very Young' and 'Young' females were involved in significantly more interactions than expected, but 'won' none of their interactions if the other interactor was an older female. In general, the proportion of interactions that females won of the total number they were involved in was significantly and positively correlated to their 'age'. Also, younger females tended to be involved in significantly more interactions than older females. The interactions in which younger females were involved tended to involve a more intense threat from the other female (table 58). However, females were no more or less likely to initiate an interaction according to their 'age'.

I did not find that a female's rate of rearing young to weaning was significantly correlated to the number of interactions she was involved in, their intensity, or the probability that she would win an interaction or initiate it.

In summary, young females were as likely as old females to initiate an interaction, even though they were less likely to win, and were more likely to be subjected to an intense threat. Younger females tended to be involved in absolutely more interactions than older

females. Despite the lack of a significant relationship between any of the various 'interaction' variables and the females' rate of rearing young to weaning, a female's social relationships with others may affect her tactics of rearing young by way of an age-related effect on her social relationships with others. 'Young' females were noted in previous sections to be less gregarious and to range less widely per trip. Perhaps this was related to being more likely to be threatened than older females.

4.6 Discussion

4.6.1 The female social organisation

The eastern grey kangaroo society is based on open membership groups; individuals may change groups several times per day. At Wallaby Creek a group may comprise 1 to 40 individuals. The individuals constituting the group may aggregate into one or more subgroups.

The adult males of the population may range over an area which includes all of the females' home ranges (Jarman, unpubl. see also Jarman and Southwell, 1986; pers obs.). Females on average ranged over 42 ha, which is less than 50% of a large male's home range. The females' home ranges overlapped considerably: a typical female shared her home range with 25 other kangaroos of either sex. A female ranged over approximately 30% of her annual home-range during a 10-day period, and regularly shifted her centre of activity around her home range.

'Old', 'Very Old' and 'Young' females were less gregarious and ranged over a smaller area per 10 days than the 'Very Young', and 'Mature' females. The difference between the behaviour of these classes of females might have been related to a greater vulnerability to predation of the older classes, and the greater levels of harassment received by the 'Young' females.

The females were divided into two distinct 'sets', North and South. The sets were not just spatially defined; the females within 'sets' associated with each other, according to cluster analysis, to a greater extent than they did between 'sets'. There was no obvious geographic barrier between the North and South females' home-ranges. Since the known subadult and adult daughters were found in their mothers' subgroups relatively frequently compared to the mothers' peers, and the home ranges of daughters overlapped their mothers' home ranges considerably, it is probable that the females within 'sets' were significantly more closely related than were the females between 'sets'.

Adult females can be very aggressive to young females, so it may be to a young female's advantage to remain in her natal home range and associate with kin. According to current theory (Hamilton, 1964; Bertram, 1976; Wasser, 1983; Dunbar, 1984), kin are probably more tolerant of each other. Indeed, mother eastern grey kangaroos are more tolerant of their subadult daughters than they are of their subadult sons (section 6.9). I did not investigate whether females differentiated between their peers when threatening other adult females in a consistent manner. This would be the next step in an investigation of whether females interacted with each other in a rank-related manner, and be a part of investigating whether relatives were more tolerant of each other.

Within 'sets', apart from the mother-daughter association, the females were not obviously retaining preferential associates between years. The closest associate for each female tended to be reproductively synchronised with her and there was some indication that females would change their closest associate between years toward females who were more closely synchronised than their previous closest-associate currently was. However, the closest associate who was chosen was not necessarily the female with the closest home-range centre who was reproductively synchronised. Some other factor was involved; it was not age. It is possible that females may have been choosing to associate preferentially with females who were reproductively synchronised and were also close relatives. Some females did not associate strongly with any other female. They may not have had any close relatives who were synchronised. This deserves further investigation. However, it may explain some of the considerable variation found between the females in the average size of subgroup in which they were found. The females' age index and rate of rearing young to weaning explained some of the variation in the average subgroup size of females, but there was still much unexplained variation.

In addition to the above, the females within the study area were very rarely found in groups that included females from outlying populations, even though there was no obvious geographic barrier between the study population's general ranging area and the area the other populations ranged over (see section 2.3 and Southwell, 1987). It is likely that the study population constitutes a social unit defined by Kaufmann, (1974, 1975) as a 'mob'. This holds if the male home-ranges are used to define the 'mob'. However, this area which the males ranged over included two 'sets' of females. Each female of a 'set' ranged over an area which overlapped considerably with the area other females of her 'set' ranged over, but overlapped much less with the home ranges of females of the other 'set'. Further, the

females were divided distinctly into these same two 'sets' by cluster analyses of the degree they associated with other females. Consequently, a 'set' may constitute another level in the eastern grey kangaroo's social organisation. Since females were not observed to migrate into the study area, or move their home range between 'sets', and relatively few females emigrated, 'sets' may be based on matriline.

4.6.2 Changes in the mother's social behaviour while rearing a young: sons versus daughters

Adult female kangaroos are typically rather gregarious, except for the period lasting from a month prior to the permanent emergence of a young until the young is several months past permanent emergence.

The females' ranging behaviour does not change to exactly the same schedule as found for their level of gregariousness, as they do not restrict their ranging area until the young is at permanent emergence. At this time, females also tend to localise their activity to an area on the boundary of or at a distance from the general cluster of females' home-range centres.

It should be noted that the mothers are not completely segregated from their conspecifics while with a recently emerged YAF: rather they are just relatively less gregarious and more sedentary. They are found by themselves more often than expected. The females may behave in this manner for several months, especially if they have a daughter. If they have a son, they appear to return to their typical behaviour after about a month.

Why do females tend to isolate themselves as their young permanently emerges? If the period of permanent emergence in kangaroos is comparable to birth in ungulates, then some of the many reasons which have been proposed for the tendency of ungulate mothers to isolate themselves during and subsequent to birth may similarly apply for permanent emergence.

Isolation might reduce the risk of predation for both mother and young, as they can appear outstanding members of a group (Jarman, 1974). A corollary of this is that when there is a seasonal peak in births, mothers may not isolate themselves (Estes and Estes 1979). However, the argument may be extended in another direction. Since the young is uncoordinated and physically weak, then it may be particularly vulnerable to predation when in a group regardless of the number of other young present. Thus, mothers with neonates may isolate themselves from conspecifics until the young is physically developed enough

to have some chance of escaping a predator by flight (Shackleton and Haywood, 1985). Isolation may also be a means of avoiding harassment of the young by others (Jarman, 1976). Alexander *et al.*, (1979) have suggested that female sheep may isolate themselves during birth to shelter the young from inclement weather. Finally isolation might reduce the risk of a young becoming 'bonded' to the wrong female or of the mother mistaking a foreign young for her own (Lott and Galland, 1985). In species where the females typically do not isolate themselves, but instead remain in a large herd to give birth, Estes and Estes (1979) suggests that there is a high risk of separation by mistaken identity.

Kaufmann (1974, 1975) and Croft (1981a and b) have reported that mother kangaroos with small YAF are seen alone more often than expected. These authors have suggested that this behaviour of mother and young occurs because the young are not physically capable of ranging around their mothers' typical home-range, or that the young are prone to following the wrong female when in a group.

I believe that the tendency for mother kangaroos to isolate themselves while their young is permanently emerging probably arises from a combination of factors. This is because the mother's level of gregariousness and ranging behaviour do not change in concert with each other. A mother begins to reduce her gregariousness as her young becomes a large pouch-infant, but she does not reduce her ranging area until it permanently emerges. Mothers with large pouch-infants appear as outstanding members of a group, and might be more vulnerable to predation. Consequently, they might become less gregarious without simultaneously reducing the area they range over.

Small YAF may also be considered outstanding members of a group, especially during the offpeak season, when there are fewer young in the population. Mothers with offpeak young are more solitary than mothers with peak young, particularly if they have sons. The offpeak sons are young who are most likely to have had very short pouch lives (section 3.6). Thus, they may be particularly physically immature and highly vulnerable to predation.

But in contrast to this, mothers with either peak or offpeak sons show a more rapid return to their typical level of gregariousness than do mothers with daughters. This was perplexing. I could see no evidence that mothers with daughters were harassed more frequently than mothers with sons, as is reported for macaques (Silk *et al.*, 1981, Simpson and Simpson, 1985)

If I assume that isolation reduces the young's risk of predation, but isolation also imposes

costs on the mother (for example, her time budget may be less favourable to her self-maintenance, see chapter 5), then mothers might differentially invest in young. Daughters may be more consistently invested in (see also section 3.8) by being given a relatively longer isolation phase than are sons. This investment in daughters may not function to increase the daughter's quality, that is size or weight, but may function to increase her chance of survival. This type of investment might be more adaptive to mothers when rearing daughters; while the type of investment which increases a son's weight or size, or the number produced (section 3.7) might be more adaptive to mothers when rearing sons. In this study daughters were not significantly more likely to survive than sons, but there was a trend in that direction (section 3.5). A significant difference in the survival of daughters versus sons may have been obscured by the very high loss of young during the middle of the field study (1983 and part of 1984).

The degree to which mothers reduce their ranging area during permanent emergence was not related to the sex of the young or the season in which it emerged, although it was related to the 'type of mother'. Mothers might reduce the size of their ranging area while the young is physically less mature, because, though the young is quite well co-ordinated, it may not have developed enough stamina to escape by flight from a predator, or follow the mother around a large home-range. However, a small ranging area during permanent emergence and subsequent gradual increase could also function to allow the young to become acquainted with its local environment and its relative location within this environment in a manner which minimised the chances of the young becoming separated from its mother in an unfamiliar environment.

However, 'peak only' mothers were less likely than 'offpeak also' mothers to reduce the area they ranged over while their young permanently emerged. It is possible that reducing the area that a mother ranges over from her typical ranging area may involve a cost. Not all mothers may be able to afford this cost. 'Peak only' mothers did tend to lose more of the young they produced than did the 'offpeak also' mothers; this might have been related to them having not reduced their ranging area while their young was permanently emerging. Alternatively, one other interpretation is that, since 'peak only' mothers include more of the 'Old', 'Very Old' and 'Young' mothers, who tend to have small trip-home-ranges in general, these females may not need to reduce their home range. Further study is required to investigate this difference between the mothers.

Overall, the relative isolation of mother and young during permanent emergence might

reduce the young's likelihood of becoming separated from its mother, for a variety of reasons. The mother-young relationship appears insecure during this period and consequently separation of mother and young may be more imminent than for other stages. I discuss this in chapter 6.

4.6.3 Mothers and subadults

YAF typically follow their mother about her home-range. When weaned, the young, now defined as a subadult, significantly reduces its association with its mother to on average 39% and 51% of the time for a son and a daughter respectively. Subadult sons tend to range around the study population's home range in a manner which is less tightly related to their mothers' current ranging areas than do subadult daughters. Both sons and daughters when subadults are attracted to subgroups which contain other subadults, regardless of the sex of the subadult. This attraction of sons for other subadults is negatively correlated to their association with their mother, while no such relationship was found for the subadult daughters. Thus, I suggest that mothers may be as much responsible as their daughters for maintaining the pairs association. In other words mothers might be investing in their subadult daughters in an active manner. Further, mothers are more likely to actively discourage an approach by their subadult son (section 6.9).

There could be many advantages to subadults of associating preferentially with each other. Subadult males are often seen sparring in a 'playfull' manner with each other (Croft, 1983; Jarman, unpubl.; pers obs.). The association of individuals who are of similar appearance may also reduce their risk of predation (Jarman, 1974). Subadults are relatively small individuals and may be harassed by the adult females. Thus, if they associate with similarly sized individuals or tolerant kin, they might suffer less harassment than they ordinarily would receive. The level of harassment received by individuals may be negatively correlated to their feeding efficiency and their physical condition (Altmann, 1980). Indeed, subadults might also be associating with 'tolerant kin' when aggregating, because the alpha-male sires most of the young of an annual cohort.

4.6.4 Dispersal

The class most likely to disperse was the small males. There are quite a number of theories concerning the mechanisms which drive dispersal. For example some of the proximate factors which may trigger dispersal are maternal or paternal aggression (Cockburn *et al.*,

1985; Franklin, 1983), competition for the local resources (Greenwood, 1980; Wasser, 1985), the onset of physical maturity (van Noordwijk and van Schaik, 1985) or a perceived elevated reproductive expectation in a nearby social group (*ibid.*). Gaines and McClenaghan (1980) have suggested that there is probably no one universal mechanism and there may be several operating within a species. This study was not conceived, and is not able, to delineate the causes of dispersal in the kangaroos at Wallaby Creek, but I can suggest some possible influences which might be involved. Principally, I was interested in finding whether the age of dispersal for a young male could have been related to the maternal investment or rearing schedule he received.

The age at which the young males were disappearing from the study site was not correlated with their level of association with their mother or with their peers. Consequently, the trigger for dispersal was probably not social, for example maternal aggression. It was not correlated to the duration of the male's YAF-phase, but it was negatively correlated with the mother's age. In addition, males were more likely to delay dispersal if they permanently emerged in the peak season and had a mother who was known to have produced at least one offpeak young.

The males who delayed dispersal might have done so because they were small individuals. The red deer sons on Rhum are more likely to disperse at younger ages if their birth weight is above the median weight for newborn sons (Clutton-Brock *et al.*, 1982b).

Young mothers of iteroparous species are presumed to invest in individual young to a lesser extent, or rather at a smaller cost to themselves, than are older females, for whom there is a smaller probability of reproducing again (Charlesworth and Leon, 1976). On the whole, the younger kangaroo mothers at Wallaby Creek were producing young at a greater rate than were the old mothers (section 3.3). Hence, it is possible that individual sons of young mothers were less intensely invested in than were the sons of the old mothers.

The peak-season sons of 'offpeak also' mothers also may have been smaller than the other sons. If 'offpeak also' mothers wean both their peak and offpeak sons at a similar average weight, then off-peak sons may grow faster during their subadult-life than peak sons because their subadult stage is timed to span the spring-summer pasture, as compared to peak males who are weaned prior to the onset of the winter frosts and a probable reduction in pasture quantity and quality (seasonal changes in pasture are currently being analysed by other researchers). Peak sons of 'peak only' mothers may be more intensely invested in, as these mothers produce young at a lower rate than the other mothers.

The above is a *post-hoc* interpretation and assumes that offpeak sons reared to weaning are in as good 'physical condition' as peak sons reared by the same mothers. It is possible to construct an argument for why sons of old mothers and peak-season sons of 'offpeak also' mothers might be larger than their peers of the same age. However, when in the field I gained the impression that early dispersers were generally larger than those who were delaying dispersal. This is currently being investigated by Jarman and associates.

If it is true I would expect that the season of a son's emergence should not affect the amount of investment he receives from his mother, although the 'type of mother' may influence the level of investment the son receives. It should be noted that the 'benefit' from the investment a young receives may be a very different quantity from that of the 'cost' to the mother of producing and rearing a young (see chapter 1). I investigate seasonal influences on the quality of the mother-young relationship in chapter 6.