

Chapter 6

The social development of the young



Figure 77: *"Time to come out now!"*

A mother letting her very small pouch-infant out of the pouch.



Figure 78: "Alright, inside NOW!"

A mother in pouch-entry posture. Note that her forepaws are spread apart and her posture is hunched.

6.1 Introduction

It is commonly accepted that parental investment in young can take many forms apart from nutritional provisioning (Hinde, 1979; Altmann, 1980); as I have shown in the previous chapters, investment may involve a disruption to the mother's typical activity schedule, energy expenditure and risk from carrying the young, and possibly post-weaning investment in young. This chapter explores how active the mother kangaroo may be in rearing her young, for example in directing its behavioural development toward that of an adult and in maintaining the relationship.

According to current theory the mother-young relationship may involve conflict; some young may attempt to obtain a greater share of a parent's resources than the portion which the parent, who would invest in future young, would optimally provide (Trivers, 1974; Parker and MacNair, 1979; MacNair and Parker, 1978; see chapter 1). This situation is most likely to arise when it is adaptive for the parent to monitor the young's development, such as when young are reared in varying social and environmental conditions; the parent is most open to the young providing misinformation about its status and hence misleading the parent. Thus the mother-young social relationship may involve behavioural manipulation of one individual by the other (Dawkins, 1976; and above references) and the 'mother-young bond' becomes a difficult entity to define. With these ideas in mind, in this chapter I look at who is responsible for maintaining or initiating changes in the mother-young relationship, and whether conflict might be involved.

Overall, the mother and young may have quite different roles in maintaining the association, and these roles may vary in form according to the sex and the developmental state of the young, and the social and physical environment. Consequently, a variety of variables need to be investigated when defining these roles. In this chapter the mother-young relationship will be described with respect to:

1. who is responsible for pouch entry and exit
2. who initiates and terminates suckling,
3. how separation arises and who is responsible for reunion,
4. who is responsible for their spatial relations,
5. how co-ordinated they are,

6. what the types of contact between them are, and
7. how weaning arises.

Also, I will briefly discuss the interactions of the young with other kangaroos.

6.2 Leaving and entering the pouch

The pouch provides an infant with shelter, warmth, nutrition, and some degree of protection from danger. Thus a pouch-infant might be expected to be strongly oriented toward the pouch. However, during the pouch-infant phase the young is seen to leave the pouch for short excursions which increase in frequency and duration as the pouch-infant ages, but particularly accelerate in duration over the short permanent-emergence phase. Who is responsible for these excursions and the final vacation date and might there be a conflict of interests between mother and young?

Conflict has been reported in the primate literature: for example, the infant primate may seek to ride on its mother to a greater extent than the mother is willing to accommodate (Altmann, 1980; Locke-Haydon, 1984; Nash, 1978). Alternatively, some primate mothers are observed to restrain their infants from moving away during certain stages of their infant's ontogeny (Bolwig, 1980; Dolhinow and Murphy, 1982; Berman, 1980).

By investigating the roles of both mother and young kangaroo in determining when the infant leaves and how long it spends outside the pouch, it may be possible to suggest whether a conflict of interests might be involved and, if it is, in what manner each might manipulate the other. I discuss the latter in chapter 7.

6.2.1 Pouch exit

In the previous chapter I suggested that mothers of pouch-infants may restrict the times these young leave the pouch to particular times of the day and to a total percentage of the day spent out of the pouch typically less than 30%. However, some authors (Russell, 1973; Osazuwa, 1978; Kaufmann, 1974) have suggested that the young can but do not usually, leave the pouch whenever they desire. In this section I provide evidence for the wild eastern grey kangaroo mother's ability to control the exit of her infant from the pouch.

I observed only two occasions of all pouch exits when I was in some doubt about who was responsible for the exit. In one case the young appeared to crawl out while the mother

was resting, and in the other the young appeared to drop or over-balance out of the pouch while the mother was feeding. In all other cases ($N > 71$) the mother appeared to expel the young from the pouch by relaxing her pouch muscles and often even appeared to force the young out by hunching into a crouched stance with her forearms splayed apart (see fig. 77).

In order to substantiate this observation that mothers were primarily responsible for their infants' exits from the pouch, I looked to see whether the mothers' behaviour prior to their infants' exits were significantly different from their typical behaviour. If the young were primarily responsible for their exit from the pouch, I would expect that the average durations of time spent by mothers in the various activity states would approximate their typical probability of being in those activity states (as determined in the previous chapter). Conversely, if the mother was responsible, it is likely that her behaviour would differ significantly from her typical behaviour. I suggest this because it appeared to me that mothers did not let their young out of the pouch when there were disturbances in the environment, and further, that mothers tended to survey more frequently just before their young left the pouch.

I quantified the duration of time mothers spent in three categories of behaviour in the minute prior to the young's exit. The three categories were: 1) surveying, 2) grooming and interacting (with the young), and 3) all else (feeding, resting, travelling, etc.). The respective probabilities for the three categories of behaviour when the young is in the pouch in general are: 0.22, 0.043, and 0.737 (these figures slightly over-estimate the 2nd category and under-estimate the 3rd); and the respective probabilities for when the young is out of the pouch in general are: 0.507, 0.179, and 0.314. The percent of time which mothers spent in each of the three activity-state categories in the minute prior to their young's exit from the pouch is presented in table 76. The percentages for the various female classes are given separately.

For classes with very small to medium (10 to 12) pouch-infants, the mother is most likely to be grooming or interacting with her young just prior to its exit. This is an overwhelming increase compared to the extremely small probability of the mother typically exhibiting these activities when her young is in the pouch, and it is even a significant increase compared to the probability of her grooming or interacting with the pouch-infant when it is out of the pouch (table 78). When not grooming or interacting with their infants, these mothers were surveying; and significantly more than they would ordinarily when the young was in the pouch.

Table 76: *Percentage of time mothers spent in each of 3 activity categories: survey, groom/interacting with the young, and all-else, in the minute intervals prior to and following an exit from or entry into the pouch by a young. Data presented separately for mothers of males (m) and females (f) and for the different classes. Also the percentage of time mothers spend in general in each of the three categories when their infant is either in or out of the pouch is included at the bottom of the table. These data come from a separate data set.*

sex of young: class		behaviour category		percent time in the minute:								
				prior to exit		subsequent to exit		prior to re-entry		subsequent to re-entry		
				m&f	m	f	m	f	m	f	m	f
<i>v. small PI</i>	10: survey	18.3	31.7	76.7	67.0	81.7	20					
	groom/interact	80.8	68.3	21.7	35.0	16.0	50					
	all-else	0.9	0	1.6	0	2.3	30					
	(sample size)	(2)	(2)	(1)	(2)	(1)	(1)					
<i>small PI</i>	11: survey	20.3	100	49.9	88.3	55.4					44.1	
	groom/interact	63.7	0	38.9	11.7	26.7					27.3	
	all-else	16.0	0	7.2	0	18.8					27.2	
	(sample size)	(7)	(1)	(15)	(1)	(19)					(15)	
<i>medium PI</i>	12: survey	34.3	59.4	36.1	71.7	57.2	54.8				59.0	
	groom/interact	49.7	39.4	54.4	15.4	12.8	3.8				0	
	all-else	16.0	1.2	9.5	11.9	30.0	41.3				41.0	
	(sample size)	(10)	(11)	(6)	(16)	(10)	(10)				(5)	
<i>large PI</i>	13: survey	47.6	74.0	80.4	54.8	78.3	44.6				82.8	
	groom/interact	46.2	65	12.1	6.7	0.2	1.9				3.3	
	all-else	6.2	17.5	7.5	38.5	21.5	53.4				13.9	
	(sample size)	(7)	(10)	(4)	(18)	(7)	(12)				(3)	
<i>v. large PI</i>	14: survey	61.6	54.7	90.6	61.9	79.0	76.3				82.1	
	groom/interact	23.5	3.9	3.9	3.2	1.9	0				0	
	all-else	15.0	41.4	5.6	34.9	19.0	23.8				17.9	
	(sample size)	(6)	(11)	(3)	(12)	(7)	(4)				(4)	
<i>PEP young</i>	15: survey	45.1	74.4	26.7	33.8	58.3	81.7				70.0	
	groom/interact	32.4	9.4	50	5.8	0	0				0	
	all-else	22.5	16.1	23.3	60.4	41.7	18.3				30.0	
	(sample size)	(5)	(3)	(3)	(4)	(2)	(2)				(2)	
<i>for classes females with small PI to with large PI inclusive:</i>												
		when young in pouch						when young out of pouch				
survey		22.0						50.7				
groom/interact		4.3						17.9				
all-else		73.7						31.4				

Table 77: *T tests are presented comparing time mother spent in each of 2 behaviour states when her infant was about to exit within a minute, had just exited within a minute, was about to re-enter the pouch within a minute, had just re-entered the pouch within the last minute, with the mean time mothers spend in these activity states when their young is in general in (μ_1) or out (μ_2) of the pouch. Data are from the classes 11 to 13 combined. Probabilities less than 0.05 are presented as *.*

\bar{x}	N	SE	position of young					
			in μ_1	out μ_2	in t_1	out t_2	in p_1	out p_2
in 1' prior to exit:								
<i>mother surveyed</i>								
21.1 sec	22	4.61	13.2	30.4	2.230	2.603	*	*
<i>mother groom/interacted</i>								
30.9	22	4.43	2.6	10.7	6.393	4.552	*	*
in 1' subsequent to exit:								
<i>mother surveyed</i>								
34.9	37	3.15	13.2	30.4	6.979	1.400	*	ns
<i>mother groom/interacted</i>								
20.9	37	3.40	2.6	10.7	5.391	2.989	*	*
in 1' prior to entry:								
<i>mother surveyed</i>								
34.3	52	2.64	13.2	30.4	7.986	1.466	*	ns
<i>mother groom/interacted</i>								
7.6	52	1.929	2.6	10.7	2.581	1.650	*	ns
in 1' subsequent to entry:								
<i>mother surveyed</i>								
30.7	39	3.02	13.2	30.4	5.789	0.097	*	ns
<i>mother groom/interacted</i>								
5.0	39	1.66	2.6	10.7	1.445	3.479	ns	*

Table 78: *G* tests on the frequency of mothers' predominant activity state (3 categories), in the minutes prior to, and after pouch exit or pouch entry. Mothers of sons and daughters are compared for classes 11 to 13 (medium pouch young) combined, and 14 and 15 (very large P1 and PEP young) combined. These two categories of classes are compared and the before and after pouch exit or entry minutes are compared.

class of mother		frequency			G tests:		
		surv	grin/int	all else	G	df	prob.
<i>in 1' subsequent to exit:</i>							
11 — 13:	mothers of sons	14	6	2	0.550	2	ns
	mothers of daughters	13	9	2			
14 & 15:	mothers of sons	8	0	-	Fishers exact test	1	0.128ns
	mothers of daughters	3	2	-			
<i>in 1' prior to entry:</i>							
11 — 13:	mothers of sons	20	3	11			
	mothers of daughters	20	6	10			
14 & 15:	mothers of sons	8	1	7			
	mothers of daughters	6	0	3			
<i>in 1' subsequent to entry:</i>							
11 — 13:	mothers of sons	11	0	9			
	mothers of daughters	14	3	6			
14 & 15:	mothers of sons	5	0	1			
	mothers of daughters	5	0	1			
11 — 13:		5	17	2	4.147	2	ns
14 & 15:		6	4	1			
<i>in 1' subsequent to exit:</i>							
11 — 13:		27	15	4	5.640	2	< 0.1†
14 & 15:		11	2	5			
<i>in 1' prior to entry:</i>							
11 — 13:		40	9	21	2.209	2	ns
14 & 15:		14	1	10			
<i>in 1' subsequent to entry:</i>							
11 — 13:		25	(3)	15	1.988	1	ns
14 & 15:		10	(0)	2			
<hr/>							
11 — 13:							
	<i>in 1' prior to exit</i>	5	17	2			
	<i>in 1' subsequent to exit</i>	27	15	4			
	<i>in 1' prior to re-entry</i>	40	9	21			
	<i>in 1' subsequent to re-entry</i>	25	3	15			
	<i>prior vs subsequent to exit</i>				10.396	2	< 0.05 *
	<i>subsequent to exit vs prior to entry</i>				11.726	2	< 0.05 *
	<i>prior vs subsequent to entry</i>				1.123	2	ns
14 & 15:							
	<i>in 1' prior to exit</i>	6	4	1			
	<i>in 1' subsequent to exit</i>	11	2	5			
	<i>in 1' prior to re-entry</i>	14	1	10			
	<i>in 1' subsequent to re-entry</i>	10	0	2			
	<i>prior vs subsequent to exit</i>				3.377	2	ns
	<i>subsequent to exit vs prior to entry</i>				11.255	2	< 0.05 *
	<i>prior vs subsequent to entry</i>				3.212	2	ns

Mothers with larger pouch-infants were even more likely than the mothers of small to medium pouch-infants (though not significantly, since the data are scant) to be surveying prior to their young's exit. They were also still grooming and interacting with the young with a high probability.

In the minute subsequent to their pouch-infant's exit from the pouch the mothers were still tending to survey and groom-interact with the infant more than they ordinarily do during the infant's egress (tables 76 and 77). Despite a larger data-set I found no significant differences in behaviour between the mothers of sons and daughters.

Overall, it would seem that the mother eastern grey kangaroo at Wallaby Creek is primarily responsible for the timing of her infant's exit from the pouch.

6.2.2 Pouch entry

If mothers are primarily responsible for determining the duration of time a infant spends outside of the pouch (as I have suggested in the previous chapter), then most probably they rely on the infant being ready and willing to enter the pouch whenever the mother calls or posturally signals for it to enter. Mothers were never observed to pick an infant up and forcibly put it into the pouch.

However, entry by the infant did not occur unless the mother crouched in a hunched position and splayed apart her forelimbs (see fig. 78). This posture can be rather subtle to quite exaggerated in appearance. A similar maternal posture has been noted by E. Russell (pers. comm.) for tammars, C. Johnson (1985, pers. comm.) for red-necked wallabies, and P. Jarman (pers. comm.) for wallaroos, whiptail wallabies, rufous bettong, and swamp wallabies. I have observed it in red-necked wallabies, tammars, red-necked pademelons, and rufous bettongs.

In at least the eastern grey kangaroos and red-necked wallabies this pouch-entry posture may be accompanied by a vocalisation. I was not able to quantify the frequency of occurrence of the kangaroo mother's call to the infant prior to pouch entry as the noise was a very soft "chkk chkk" which I could hear only when I was very close. Nevertheless, I believe the infant could hear it from quite some distance as the following excerpt from my field notes exemplifies.

Eucalypt exits from the pouch at 08.11.45 hours ... Eucalypt hops away out of sight, >30m, (08.21h) and Dew (mother) immediately chkks and surveys. Eucalypt returns promptly and pokes her head in the pouch.

This routine occurred again at 08.22 hours and 08.29 hours. At 08.31 hours Eucalypt was in close proximity to her mother, but as a tractor started up in the distance Dew 'chkk'ed while assuming the pouch-entry posture and Eucalypt dived into the pouch. This was not an uncommon observation and shows how easily a mother could call her infant to her, with the infant's first response being to poke its head in the pouch, and if the mother was in the appropriate posture it would then enter the pouch. There were only 3 occasions when mothers of pouch-infants who were out of the pouch chased their infant around in circles 'chkking' and exhibiting the pouch-entry posture, without the infant responding appropriately and promptly. In these cases the infant had just interacted with an aggressive female, and appeared rather 'confused'.

I believe that, at least in part, mothers might train their infants to respond to the above-mentioned cues which invite pouch-entry by the infant. If I was close enough, I heard mothers of very small pouch-infants produce a very soft and continual "chkk chkk" noise while letting their infant out of and back into the pouch. I observed 11 mothers with very small pouch-infants who appeared to be leaving the pouch for one of their first few occasions. The infants were let back into the pouch almost immediately. For the very short span of time they were out they had their head in the pouch and were often on the tips of their toes, and appeared to be trying to dive back into the pouch. Once back in the pouch the mother repeated this routine on average two more times, and on one occasion 7 more times.

Prior to a pouch-infant re-entering the pouch, all classes of mother, excepting those with permanently-emerging sons, averaged a greater percentage of their time surveying compared to the other two categories of behaviour. However, it was not significantly more predominant than expected for mothers whose infants were out of the pouch. Mothers averaged a lower or typical percentage of time spent grooming/interacting compared to their general behaviour while the infant was out of the pouch. There were no consistent differences in the mothers' behaviour according to the sex of their infant (table 78).

Subsequent to pouch entry the mothers were still tending to survey more than they typically would when the infant was in the pouch (tables 76 and 77). I would expect this if a disturbance caused the entry of the infant into the pouch.

While it would appear that the mother was in immediate control of the time of the infant's entry into the pouch, it is still possible that the infant's activities prompted the mother to let it into the pouch. Prior to entering the pouch, small to medium pouch-infants,

Table 79: *G* tests comparing frequencies of the activity state of pouch-infants prior to a pouch entry with those in general for pouch-infants. The series of MPY and *v* large PI or PEP young were tested separately.

	frequencies of activity categories			G test	probability
	'sucking'	interacting, hopping, & all-else			
small to large pouch-infant sons					
<i>in 1' prior</i>	15	16		0.092	<i>ns</i>
<i>typically</i>	170	203			
small to large pouch-infant daughters					
<i>in 1' prior</i>	11	15		1.815	<i>ns</i>
<i>typically</i>	104	250			
small to large pouch-infants (excluding sucking)					
		interacting	hopping	all-else	
<i>in 1' prior</i>		14	11	6	13.879
<i>typically</i>		83	145	210	<0.01*
very large pouch-infants and PEP young					
<i>in 1' prior</i>	11	1	0	4	

whether a son or daughter, were not 'sucking' any more frequently than expected (table 79). However, they were significantly more likely to have been interacting with a kangaroo other than the mother, compared to the frequency of interactions typical of their time out of the pouch (even including interacting with the mother) (table 79).

Infants at or near permanent emergence were predominantly 'sucking' prior to entering the pouch (table 79); of 16 pouch entries of this class one involved the infant interacting with a foreign kangaroo immediately beforehand. Although the data are rather scant, it is probable that older pouch-infants were less likely to enter the pouch after interacting with another kangaroo than were the younger pouch-infants.

In the field it appeared to me that these older infants were entering the pouch predominantly after a palpable environmental disturbance. Of 21 pouch entries by these older pouch-infants at least 14 (67%) were preceded by a loud noise, a vehicle or person or cattle's approach, or a wallaby's rapid movement. Of 69 pouch-entries by small to medium pouch-infants 19 (28%) were preceded by a disturbance. I do not believe that these younger infants were less likely to enter the pouch upon an environmental disturbance, but rather that older pouch-infants, who spend a greater proportion of their time out of the pouch, might be less likely to enter the pouch after a social interaction or might be less likely to interact socially. I look at the young's interactions with others in section 6.8.

It is not possible for me to state categorically that disturbances in the environment cause mothers to let their infants into the pouch, because I was not able to quantify the occasions on which a disturbance occurred but was not followed by the infant's entry into the pouch. However, it is biologically logical and in the field consistent with the mother's behaviour. Mothers probably even rated disturbances relative to the age of their infant. This aspect deserves further study. Apart from these possible causes of pouch entry, the pouch-infant, especially when small to medium in size, may have been responsible, since infants were typically let into the pouch following their having interacted with another kangaroo. In this way the mother is perhaps open to manipulation by the infant. Alternatively, the mother may view an interaction between her infant and another as an environmental disturbance which potentially threatens her infant.

Overall, the mother appears to be responsible for initiating the infant's exits from the pouch and for determining when an infant re-enters the pouch at least proximately. However, the infant is responsible for the typically prompt entry into the pouch upon the mother's invitation to enter. In this way the mother might be in control of the times and duration of the infant's egress from the pouch; and the infant might rely upon the mother to identify when danger threatens and hence when it should remain inside or return to the pouch.

6.3 Initiation and termination of 'sucking'

While out of the pouch, pouch-infants had their head in the pouch, and were assumed to be sucking on average 50% of the time if male and 30% of the time if female (previous chapter); and they dived into the pouch or 'sucked' very readily upon a signal from the mother (previous section). Thus, pouch-infants could be described as strongly oriented toward the pouch. In comparison YAF suck only about 4 to 6 times per day (section 5.2). How does this transition occur? While the infant returns to the pouch it is probably advantageous to the mother to have a young which is pouch-oriented: the mother need spend very little time, energy, or risk in enticing her young into the pouch when danger threatens. Consequently, I would hypothesise that the time of permanent emergence might be a critical stage in the young's development with the mother rejecting much of the young's attention toward the pouch by terminating more of its 'sucking' bouts. At the same time, however, rejection of the young by the mother should not be too intense as there could be

Table 80: *Hinde and Atkinson's (1970) proximity index used as an indicator of a mother's responsibility in initiating and terminating suckling bouts, as compared to her young's responsibility. Also the proportion of bouts initiated by the mother are included.*

	class						
	10 <i>v</i> small PI	11 small PI	12 medium PI	13 large PI	14 <i>v</i> large PI	15 PEP young	16 small YAF
<i>sons</i>							
<i>N</i>	5	5	13	8	16	9	
\bar{x}	-0.005	0.078	0.243	0.232	0.310	0.483	
<i>SE</i>	0.055	0.087	0.057	0.038	0.074	0.083	
<i>proportion mother</i>							
<i>initiated</i>	2/18	0/33	9/189	5/191	10/446	1/168	0/68
<i>daughters</i>							
<i>N</i>	4	8	15	9	12	7	
\bar{x}	-0.057	-0.003	0.174	0.194	0.417	0.332	
<i>SE</i>	0.038	0.049	0.046	0.103	0.076	0.065	
<i>proportion mother</i>							
<i>initiated</i>	7/56	6/73	17/270	14/191	3/266	0/168	0/60

a risk of the young being prematurely weaned or alienated from its mother. There is a high risk of mortality of young at this age (section 3.5).

Mothers of many eutherian species (Lent, 1974; Espmark, 1969; Underwood, 1979; Gauthier and Barrette, 1985; Lee and Moss, 1986; Renouf and Diemand, 1984; Pratt and Anderson, 1979; Berman, 1980) reject or terminate a steadily increasing percentage of suckling bouts. However this pattern is not always observed. Berger (1979a) has reported that, while mountain bighorn sheep exhibit this pattern, desert bighorn sheep wean their young quite suddenly by increasing, within the duration of a week, the proportion of the young's sucking attempts which they rejected (from 13% to 52%). Tyler (1972) and Duncan *et al.* (1984) have noted that pony and camargue horse mothers, after initially terminating a high proportion of their young's suckling bouts, maintain a rather low termination level of 20% or less right until near weaning, whereupon they again reject a high proportion of the young's attempts to suck. Which pattern is observed in eastern grey kangaroo mothers? A slow or rapid method of weaning may affect the spatial relationship of mothers and YAF. This I discuss in section 6.5.

In order to look at the change in the responsibility between mother and young in initiating and terminating 'sucking' bouts as the young develops, I calculated Hinde and Atkinson's (1970) proximity index for various mother-young pairs and determined an average for each

class of male and of female pouch-infant (table 80). The index is:

$$\frac{(\text{no. of terminations by mother} - \text{no. of initiations by mother})}{\text{over}} \\ (\text{no. of initiations by mother} - \text{no. of initiations by infant}).$$

I would point out that the results probably underestimate the mothers' involvement in initiating 'suckling' as I could not be certain of hearing their call to the young. However, I will assume that I am equally likely to miss the vocalisations of the mothers of the different developmental classes.

Mothers were more responsible for initiating than terminating 'suckling' by their very small infants, but became increasingly responsible for terminating rather than initiating 'suckling' as their infant developed. Indeed initiations by the mother became almost nonexistent as the young neared permanent emergence (table 80). This state continues through the YAF stage and consequently the index becomes uninformative.

The averages of the indexes of very small to medium pouch young differed significantly between the sexes; mothers were more responsible for initiating 'suckling' by daughters than sons ($G=7.650, df=1, p < 0.01$).

However, mothers were observed to initiate only a small percentage of 'suckling' bouts, even for small to medium pouch-infants (3% sons and 7% daughters). Much of the change in the roles of mother and young in determining the timing and duration of sucking bouts resulted from a change in the percent of bouts a mother terminated rather than the percent she initiated (fig. 79). The mother terminated significantly more bouts (the young terminated relatively fewer) ($G=71.563, df=1, p < 0.001$) when her young was near permanent emergence (approximately 40%) than she did when it was a small to medium pouch-infant or a YAF (approximately 20%). The mother's low rate of rejection continues until weaning, whereupon the mother rejects most of the young's attempts to suck over a rather sudden and brief period. This is discussed further in section 6.9.

The mothers did not terminate significantly more sucking bouts of YAF sons (22%) than they did of YAF daughters (20%) ($G=0.149, df=1, p > 0.1$). Nor did mothers terminate significantly more bouts during the offpeak season (82%) compared to the peak season (81%) or terminate significantly more if their young was an offpeak-season emerger (84%) compared to a peak-season emerger (78%) ($G=1.310, df=1, p > 0.1$). Mothers who had

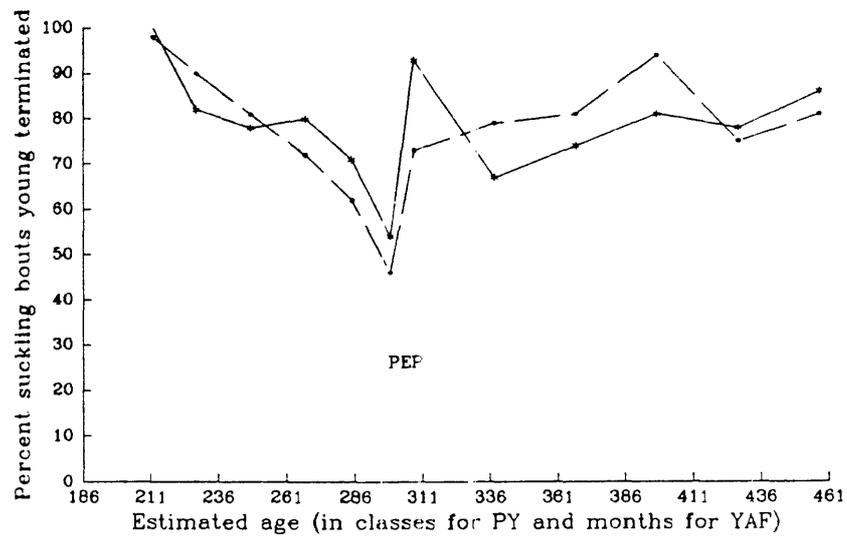


Figure 79: *The percentage of all sucking bouts which were terminated by the young according to the age of the young (in days on the x-axis). Males are represented by the continuous line with stars, and females are represented by the broken line with points.*

young permanently emerge in the peak season only were also no more likely to terminate their YAFs' sucking bouts (85%) than were the 'offpeak also' mothers (86%).

Mothers of very small pouch-infants did terminate significantly fewer bouts (1%) than mothers with small to medium pouch-infants (20%) ($G = 16.849$, $df = 1$, $p < 0.01$).

Overall, throughout the young's ontogeny mothers terminate comparatively few of their young's 'sucking' bouts, with the exception of the brief periods of permanent emergence and weaning. Permanent emergence, as I predicted, involves a significant increase in the mother's rejection of the young's sucking bouts. This rejection period is brief but not intense. The young rapidly changes toward a YAF sucking pattern. I discuss weaning further in section 6.9. Mothers were observed to initiate only a small percentage ($< 10\%$) of their pouch-infants' sucking bouts, but they initiated significantly more of the daughters' bouts than the sons' bouts.

6.4 Identification, separation, and reunion

The current form of a relationship is determined by the past history of the individuals' interactions with each other, and not just with their immediate requirements of each other (Hinde and Davies, 1972; Hinde and Spencer-Booth, 1971; Coelho and Bramblett, 1984). For example, the occurrence of a separation in a mother-young relationship can lead to the young increasing its role in maintaining a close proximity to the mother, especially if the mother left the young rather than vice versa (Hinde and Davies, 1972). One method of discerning the nature of a relationship and the responsibility of the partners in maintaining it, is to look at how separation and reunion arise (Walser *et al.*, 1984; Alexander *et al.*, 1983). The cues each use in identifying the other often can be inferred from observing reunions. The frequency of separation and types of reunion may vary with the young's developmental stage or according to its sex. These variations can help identify the roles of the individuals in maintaining their association.

6.4.1 Separation

I define a separation as a state when either the mother and young were found in different subgroups or if in the same subgroup then the young or the mother behaviourally indicated their uncertainty of the position of the other by, for example, calling and 'checking the identity of others nearby'.

Not only was there a greater likelihood of permanently emerging young being permanently lost than there was for either pouch-infants or large YAF (section 3.5), there also was a significantly greater likelihood of PEP young than the other classes of young being temporarily separated from their mothers (table 81). Pouch-young and YAF were observed

Table 81: The frequency of separations for young of different classes compared to the expected. The expected was calculated by the relative time an infant spent in each class multiplied by the number of young which entered that class. The classes are pouch-infants (PI), PEP young (PEP), small YAF (SYAF), and large YAF (LYAF).

	classes of young				total
	PI	PEP	SYAF	LYAF	
<i>total separations:</i>					
observed frequency	52	40	31	53	176
(days in class)	(71)	(9)	(84)	(120)	
(no. individuals)	170	159	116	82	
expected frequency	65	7	51	53	176
χ^2	2.6	155.57	7.84	0	166.01 *
<i>PI vs YAF:</i>					
observed frequency	52			84	136
expected frequency	53			83	136
<i>separation in different subgroups:</i>					
observed frequency	5	12	22	36	75
expected frequency	28	3	22	22	75
χ^2	18.89	27.00	0	8.91	54.80*
<i>the sexes:</i>					
	males	female	total		
observed frequency	94	82	176		
expected frequency	105	71	176		
χ^2	1.15	1.70	2.86	$p > 0.05ns$	

separated from their mothers to a similar extent relative to their frequencies in the population. However, separation was less likely to develop to the extent where the mother and young were in different subgroups for pouch-infants and PEP young, than for YAF (table 81).

There was a non-significant tendency for female young to be temporarily separated more often than male young, compared to their frequency in the population (table 81).

Of all YAF reared to weaning during this study, 62% (19/31) of males and 75% (15/20) of females were seen separated from their mother at least once to the extent of being in different subgroups. Since I was in the field for only about a third of the duration of most young's YAF phase, it is probable that most YAF became separated at least once.

I observed 39 separations of mother and young from the outset. Some of these did not extend to the two moving to different subgroups. In these cases separation was defined by the young or the mother behaviourally indicating their uncertainty of the position of the other by, for example, calling and 'checking the identity of others nearby'. I distinguished four basic patterns in the occurrence of separations.

1. 18 occurred by the mother hopping away and the young not following. Of these, 2 involved a mother being courted and 1 involved a mother interacting with a foreign young and then hopping away leaving her very small pouch-infant behind.
2. 7 occurred with the young interacting with another and then appearing uncertain as to who or where its mother was.
3. 9 occurred because the young followed other kangaroos who were leaving a group, but the mother did not immediately do so too.
4. 5 occurred during a disturbance, and the mother and young either went in different directions or the young left and the mother did not.

Accordingly, movement of the mother away from her original position was the commonest cause of a separation (46%). Young of all ages, from pouch-infants to YAF almost weaned, were separated in this manner (table 82). However, the type 2) separation was predominantly seen in pouch-infants, and the type 3) separation included pouch-infants and young who had recently emerged permanently. Possibly YAF are more likely to be separated by failing to follow their mother when she moves away or by a disturbance. Pouch-infants are typically carried inside the pouch when the mother moves between groups and they

Table 82: *Frequencies of separation for young of different classes or sex.*

	Mother moved away	young interacted with another	young followed another	following a disturbance
<i>PY</i>	1	5	2	1
<i>PEP</i>	3		6	1
<i>YAF (age by month post-PEP)</i>				
<i>I</i>	7		1	
<i>II</i>	1	1		
<i>III</i>	4			
<i>IV</i>	1			
<i>V</i>	1			1
<i>unknown</i>		1		2
according to sex of young:				
<i>male</i>	10	2	6	2
<i>female</i>	8	3	3	1
<i>unknown</i>	0	2	0	2

quickly return to the pouch during a disturbance. However, my data set is too sparse to test for these differences between young of different ages statistically.

Overall, I would suggest that, as compared to YAF, pouch-infants may have a less strongly defined sense of who their mother is or at least where she is positioned in the environment. I discuss this hypothesis further in section 6.5. Since YAF are more likely to become ‘lost’ by not following their mother when she moves away, and since they are probably ‘lost’ at least once during their YAF stage, separation may be correlated with most YAF’s increased responsibility in maintaining a close proximity to their mother (section 6.5) (Hinde and Davies, 1972). In the next section I look at whether inter-subgroup separation becomes more frequent following the young’s permanent emergence because mothers might become less active in seeking their separated YAF.

6.4.2 Reunion

The mother and young may both take an initiative in relocating the other after a separation. I watched 176 reunions. There appeared to be several tactics a partner could use in increasing the probability of a reunion.

1. both mother and young could return to the location where they were last together. I observed 21 cases of separation followed by a reunion, excluding cases where the mother was observed immediately hopping to an errant young following the wrong

kangaroo. Of these 21, 14 (66%) involved the young and mother returning to the spot where they were last together. Young of all ages were observed to do this (1 pouch-infant, 8 small YAF, and 3 large YAF).

2. lost young will check kangaroos in the vicinity by hopping toward them, especially if these individuals move, and by stretching their nose toward the kangaroo. Forty-six young were observed doing this and 14 were observed following others. Mothers too will 'check the identity' of young in the vicinity by 'nose stretching' toward them. I observed fewer instances of this behaviour in separated mothers than in young, possibly because mothers were more visually discerning in identifying their young than were the young in identifying their mothers.
3. both mother and young will call intermittently while separated. Almost all lost young called; but I am invoking a tautology as I have used this behaviour in defining a 'lost young'. The mothers were heard to call in 30% (53/176) of the observed reunions. There are possibly two types of maternal calls. One is the soft "chkk chkk" previously mentioned (section 6.2), and the other is a very loud cough call. This latter call I heard given by only two females, who were travelling widely over their home range calling, unaccompanied by males or by their young.

On the two occasions when I saw a pouch-infant become caught on some barbed wire, the young called continuously. On both occasions the mothers were close, but other kangaroos in the vicinity and up to 100m away hopped to the infant. Both adult males and females responded.

In order to investigate whether a mother and young's reunion strategies change with the age or sex of the young, or the season of separation, or the 'type' of mother, I divided the reunions into 4 categories. The categories were:

1. the young called eventually the young hopped to the mother (N=63);
2. the young hopped away from its mother ..., and the mother hopped to the young (the mother might or might not have called) (N=35);
3. the young called and the mother hopped to the young (the mother might or might not have called) (N=53); and
4. the mother called and the young hopped to the mother (N=25).

I have presented the frequencies of these reunion types against the age and sex and 'mother type' separately in table 83. Since type 2) and 3) both involve the mother travelling

Table 83: Frequencies of types of reunion according to the age of the young, the sex of the young and the 'type' of mother.

	Type 1 young calls and relocates mother	Type 2 young hops away mother retrieves	Type 3 young calls mother hops to it	Type 4 mother calls young hops to her	total
age:					
<i>PY</i>	15	9	15	13	52
<i>PEP young</i>	16	5	11	8	40
YAF age: by month post-PEP					
small YAF:					
<i>I</i>	8	5	6	0	19
<i>II</i>	2	6	3	1	12
large YAF:					
<i>III</i>	5	4	8	1	18
<i>IV</i>	7	3	4	0	14
$\geq V$	10	3	6	2	21
<i>total</i>	63	35	53	25	176
sex:					
<i>male</i>	31	22	31	10	94
<i>female</i>	32	13	22	15	82
type of mother:					
<i>'peak only'</i>	28	15	18	6	67
<i>'offpeak also'</i>	35	20	35	19	109

Table 84: *G* tests comparing frequencies of reunion types between young of the sexes, of different ages and of different 'types' of mother. Reunion types 1 and 4 refer to reunions actively brought about by the young, and reunion types 2 and 3 refer to reunions actively brought about by the mother.

reunion type	variables compared	test	df	probability
1&4 vs 2&3	age: pouch-infants PEP young small YAF large YAF	$G=4.741$	3	$p > 0.1ns$
1&4 vs 2&3	sex: males females	$G=3.299$	1	$p > 0.05ns$
1&4 vs 2&3	mother: peak only offpeak also	$G=0.024$	1	$p > 0.1ns$

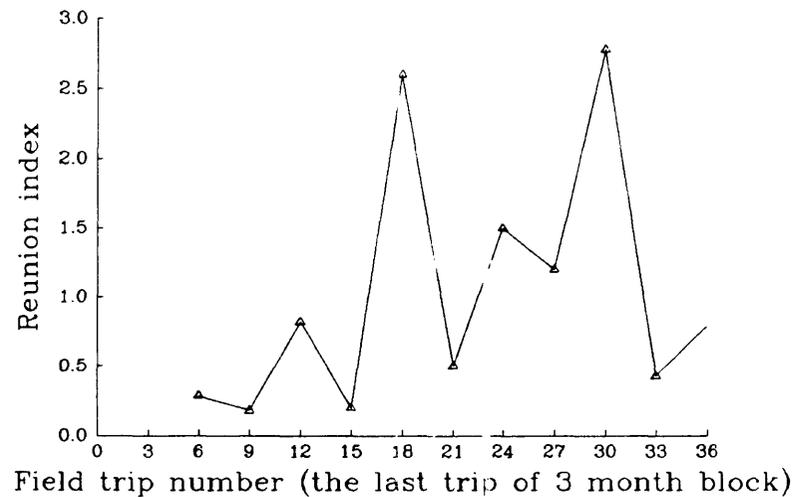


Figure 80: *Reunion index calculated from 3 month blocks related to the relevant field trip dates. The reunion index was calculated by all reunions initiated by the mother over all initiated by the young.*

to the young and consequently expending energy and time in initiating the reunion, I combined them, against the types 1) and 4), and tested for significant differences over the age or sex of the young or the 'mother type' (table 84). The test results were nonsignificant. To check for a relationship between the type of reunion and the season, I used the following index of reunion types: $(1+4)/(2+3)$. The index did not vary consistently with season (fig. 80), but it was significantly correlated to the percentage of young in the study area who permanently disappeared in each 3 month block ($R^2 = 0.439$, $\%Disp. = 2.76 + 35.47x(R.Index) - 11.02(R.Index)^2$, linear $p = 0.039$, quadratic $p = 0.049$, fig. 81). Young were more likely to be permanently lost when the mothers were initiating a smaller proportion of the reunions.

In sum, the mothers were not necessarily responding to their lost young's calls in a uniform manner. However, the increased separation (mother and young in at least different subgroups), for YAF as compared to pouch-infants does not appear to have arisen because the mothers of YAF were any less active in seeking their young compared to mothers of pouch-infants. The difference may be caused by the mothers of pouch-infants moving less, and not changing subgroups while their pouch-infant is out of the pouch. I look at the

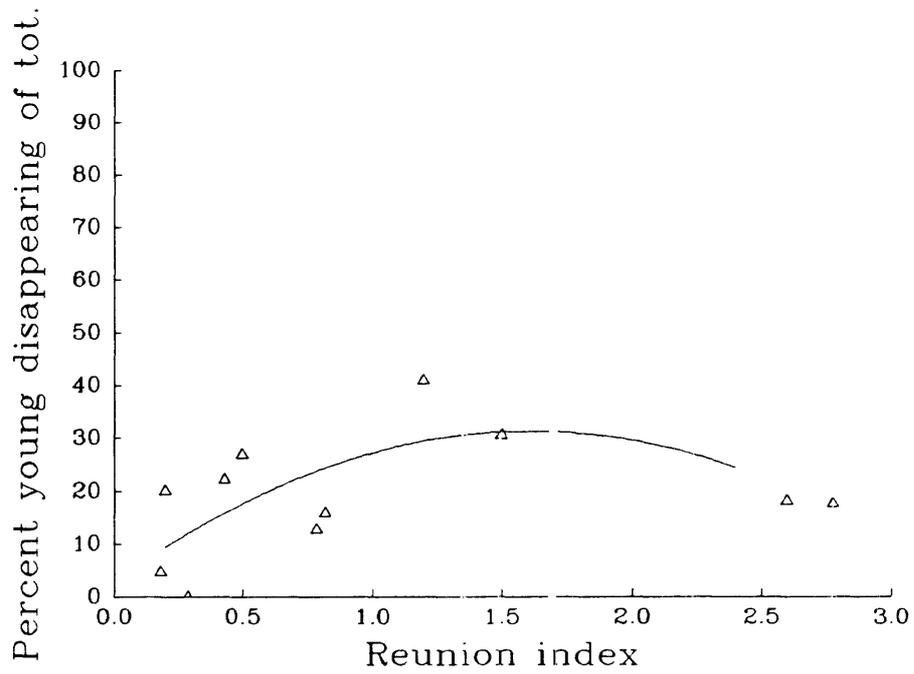


Figure 81: *Reunion index calculated from 3 month blocks and related to the percentage of young who disappeared in that 3 month block. The continuous line represents the equation which best-fitted the data, see text.*

mothers' rate of movement in section 6.5.

I have previously suggested (section 3.5) that the increased permanent loss of young which occurred in the middle of my study may have been related to a reduction in the condition of the mothers. If this is true, it may have been mediated in part by a reluctance of mothers in poor condition to seek lost young actively. It would be worth while investigating the extent of the effect of a mother's condition on the mother-young relationship.

6.4.3 Identification

A series of elegantly structured experiments are really required for discerning what type of cues mother and young respond to when locating and identifying each other. Previous research in this area for eutherians is quite varied in the findings (Lent, 1975; Lillehei and Snowdon, 1978; Cheney and Seyfarth, 1982; Wolski *et al.*, 1980; Walser *et al.*, 1984). However, from the kangaroos' behaviour in the field I can make a few inferences.

Firstly, I doubt that they use visual cues to make an identification at an individual level, as both mothers and young, when separated, approach others and 'nose-stretch' toward them. Mothers then cuff the young if it is not theirs or accept it if it is. The behaviour of the young, especially if it is a pouch-infant, subsequent to a 'nose-stretch' appears to rely on its reception by the other. YAF probably can discriminate their mothers from other kangaroos by smell. Both mothers and young respond to each others' vocalisation, but I am not able to infer whether they respond to any vocalisation of the relevant class when separated, or whether they can use a vocalisation to identify each other.

Although visual cues may be used in identifying individuals at a relatively gross level only, the spatial position of an individual appears to be very important to a kangaroo. After a separation, mothers and young readily return to the location where they were last with each other. Young often appear to consider themselves separated when their mother changes her position within a subgroup. Pouch-infants, especially, appear to rely on a mother's spatial location within a subgroup while making rapid hopping excursions around the subgroup. These infants typically maintain particular routes to and from the mother. Pouch-infants easily become confused if another kangaroo interacts with them while they are on a hopping route (see previous subsections).

Thus I suggest that the mother's stability of spatial position may be particularly important to a pouch-infant's identification of its mother. YAF may have to monitor their mother's movements continually. I explore the mother's rate of movement against the age

of her young in section 6.5. Such a difference between pouch-infants and YAF in the way they identify their mothers would have important consequences for the permanent emergence stage, and may be a contributing factor in the pair's isolation at this time. Young were particularly likely to follow the wrong kangaroo around the time of their permanent emergence.

6.5 Spatial relations of mother and young

Studies of who initiates and terminates the spatial positions in a mother-offspring pair may be used in identifying periods when conflict between mother and offspring might be particularly prominent in a relationship (Trivers, 1974; MacNair and Parker, 1978; Parker 1985). The spatial relationship of mother and young can be quite dynamic, varying in form as the young ages, and between mother-young pairs according to the sex of the young or a wide variety of environmental variables (Altmann, 1980; Hinde, 1976; Nash, 1978; Rosenblum, 1974; Guinness *et al.*, 1979; Johnson, 1985; Bolwig, 1980; Dolhinow and Murphy, 1982; Lee, 1984a; Berman, 1980). There is some dispute as to how significant the environmental variables are in affecting mother-young spatial relations (Johnson and Southwick, 1986; Simpson *et al.*, 1986; Locke-Haydon, 1984) as compared to the effect of species-specific developmental mechanisms. This means that the opportunity for parent-offspring conflict in the relationship may not be as great as earlier researchers (Ransom and Rowell, 1972; Hinde and Spencer-Booth, 1967) had intimated.

Nevertheless, there are differences within species: for example, the spatial relations between mothers and sons versus daughters has not been found to be consistently different within various primate species (Bolwig, 1980; Lee, 1984a; Rosenblum, 1974; Altmann, 1980; Nash, 1978; Hinde and Spencer-Booth, 1967). Behavioural flexibility on the part of the mother should enable her to invest differentially in young according to her condition and, perhaps, her strategy of offspring production (chapter 1). However, flexibility in a mother's behaviour might also be associated with some parent-offspring conflict (Altmann, 1980).

Conflict is most likely to arise in the mother-young relationship of the eastern grey kangaroo during the stage of permanent emergence, with mothers increasing their rejections of the young's frequent attempts to 'suck' or dive into the pouch. The duration of pouch-life varies considerably, especially for male pouch-young. Furthermore, as male pouch-infants show greater orientation toward the pouch than females, conflict at permanent emergence

might be more apparent within the spatial relations of sons and mothers than of mothers and daughters.

However, according to one current hypothesis, when the environment is particularly hazardous mothers are likely to be more responsible for maintaining close spatial relations (Johnson and Southwick, 1986; Simpson *et al.* 1986). This could be extended: mothers may be more responsible for maintaining close spatial relations during the periods of the young's ontogeny with the highest probability of loss of the young, which would be at permanent emergence in the eastern grey kangaroo.

Do mother kangaroos determine the spatial relations at permanent emergence by increasing or decreasing the spatial distance between themselves and their young? A third possibility is that the young might determine the date of permanent emergence. The young might have to learn to change from 'sucking' frequently for short durations to sucking on only a few occasions per day, but for longer durations. The mother might be responsible for this behavioural change in the young by increasing the percentage of suckling bouts she terminates (section 6.3), but the relationship between mother and young may not necessarily involve conflict. In this case, the rate of contact attempts made by the young and terminated by the mother around permanent emergence should not be related to the duration of the young's pouch-life. However, if conflict can be a significant part of the relationship at this time, I would expect it to be greater within pairs in which the young is emerging after a short pouch-life than in pairs where the young had a long pouch-life.

The approach of weaning might also be marked by increasing conflict in the spatial relations of the mother and young (Altmann, 1980; Taber and Thomas, 1982). If conflict is involved, it might be greater between mothers and sons than mothers and daughters. I suggest this because male subadult grey kangaroos were found to associate less with their mothers than were the female subadults (chapter 4). It is possible that this difference between the sexes might be related to a greater rate of spatial leavings by the mothers of sons than daughters.

In order to discuss the ontogeny of spatial relations in the mother-young pairs of the eastern grey kangaroo and differences according to the sex of the young, I first describe separately the average distance between mother and young, and the time mother and young spend in each of four spatial positions, then describe who initiates and terminates these four spatial positions, the mother's movement rate, and the mother's behaviour while her pouch-infant is more than 10 metres from her. The data analysed in this section, as for much of the

Table 85: Mean distances between mother and young. Means have been calculated for the sexes and for the classes of young separately. The units are metres.

females classes	Pouch Young						YAF					
	medium to large			very large to PIP			small			large		
	11 → 13			14 & 15			16			17 & 18		
	\bar{x}	SE	N	\bar{x}	SE	N	\bar{x}	SE	N	\bar{x}	SE	N
males	1.4	0.58	6	1.8	0.709	7	3.5	0.80	5	4.8	1.13	8
females	1.5	0.30	8	1.9	0.39	6	4.4	0.31	6	4.2	1.22	7

as measured by mean distance between mother and young when first sighted (not average of individual pairs' averages)

	Year	YAF	
		small	large
males	1982	4.78	3.7
	1983	3.4	4.9
	1984	4.0	4.8
females	1982	3.2	4.3
	1983	2.9	4.7
	1984	4.1	4.9

data analyses in the previous chapter, were gathered during observation periods in which the mother and young were not resting.

6.5.1 Average distance between mother and young

The average distances between mother and young for various classes and both sexes of young are presented in table 85. Pouch-infants spend a high proportion of their time 'sucking', and consequently they average a close distance to their mother. After permanent emergence, mother and young are on average further apart, but only by 2 to 3 metres. There were no consistent differences between the sexes of young. However, averages can obscure meaningful variation, within and between pairs, so on the basis of these results I have divided the mother and young spatial positions into four exclusive categories: contact, less than or equal to 2m, less than or equal to 10m, and greater than 10m.

6.5.2 Average bout durations and percentage of total time spent in each of four spatial categories

Once pouch-infants reach class 12 they hop quite adeptly, and therefore are able to

Table 86: Mean durations of bouts mothers and infants spent in each of 4 spatial categories. The spatial categories are mutually exclusive; 'cntc' refers to the category in contact. The number of individuals used to obtain the means (of their averages) are presented in brackets (*N*) to the left of the means. Since some YAF were not observed in a particular spatial category, the sample size did not include these individuals. In these cases the relevant sample size is presented in brackets immediately to the left of the appropriate mean. Units are seconds.

class	sons:					daughters:				
	(<i>N</i>)	cntc	< 2m	< 10m	> 10m	(<i>N</i>)	cntc	< 2m	< 10m	> 10m
<i>v. small</i>										
PI	(1)	50.4	6.4	-	-	(1)	8.8	4.8	-	-
<i>small</i>										
PI	(1)	10.5	8.2	-	-	(6)	13.7	9.4	3.1	-
<i>medium</i>										
PI	(7)	35.5	12.2	6.7	0.8	(7)	20.6	12.2	11.0	4.8
<i>large</i>										
PI	(4)	24.0	18.2	17.7	5.1	(4)	13.3	17.4	13.1	11.4
<i>v. large</i>										
PI	(7)	44.1	26.4	26.8	27.2	(6)	33.8	36.0	23.4	22.9
PEP										
<i>young</i>	(3)	29.3	58.9	32.6	31.8	(3)	39.1	42.8	29.7	26.1
months past PEP										
0	(4)	36.3	189.7	184.0	(3)143.3	(2)	4.9	234.7	156.2	-
I	(4)	10.2	(5)163.9	(5)328.9	(2)285.5	(4)	14.9	(5)237.3	(5)526.7	(2)18.5
II	(2)	3.8	(4)129.1	(4)592.2	(3)5.8	(5)	58.2	317.9	230.4	(4)401.7
III	(2)	30.3	(4)226.1	(4)210.2	(4)195.6	(1)	2.0	(4)266.9	(4)190.6	(1)822
IV	(3)	6.8	(4)192.5	(4)189.3	(3)413.9	(3)	5.3	132.6	267.6	(1)6.0
V	(3)	2.9	142.2	326.2	354.9	(2)	38.8	28.4	244.0	(1)289.0
VI	(1)	-	164.0	1676	-	(2)	78.8	36.9	237.3	218.8

Table 87: The percentage of total spatial transitions observed that were initiated by mother and by the young. Data for pairs of mothers and young are presented separately according to the sex of the young. G tests comparing frequencies for different classes are included. Also included are G tests comparing for mothers of sons and daughters separately a) classes of infants combined, with both classes of YAF, and b) small YAF and large YAF.

class	no. of spatial transitions	percent initiated by:					
		mother with son	mother with daughter	son	daughter		
r small PI	10	48	79	8%	92%	8%	92%
small PI	11	54	152	19%	81%	17%	83%
medium PI	12	715	1305	12%	88%	11%	89%
large PI	13	819	947	11%	89%	15%	85%
r large PI	14	1463	1122	15%	85%	15%	85%
PEP young	15	567	635	11%	79%	25%	75%
small YAF		397	478	18%	62%	40%	60%
large YAF		396	486	14%	56%	42%	58%

combined χ^2 test on pouch infants and mothers $\chi^2 = 3631.318 p < 0.001*$

Test Variables		Test Statistic	df	p	
mothers and sons:	small YAF vs large YAF	G = 3.104	1	p > 0.05	ns
	pouch infants vs YAF	G = 277.748	1	p < 0.05	*
mothers and daughters:	small YAF vs large YAF	G = 0.694	1	p > 0.05	ns
	pouch infants vs YAF	G = 332.549	1	p < 0.05	*

Table 88: The mean percentage of time spent by mothers and young at various distances (metres) apart. The spatial positions are mutually exclusive: 'cntc' refers to in contact. The means have been calculated from averages obtained from individual mother-young pairs. The number of these pairs is presented in the column to the left of the means (N).

class	(N)	sons:				(N)	daughters:			
		spatial categories					spatial categories			
		cntc	$\leq 2m$	$\leq 10m$	$> 10m$		cntc	$\leq 2m$	$\leq 10m$	$> 10m$
<i>v. small</i>										
<i>PI</i>	(1)	88.7	11.3	-	-	(1)	64.6	35.4	-	-
<i>small</i>										
<i>PI</i>	(1)	56.3	43.8	-	-	(6)	48.3	49.4	2.6	-
<i>medium</i>										
<i>PI</i>	(7)	65.2	30.2	4.4	0.2	(7)	50.2	36.0	11.7	2.1
<i>large</i>										
<i>PI</i>	(4)	41.6	42.0	14.3	1.7	(4)	32.6	51.8	12.7	3.0
<i>v. large</i>										
<i>PI</i>	(7)	51.9	39.9	6.5	1.7	(6)	40.0	53.4	5.2	1.4
<i>PEP</i>										
<i>young</i>	(3)	25.0	63.1	7.3	4.7	(3)	36.2	52.8	9.9	1.0
months past PEP										
<i>0</i>	(4)	3.4	56.0	36.4	4.2	(2)	0.5	82.5	17.0	-
<i>I</i>	(5)	0.7	44.1	44.6	10.6	(5)	0.4	44.6	54.8	0.2
<i>II</i>	(4)	0.2	35.2	64.1	0.5	(5)	1.9	48.4	42.5	7.1
<i>III</i>	(4)	2.7	45.7	37.2	14.5	(4)	0.0	51.1	35.1	13.8
<i>IV</i>	(4)	1.4	49.6	29.5	17.1	(3)	0.7	52.3	46.1	0.1
<i>V</i>	(3)	0.4	40.9	45.9	13.0	(2)	4.0	33.3	59.9	2.8
<i>VI</i>	(1)	-	8.9	91.1	-	(2)	0.1	26.1	37.7	12.1

move around their mothers with ease. They do so rather rapidly compared to YAF. This is reflected in the short average durations ($< 1\text{min}$) they spend in the four spatial categories presented in table 86, and their initiation of significantly more spatial transitions ($> 85\%$) between the four spatial categories than their mothers initiate (table 87). This pattern changes rapidly as the young permanently emerges. YAF are far more stable in the position they maintain relative to the mother (2 to 10 minutes per bout), and the mother contributes to about 40% of the transitions instead of 15% or less. I have excluded the durations of contact time in which YAF were sucking when calculating the average contact bout (and also the percentage of time they were in contact) because YAF sucking bouts, being 12 to 20 minutes in duration and infrequent, considerably distorted the individual's averages, from which I calculated the gross class averages.

Sons and daughters, regardless of their age, initiate a very similar percentage of spatial transitions from their mother (table 87).

The percentages of time mother and young were observed within each of the four spatial

Table 89: Tests comparing the percentage of time (%Sq) mothers and sons versus mothers and daughters spent in different spatial positions apart. As this % of time changes with class of the young I include a test comparing the slopes of the linear best-fit equations which describe the change in contact association. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

best-fit equations:		probability	t test comparing slopes
sons	%Sq = 177.9 - 9.6(class)	0.003*	t=0.437 df=46 ns
daughters	%Sq = 97.2 - 4.2(class)	0.070†	

Mann-Whitney U test comparing sexes for class 12 infants			
% time spent in contact			
U=15	N ₁ = 7	N ₂ = 7	p > 0.1ns
% time spent less than 2 metres and out of contact			
U=17	N ₁ = 7	N ₂ = 7	p > 0.1ns
% time spent between 2 and less than 10 metres			
U=10	N ₁ = 7	N ₂ = 7	p < 0.1†
% time spent 10 metres or further			
U=3	N ₁ = 7	N ₂ = 7	p < 0.1*

positions are presented in table 88. Separate calculations are given for the different classes and according to the sex of the young. Pouch-infants spend 50% or more of the time in contact with their mother. Males spend significantly more time 'sucking' (section 5.2); they also averaged consistently more time than daughters in contact. However, the difference was not significant when comparing best-fit linear equations or by a Mann-Whitney U test comparing differences between the sexes of class 12 pouch-infants (see table 89). In contrast, medium sized pouch-infant daughters (class 12) were spending a *significantly* greater percentage of their time more than 2 m from their mother than sons were (table 89). There is a similar trend for small pouch-infant daughters to spend more time further from their mothers than sons.

After permanent emergence the young spends less than 4% of its time in non-sucking contact with the mother, and typically less than 17% of its time further than 10m from the mother (table 88). Thus, while the young has increased its radius of concentrated activity from the mother, it still predominantly remains in close proximity to her. However, large YAF males are now more adventuresome than are the daughters, as these sons spend significantly more time further than 10m from the mother (MWU test $U = 38$, $N = 12$, 11 , $p < 0.1$).

In general, the spatial positions between a mother and young change rapidly during permanent emergence. Compared to pouch-infants, YAF initiate fewer movements around their mothers and spend less time in consistent high frequency contact. There are significant

differences between the sexes in their spatial positions from their mother. Daughters while small to medium pouch-infants spend more time away from their mother than sons do, but a reversal later occurs, and by the time they are large YAF the reversal is significant.

6.5.3 Initiation and termination

Who is responsible for the various mother-young spatial positions I have just described? Since the observations I obtained were too short to analyse the frequency of spatial-state terminations on an individual level, especially for YAF, I combined the frequencies into class-related data.

In order to comprehend an overall picture of the changes in the responsibilities of the mother and young in their spatial relations, I have calculated Hinde and Atkinson's proximity index (1970, see section 6.3) for each class and by sex of the young. The results are presented in figs. 82 and 83. Since pouch-infants move around their mothers at a high rate, the index varies little from zero until permanent emergence, when the young and mother initiate spatial transitions at more similar rates.

In spite of the infant's considerable activity, mothers can play a significant role in determining the spatial relations (Hinde, 1979; Altmann, 1980; Simpson *et al.*, 1986). The indexes for pouch-infant sons and daughters lie toward the mother terminating more 'contact' and 'further than 10m' spatial positions than she initiates. Simultaneously, the mother initiates more spatial positions in the 'less than 10m' and 'less than 2m' categories than she terminates. Thus, mothers appear to be maintaining the spatial association with their infants at a position less than 10m but not in contact.

Just prior to permanent emergence the mother begins to terminate contact to a greater extent, and thereby initiates even more positions in the 'less than 2m' and 'less than 10m' categories. This was particularly apparent for mothers of very large pouch-infant sons. As sons had been in contact with their mothers more than daughters when small to medium pouch-infants, the difference is probably not an anomaly.

At permanent emergence mothers are still terminating more of the 'greater than 10m' positions than they are initiating. However, they soon cease doing this for small YAF sons, although they continue to move toward their small YAF daughters when they are more than 10m away. In general, the mothers of YAF sons and daughters show quite striking differences. Mothers of YAF sons continued to terminate more of the contacts with their sons, just as they did at permanent emergence. Also, they terminated more of the 'less than

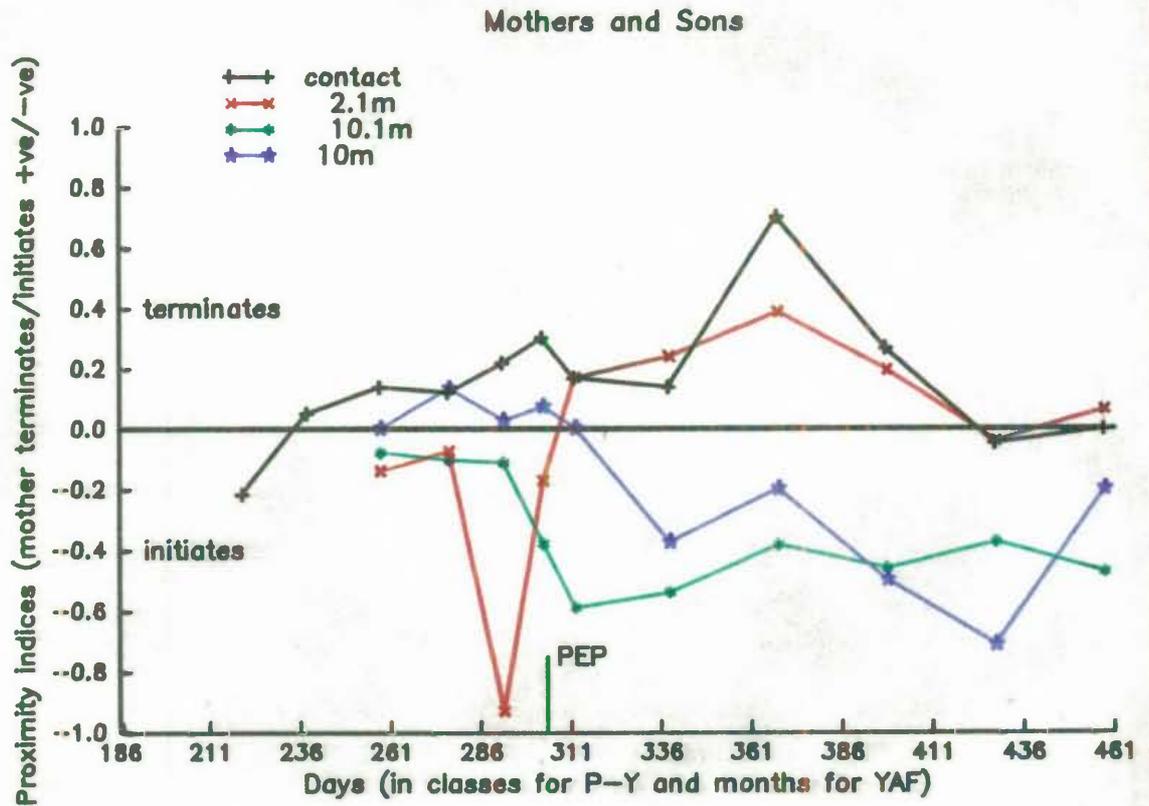


Figure 82: Values of Hinde and Atkinson's proximity index for mother and son pairs according to the age of the son and for different spatial positions. The spatial positions are mutually exclusive. When the index is positive the mother is terminating more of the bouts in that spatial position than she initiates. When the index is negative the mother is initiating more than she terminates. See text for details.

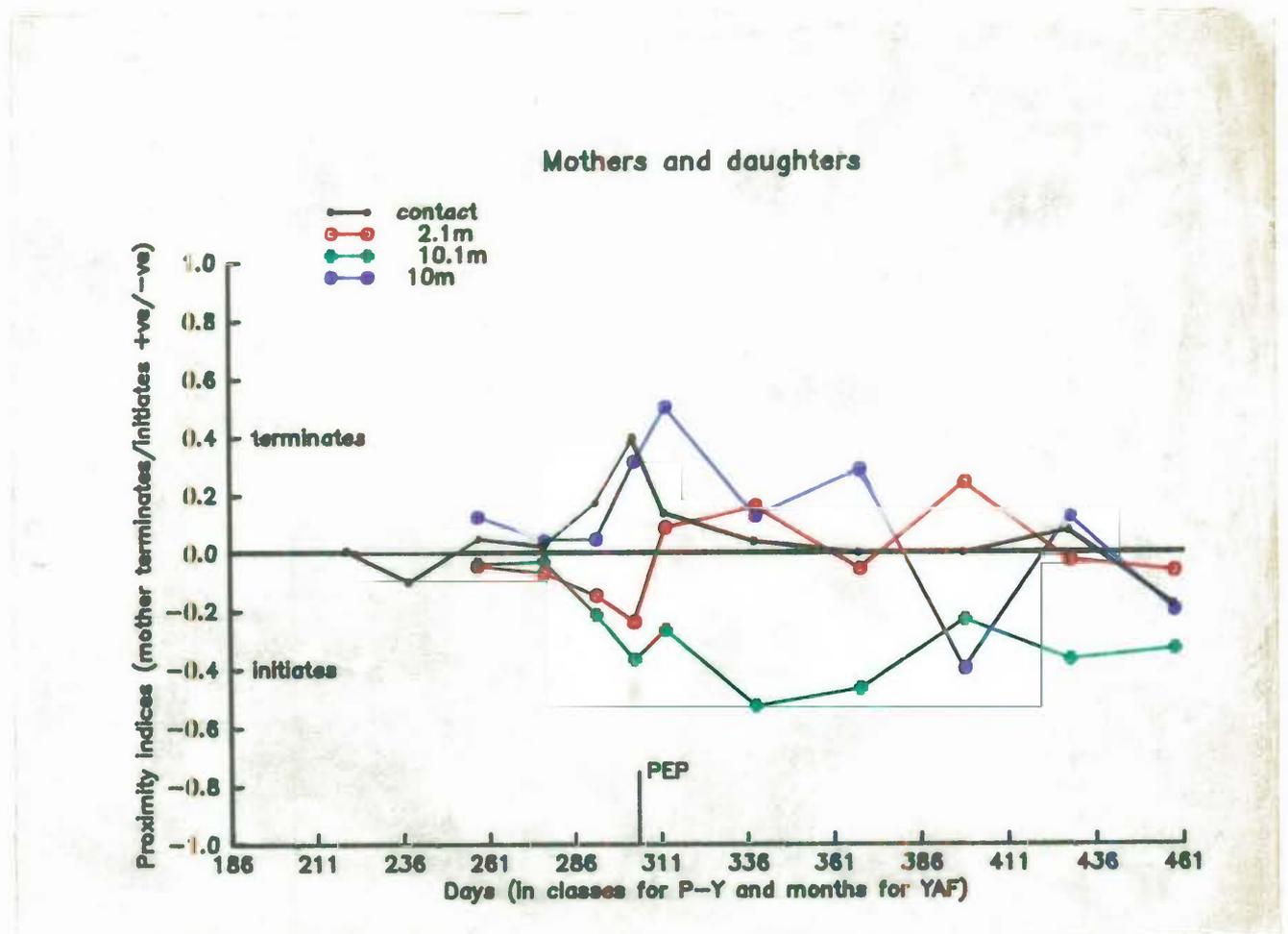


Figure 83: Values of Hinde and Atkinson's proximity index for mother and daughter pairs according to the age of the daughter and for different spatial positions. The spatial positions are mutually exclusive. When the index is positive the mother is terminating more of the bouts in that spatial position than she initiates. When the index is negative the mother is initiating more than she terminates. See text for details.

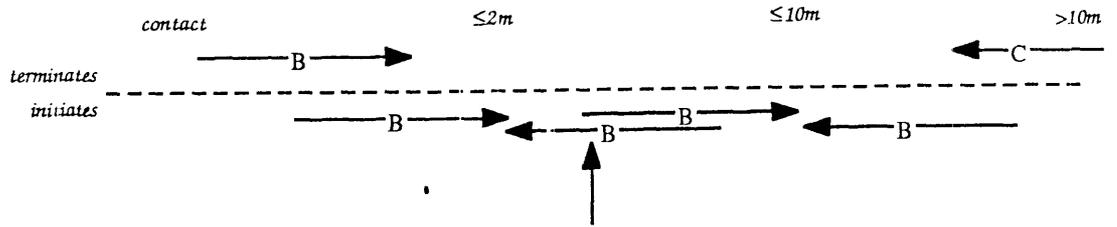
2m' positions than they initiated, and initiated more of the 'less than 10m' and 'greater than 10m' positions than they terminated. Mothers of YAF daughters initiated about as many of the 'contact' and 'less than 2m' positions as they terminated. While they initiated more of the 'less than 10m' positions than they terminated, they terminated more of the 'greater than 10m' positions than they initiated.

I have provided a rough schematic review of the spatial relations just described in figure 84. The approximate point of stability in the pairs' spatial positions increases in distance as the young ages, particularly for sons.

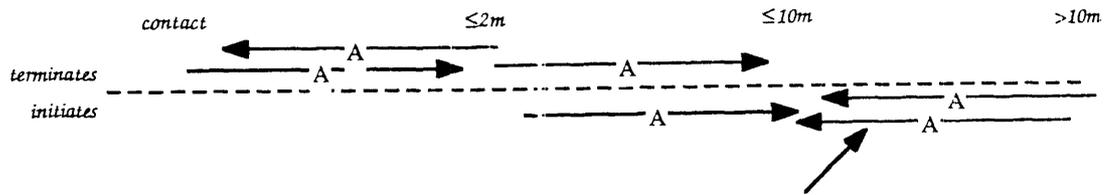
The mother's behaviour is possibly a contributing force in the differences in her YAF son's and daughter's spatial relations with her. However, it is not obvious from my data that mothers encourage pouch-infant daughters to be further from them than pouch-infant sons. The differences between sons' and daughters' spatial relations with their mother are significant according to G tests on the frequencies with which young move away from, rather than towards, their mother (table 90). G tests on the frequencies with which mothers move away from, rather than towards, their sons and daughters (table 90) substantiate the mother's greater role in determining the spatial position of her YAF than of her pouch-infant. Further, there was no significant difference between the best-fit equations for the contact proximity indices of mothers of pouch-infant sons and daughters against age of their young (table 89 and fig. 85). Thus, the greater contact and sucking of pouch-infant sons than daughters (sections 5.2 and 6.5.2) is either subtly initiated by the mother or is genetic in origin. The frequency of contact bouts per minute for daughters was very similar or slightly greater to that of sons (fig. 86), but the duration of contact bouts was not so similar in appearance (table 86). This is worth investigating further. Unfortunately my data set is too small for further analysis.

I suggested in the introduction to section 6.5 that conflict might be particularly apparent in mother-young spatial relations at permanent emergence. However, an alternative interpretation could be that the young was just in the process of learning to follow the mother around her home range rather than dive into the pouch. Thus, I predicted that if a conflict of interests was involved, then the young with short pouch-life durations should exhibit high levels of initiating contact, with their mothers terminating it, as compared to the mother initiating contact or the infant terminating it, i.e. they should have high scores on Hinde and Atkinson's proximity index for contact compared to young with long pouch-life durations. This assumes that young with long pouch-life durations are likely to gain

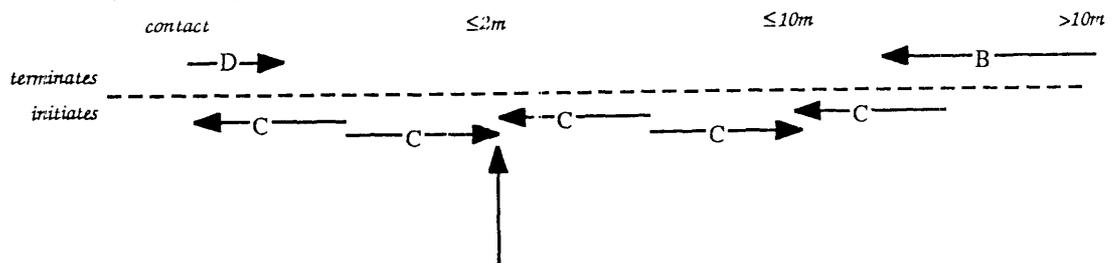
*Mothers of pouch
infant sons*



YAF sons



Pouch-infant daughters



YAF daughters

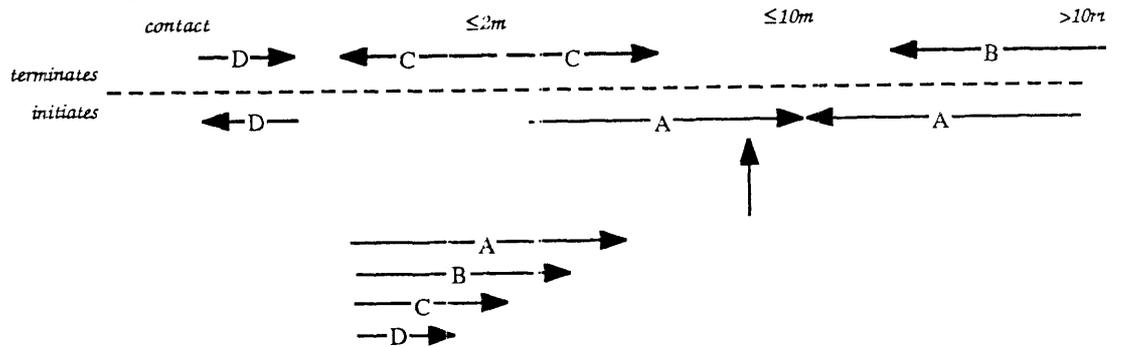


Figure 84: A schematic review of the mother-young spatial relations for mother-young pairs according to the sex of the young and whether it was an infant or a YAF. The approximate point of stability, that is the spatial position toward which the mother tends to approach more than she terminates is indicated by the vertical arrows below the arrows which indicate the direction of a mother's tendency to move between two spatial positions. The length of these latter type of arrows (the arrows are named according to their length: $A > B > C > D$) roughly indicates the relative strength of the mother's movement. The oblique arrow is used for mothers of YAF sons because the general direction appears to be away from the son rather than stabilising at some particular distance.

Table 90: *G* tests and frequencies for comparing the degree the young and mother move away from or toward each other, for different classes of young and according to the sex of the young. The frequencies refer to the spatial categories: ≤ 2 metres, ≤ 10 metres, and >10 metres, separately. *G* values with probabilities less than 0.05 are presented as *, otherwise the *G* value was deemed not significant (ns).

young	spatial categories:							
	infant moves:				mother moves:			
	$\leq 2m$		$\leq 10m$		$\leq 2m$		$\leq 10m$	
	away	to	away	to	away	to	away	to
medium PI								
sons	65(22%)	234	3(3%)	85	5(18%)	23	0	0
daughters	188(35%)	346	12(6%)	190	8(14%)	48	0	5
	<i>G</i> =16.968*				ns			
large PI								
sons	85(26%)	248	15(14%)	95	11(9%)	12	1(25%)	3
daughters	104(28%)	271	12(10%)	103	17(19%)	33	3(21%)	11
	<i>G</i> =0.433ns		<i>G</i> =0.557ns		<i>G</i> =1.300ns			
very large PI								
sons	88(15%)	483	11(13%)	73	17(50%)	17	0	4
daughters	103(22%)	375	20(15%)	110	25(52%)	23	0	5
	<i>G</i> =6.555*		<i>G</i> =0.200ns		ns			
PEP young								
sons	25(11%)	195	5(13%)	35	14(67%)	7	0	2
daughters	47(18%)	215	7(10%)	61	8	0	5	
	<i>G</i> =4.144*		<i>G</i> =0.131ns		<i>G</i> =0.623ns			
SYAF								
sons	37(46%)	44	5(5%)	87	72(84%)	14	7(39%)	11
daughters	32(35%)	60	11(10%)	95	70(66%)	36	6(23%)	20
	<i>G</i> =2.136ns		<i>G</i> =1.665ns		<i>G</i> =8.162*		<i>G</i> =1.266ns	
LYAF								
sons	25(35%)	46	4(6%)	67	61(66%)	32	16(64%)	9
daughters	49(49%)	50	7(7%)	89	69(58%)	51	5(18%)	22
	<i>G</i> =3.460*		ns		<i>G</i> =1.449ns		<i>G</i> =11.605*	
spatial category: >10m								
	all PI		SYAF		LYAF		all classes	
	frequencies of who terminates this category mother (m) or young (y):							
	(m)	(y)	(m)	(y)	(m)	(y)	(m)	(y)
sons	7(8%)	80	6(35%)	11	6(21%)	23	12(26%)	34
daughters	17(12%)	121	9(53%)	8	6(33%)	12	15(43%)	20
	<i>G</i> =1.059ns		<i>G</i> =1.081ns		<i>G</i> =0.916ns		<i>G</i> =2.507ns	

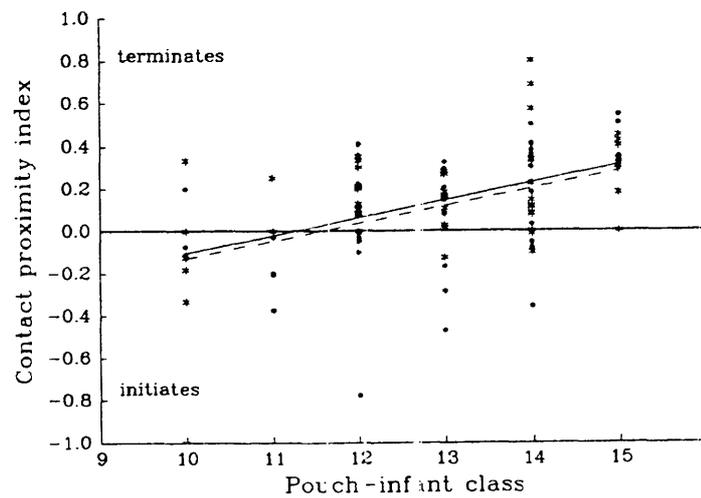


Figure 85: Values and the best-fit equations describing the relationship between the contact proximity (CP) indices for sons and daughters and their class. Sons values are depicted by stars and the equation by the continuous line. The best-fit equation was:

$$CPindex = -0.934 - 0.083(class).$$

The probability was < 0.001 . The R^2 was 0.258. Daughters values are depicted by solid circles and the equation by the broken line. The best-fit equation was:

$$CPindex = -0.948 + 0.082(class).$$

The probability was < 0.001 . The R^2 was 0.206.

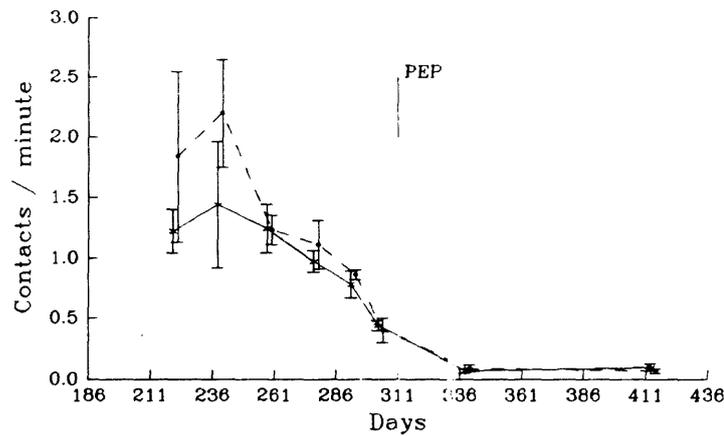


Figure 86: *The relationship between sons' and daughters' rates of contact with their mothers against their age. The sons means are represented by the stars connected by the solid line. The daughters means are represented by the solid circles connected by the broken line. Standard errors are included.*

little from increasing their stay in the pouch. Further, as sons typically have more variable pouch-life durations (section 3.6), I believe that an early termination was more likely to be maternally related rather than initiated by the young. The best-fit linear relationship of the contact proximity index against the pouch-life duration for permanently emerging sons is in accord with my prediction, and the daughters' index values showed a similar trend (fig. 87). There were too few points to analyse the daughters' indices against pouch-life duration. There was no significant relationship for large pouch-infant males' pouch-duration and their contact proximity index (fig. 88). This is to be expected if permanent emergence occurs abruptly and conflict is centred on that brief period.

6.5.4 The mother's rate of movement

In general, pouch-infants were more directly responsible for their spatial position than were their mothers. However, I have suggested that young of this age might not have a very strong sense of who their mother is, and may use her spatial position in the local environment to relocate her when on 'play hopping' excursions (sections 6.4). If this is so, then it might be important for the mother to restrict her rate of movement while her young

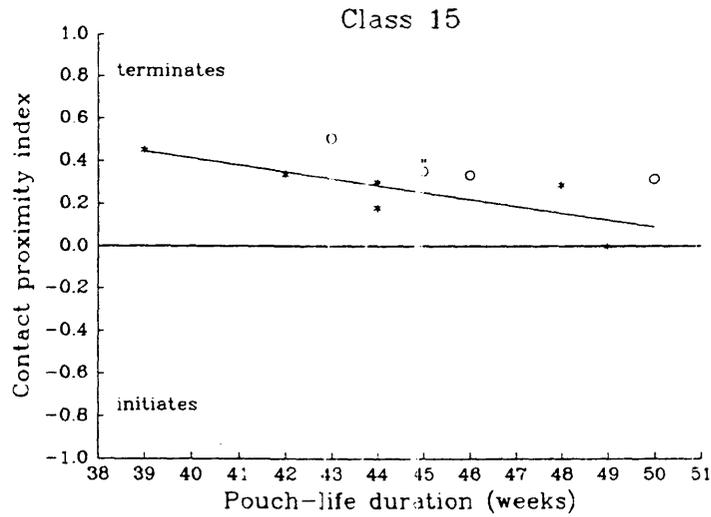


Figure 87: Values (the stars) of and the best-fit equation for PEP sons' contact proximity indices related to their pouch-life duration. The R^2 was 0.520. The best fit equation was: $CPIndex = 1.691 - 0.032(\text{pouch} - \text{life})$. The probability was 0.068. The values for daughters' contact proximity indices are included (open circles). However it was not possible to fit a significant relationship to their few values.

Table 91: Mothers' mean rates of movement according to the season or the sex of their young, and according to whether it is inside or outside the pouch. Units are bouts of walking or hopping per minute.

		offpeak season	peak season	sons	daughters
out of pouch:	sample size	9	5	13	14
	mean	0.38	0.46	0.31	0.53
	SE	0.08	0.13	0.06	0.09
in pouch:	sample size	8	14		22
	mean	0.90	1.20		1.09
	SE	0.17	0.12		0.10

t test comparing season means for mothers with PY inside
 $t=1.565$ $df=20$, $p > 0.1ns$

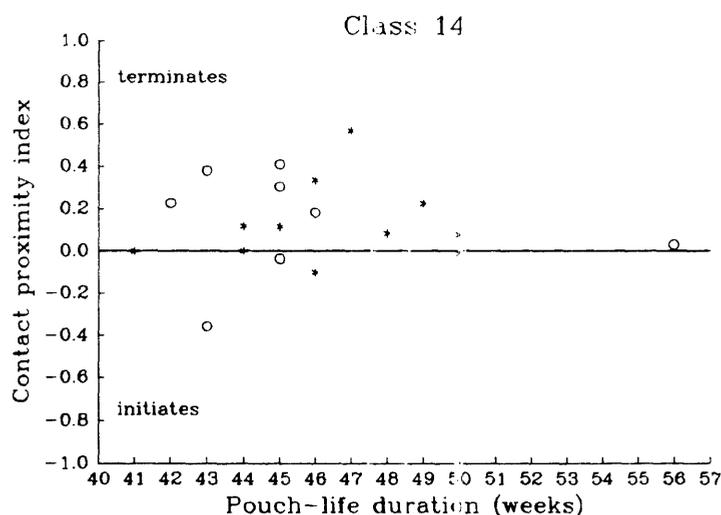


Figure 88: Values of very large pouch-infant sons' (stars) and daughters' (open circles) contact proximity indices related to their pouch-life duration. Significant relationships could not be fitted to the data.

is out of the pouch.

The averages of the various classes of mothers' rates of movement are presented in figure 89; the rates for mothers of sons and daughters are separately given. It was possible to fit significant linear equations to the mothers' rates of movement as they passed through the classes from 'with very small pouch-infant' to 'with large YAF'. The slopes differed significantly between mothers with sons and mothers with daughters (sons: $R^2 = 0.385$, Rate of Move = $-1.030 + 0.116(class)$, $p = 0.000$; daughters: $R^2 = 0.170$, Rate of Move = $-0.427 + 0.070(class)$, $p = 0.001$; slope t test $t = 3.864$, $p < 0.001$). Basically mothers of pouch-infants were moving at a reduced rate, when young were out of the pouch, compared to mothers with YAF, and also compared to their rate when their young was inside the pouch (fig. 89). This latter rate was typically more than twice as fast as the rates for mothers with infants out of the pouch. Mothers may have been maintaining a slow movement rate for daughters at permanent emergence and when small YAF to a greater extent than they did for sons. Mothers did not appear to alter their rates of movement significantly according to the season (table 91).

The rate-of-movement index just discussed, included two types of movement: walking

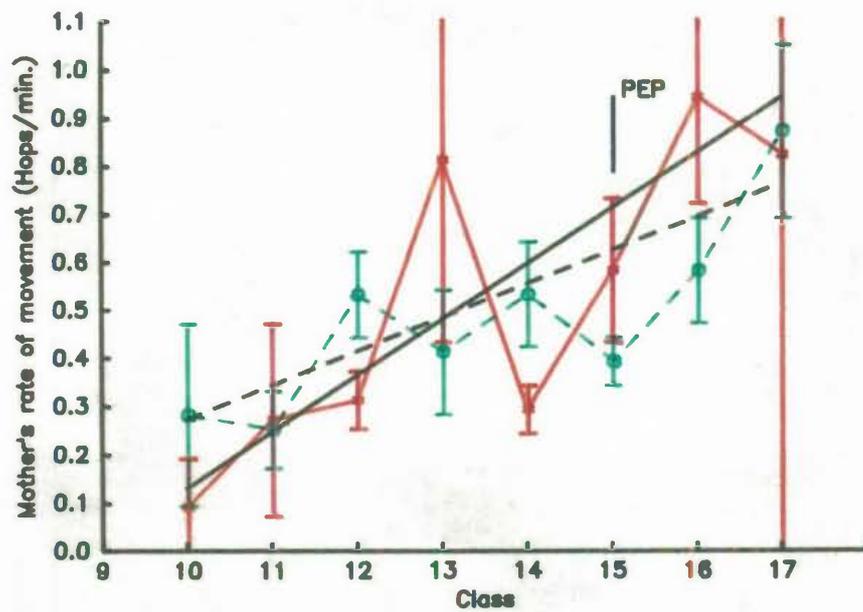


Figure 89: The averages of various classes of mothers' rates of movement. Standard errors are included. The mothers of sons' bouts of walks and hops per minute (H/min.) for each class are presented by the red stars connected by the solid red line. The best-fit equation is represented by the solid black line, see text. The mothers of daughters' bouts of walks and hops per minute (H/min.) for each class are presented by the green circles connected by the broken green line. The best-fit equation is represented by the broken black line, see text.

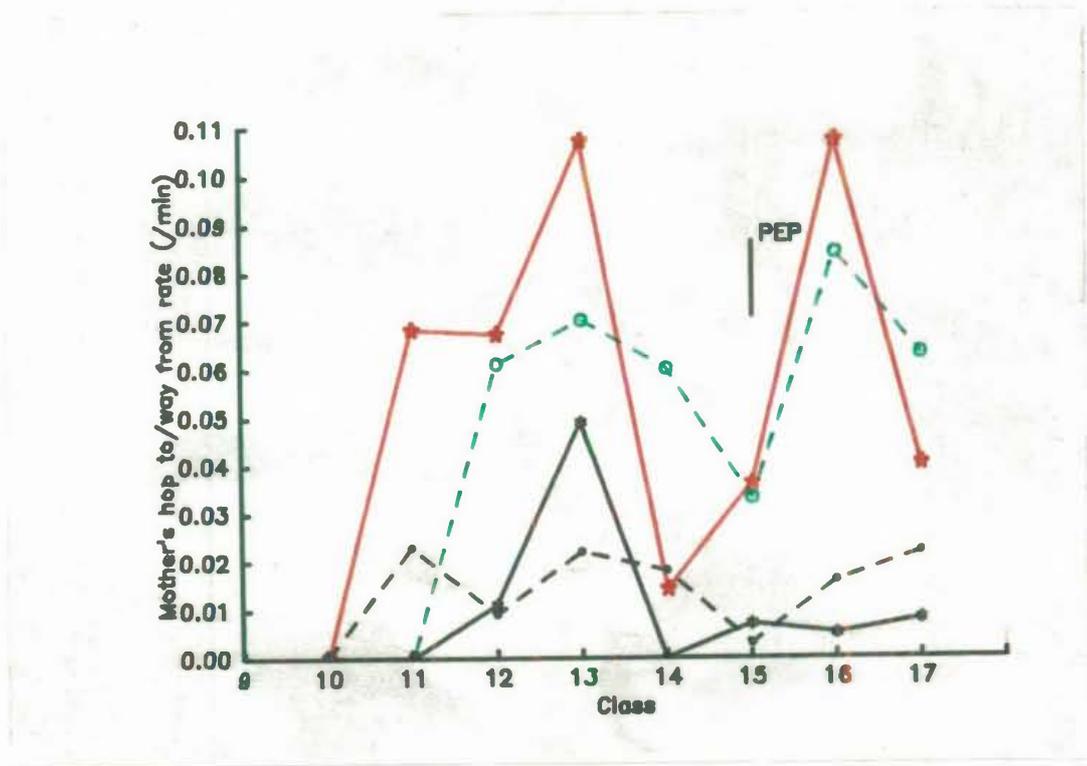


Figure 90: Mothers of sons' and daughters' rates of hopping bouts per minute related to their class for movement towards and away from their young separately. The averages for mothers of sons are presented by: the red stars connected by the solid red line for movement away, and by the black solid line for movement towards. The averages for mothers of daughters are presented by: the green circles connected by the broken green line for movement away, and by the black broken line for movement towards.

Table 92: Means and medians of the distances mothers hop from their infant or YAF. Units are metres. N refers to sample size and \bar{x} refers to the mean. SE is standard error.

class	11	12	13	14	15	16	17&18
	small PI	medium PI	large PI	large PI	PEP young	small YAF	large YAF
<i>mothers with sons:</i>							
N	4	12	11	2	9	28	19
\bar{x}	2.75	6.75	6.55	10.0	5.0	13.32	8.42
SE	0.55	1.76	1.81	7.07	2.054	4.566	1.634
median		3	5		3	8	7
<i>mothers with daughter:</i>							
N		13	16	10	9	30	38
\bar{x}		7.85	14.56	9.90	8.67	9.75	8.95
SE	2.76	3.693	3.830	3.283	1.31	1.12	
median		3	7	4-6	5	8	6

and hopping. I did not weight the hopping movement by the distance travelled, as it could have a variable effect best analysed separately. I was more concerned with the mother's general movement rate over time. However, mothers of pouch-infants might be expected to reduce their rate of hopping, and the distance moved per bout, as well as reducing their rate of movement in general. In fact, mothers with medium sized pouch-infants out of the pouch hopped as much as mothers with small YAF (fig. 90). I combined the data from individuals to obtain the hopping rates, as mothers hop infrequently. Thus I can not test for differences between the classes. However, it seems either that mothers, excepting those with very small infants out of the pouch, do not change the frequency with which they hop (which is very low anyway) according to the age of their young, or that they hop less frequently while their young is permanently emerging as well as when they have a very small pouch-infant who is out of the pouch. The median distances the mothers were hopping increased only slightly with the age of the young (table 92).

Mothers were never observed to lead pouch-infants between groups in the field, although they were observed to lead pouch-infants out of groups, whereupon they would stop and let the infant into the pouch and then hop further away. Further study on the training of infants in following their mothers prior to permanent emergence may reveal some interesting patterns.

Overall, mothers with pouch-infants out of the pouch did significantly reduce their

Table 93: Times (and proportion of records) when mothers surveyed and did not survey, while their infants were more than 10metres from them, and while their infants were out of the pouch in general. G tests comparing the frequencies of these two categories of behaviour for mothers of medium pouch-young and those of large pouch-young or PEP young are included.

	mother's activity state		
	survey	not survey	total
mothers with MPY (classes 11–13)			
when PI > 10m	69 (62%)	43 (38%)	112
when PI out			
all distances:	116 (51%)	113 (49%)	229
<i>G test for independence</i>			
<i>df = 1, G = 3.661 p < 0.1†</i>			
when PI > 10m			
MPY mothers	69 (62%)	43 (38%)	112
LPY &			
PEP mothers	68 (62%)	42 (38%)	110

movement rate compared to mothers with their infants inside the pouch and mothers of YAF. Mothers of small YAF daughters might move less than mothers of small YAF sons. This is consistent with the finding that mothers of small YAF sons moved away from them more than did the mothers of small YAF daughters.

6.5.5 The mother's behaviour when the pouch-infant is at a distance

Although mothers of pouch-infants did not appear greatly responsible for the spatial position of their infant, and they did not move much while the young was out of the pouch, they were monitoring the infant's activities. For example, they surveyed more frequently while the infant was out of the pouch than when it was in the pouch (section 5.2); they would retrieve infants who started to follow the wrong kangaroo or were 'lost' (section 6.4); and they would call the young to dive into the pouch if danger threatened (section 6.2). This surveillance of their infant's activities significantly increased when their infant moved to more than 10m away (table 93).

6.5.6 Discussion

The ontogeny of the spatial relations of the mother and young eastern grey kangaroos is different from any described for eutherian species (Nash, 1978; Guinness *et al.*, 1979; Lickliter, 1984; Taber and Thomas, 1982; Simpson *et al.*, 1986; Altmann, 1980; Berman, 1980; Dolhinow and Murphy, 1982; Byers and Byers, 1983; Shackleton and Haywood, 1984). The typical pattern for many primate species is one of gradual increase in the infant's responsibility for the spatial relations. According to Simpson *et al.* (1986) this slow change probably arises because there are several points of potential conflict in the young primate's ontogeny e.g. the termination of nipple contact, body contact, and close proximity. The occurrence of a hiding phase found in some ungulate species (Lent, 1974; Ralls *et al.*, 1986) and some macropodoid species (Johnson, 1985; pers. obs.) determines quite a different pattern for these species (Lickliter, 1984; Espmark, 1969); the mother is primarily responsible for maintaining proximity initially, but once the hiding phase is terminated the infant becomes highly responsible. In the 'follower' young of ponies (Crowal-Davies, 1986; Tyler, 1972), when the foal is not lying down, almost from birth it is primarily responsible for the spatial position between itself and its mother. The pattern for southern right whales (Taber and Thomas, 1982) involves the mother being primarily responsible for approaching the young until several weeks prior to weaning. The presence of pouch-life with a permanent emergence stage succeeded by a 'follower' type of young in the eastern grey kangaroo possibly determines yet another ontogenetic pattern of spatial relations between mother and young.

Prior to permanent emergence the young is more immediately responsible for its spatial position than its mother is. However, the mother's rate of movement while her young is out of the pouch is considerably reduced, compared to when it is inside or compared to mothers with YAF. This is similar to a pony mare's stability of position when her foal is lying down (Crowal-Davies, 1986). Mother kangaroos also survey more when their infant is at a distance. Thus mothers are indirectly quite responsible for their young's position in the environment. I discuss this further in section 6.10. On permanent emergence, the infant ceases to move around its mother at its previous high rate. There is probably parent-offspring conflict in the relationship, as the mother rejects more of the infant's contacts, particularly of infant sons with short pouch-lives. Compared to sons, there may be overall less potential for conflict to arise between mothers and daughters at permanent emergence, since pouch-life is less variable in its duration. Unfortunately my data set was too small to test for this. But overall, a mother increased the distance between herself and her young

around permanent emergence by terminating more of the young's contacts. Thus contrary to the hypotheses of Johnson and Southwick (1986) and Simpson *et al.* (1986) (see above), the critical time of permanent emergence was not marked by the mother becoming more solicitous towards her young: rather, the reverse occurred. This increased rejection by the mother of her young remained rather high for sons, but not for daughters during the YAF phase. Mothers of daughter YAF even approached their daughters more frequently than their sons when the young moved further than 10m from them. Indeed, mothers of sons were more likely to initiate a distance of more than 10m between them and their sons. Also, mothers of small YAF daughters appeared to maintain a reduced rate of movement compared to mothers of small YAF sons. There was no obvious difference between mothers of YAF sons and mothers of YAF daughters in their tendency to terminate contact.

It is also worth noting that there was little indication by the mother that weaning was approaching.

Finally, daughter pouch-infants initiated more movements away from their mothers, and spent a greater percentage of their time when out of the pouch at distances greater than 10m than did pouch-infant sons. This was not obviously related to a difference in the mothers' behaviour toward sons and daughters. So, while sons were 'sucking' more at this age than daughters (section 5.2), the daughters were making more adventuresome excursions from their mothers. A similar early independence of daughters compared to sons, which is followed by a reversal as the young ages, was also noted by Hinde and Spencer-Booth (1971) for rhesus monkeys.

6.6 Mother-young co-ordination

In chapter 5 I showed that pouch-infants when out of the pouch have very different activity budgets and structure of sequential behaviour compared to their mothers. After permanent emergence the young exhibits a behavioural structure and schedule that closely resembles those of adult females. Consequently, I would expect that, compared to YAF, pouch-infants would be significantly less often in an activity state similar to their mother. But, excluding sucking, are there differences between sons' and daughters' degree of 'co-ordination' with their mother, or differences between seasons?

The percentage of records in which the activity states of young and mothers matched are presented in table 94 for pouch-infants, small YAF and large YAF, sons and daughters. As

Table 94: Percentage of the young's activity states which matched their mothers', analysed by age and sex of the young. Tests comparing sons' and daughters' data from summer and winter and for young of different classes are included. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *. MWU test refers to Mann Whitney U test.

season	sex	sample size	mean	SE
pouch-infants:				
summer	sons	15	42.8	4.50
	daughters	26	39.5	4.34
	both	41	40.7	
small YAF:				
winter	sons	11	47.5	7.56
	daughters	11	51.6	5.29
summer	sons	16	62.8	3.51
	daughters	13	52.0	7.57
both	both	51	54.4	
large YAF:				
winter	sons	9	63.0	4.84
	daughters	6	62.6	9.36
summer	sons	30	55.1	2.67
	daughters	22	57.9	4.95
both	both	67	57.7	
test statistic probability				
<i>pouch-infants: sons vs daughters</i>				
		MWU	$z=0.785$	0.218ns
<i>pouch-infants vs small YAF</i>				
		t test	$t=3.120$	$p < 0.01*$
<i>small YAF vs large YAF</i>				
		t test	$t=0.928$	$p > 0.2ns$
<i>pouch-infants vs large YAF</i>				
		t test	$t=4.596$	$P < 0.01*$
<i>small YAF: summer vs winter</i>				
		t test	$t=1.437$	$p > 0.1ns$
<i>large YAF: summer vs winter</i>				
		t test	$t=1.267$	$p > 0.2ns$

expected, pouch-infants were significantly less co-ordinated with their mothers than either small YAF or large YAF. The difference between pouch-infant sons and daughters was not significant, and it is not obviously different for small or large YAF (table 94). The seasonal differences for YAF were also not significantly different (I combined sexes and used a t-test, as the sample size was much larger and YAF had less variable co-ordination percentages).

6.7 Types of mother-young contact

As the eastern grey kangaroo is highly sexually dimorphic, according to current theories (Fagen, 1981; Stevenson and Poole, 1982; Trivers, 1978) there might be differences between the sexes in their play behaviour (see also chapter 5), and in the schedules and rates of investment they receive from their mother (chapters 1 and 3). Female infants spent more time 'playing' than the male infants; this is assuming that male and female pouch-infants are out of the pouch for the same proportion of the day (see section 5.2). In this chapter, I noted that female infants also venture further from their mothers at an earlier age than do male infants. However, male infants might still be using as much energy playing as female infants if they are playing more 'roughly' with their mothers.

In a review of the importance of play as physical training and exercise for young, Fagen (1976) noted that 'rough and tumble' play should occur in brief and intense bouts frequently interrupted by rest periods. A second type of play, 'approach-withdrawal', according to Fagen (*ibid.* p.213) "should involve prolonged bouts of locomotion at submaximal intensity". Daughter eastern grey kangaroos might be spending a greater proportion of their time in the second type of play rather than the 'rough' play. If this play difference exists between sons and daughters, then the types of contact states of mother and young should differ between mother and son pairs and mother and daughter pairs. Mothers are the only play-partners kangaroo young have until they become subadults.

Such a difference in the behaviour of mothers with their sons and daughters would possibly entail a greater energetic investment by mothers in their sons, unless mothers were distributing their resources in a different manner between the sexes. For example, mothers might groom daughters more (Missakian, 1974; Simonds, 1974; Kurland, 1977). The grooming of young may have quite an important function (Espmark, 1969) in maintaining a bond between the mother and young, in cleaning parasites from the young, and in stimulating the young to urinate and defecate (this does occur in the kangaroos, especially in

Table 95: *Frequencies of types of contact states which sons and daughters make with their mothers.*

medium pouch-infants		'passive' states					'play-fight' states						
		allo- groom	nose	paw	touch	hug	jump- on	cuff	grab	lean over	kick	rub	high- stand
sons	freq	12	72	24	12	11	49	3	26	4	2	3	3
	%	5.4	33	11	5	5	22	1	12	2	1	1	1
daughters	freq	28	102	51	21	18	28	4	18	5	0	3	2
	%	10	36	18	8	6	10	1	6	2	0	1	1
small YAF													
sons	freq	9	40	9	2	7	7	0	3	2	0	2	0
	%	12	53	12	3	9	9	0	4	3	0	3	0
daughters	freq	9	42	5	3	8	0	0	0	8	0	0	4
	%	11	53	6	4	10	0	0	0	10	0	0	5
large YAF													
sons	freq	11	40	8	5	8	2	2	7	6	1	4	3
	%	11	40	8	5	8	2	2	7	6	1	4	3
daughter	freq	18	47	11	1	19	6	1	4	0	3	1	1
	%	16	42	10	1	17	5	1	4	0	3	1	1

the pouch, pers. obs.).

Although YAF are in contact with their mothers only a small percentage of the time (section 6.5.2), differences in the form of this contact may signify important differences in the relationships of mothers with their sons versus daughters. Thus we can ask, are there differences in the type of contact states and their relative frequency between sons and daughters, and between mothers of sons and mothers of daughters? Also, are mothers more active while in contact with sons or with daughters?

I divided the contact states of young into 12 categories and combined all observations for medium-sized pouch-infant sons and those for the similar class of daughters into a frequency table (table 95). Compared to medium pouch-infant daughters, pouch-infant sons as a class did appear to be more frequently jumping at, grabbing, and kicking (the mother), and high-standing, all of which are activity states seen in adult males' fights. The daughters were more frequently grooming or pawing their mothers than were sons. The differences were statistically significant ($G = 24.063$, $df = 1$, $p < 0.001$). However as this was a post hoc analysis I also divided the contact states into those of typically male fighting states and those of a more 'passive' set of states, and compared these frequencies found for sons and daughters. Sons were still found to be exhibiting states similar to those seen in male fights significantly more frequently than were daughter pouch-infants

Table 96: Frequencies and percentages of the types of contact states of mothers with their young.

states:		allogoom	'passive' states					'play-fight' states					freq
class			nose	paw	touch	pouch entry	hug	rub	grab	cuff	kick lean over high-stand	total	
pouch-infants													
sons	freq	106	17	5	2	1	3	1	0	0	0	135	
	%	79	'passive' states 18%					'play-fight' states 3%					
daughters	freq	81	27	3	0	4	4	1	0	0	0	120	
	%	68	'passive' states 28%					'play-fight' states 4%					
small YAF													
sons	freq	26	21	5	0	-	5	1	0	0	0	58	
	%	45	'passive' states 45%					'play-fight' states 10%					
daughters	freq	74	20	3	2	-	4	0	1	1	1	106	
	%	70	'passive' states 23%					'play-fight' states 7%					
large YAF													
sons	freq	68	19	4	5	-	7	0	4	4	4	115	
	%	59	'passive' states 24%					'play-fight' states 17%					
daughter	freq	73	40	9	2	-	19	2	6	0	2	153	
	%	48	'passive' states 33%					'play-fight' states 19%					

($G = 17.111$, $df = 1$, $p < 0.05$).

YAF were in contact with their mothers much less frequently, so again I combined data from individuals into classes and conducted G tests. First I tested whether sons' and daughters' frequencies of the 'passive' versus 'fight' contact states varied between the small YAF and large YAF classes, and between the medium pouch-infant and small YAF classes. Small YAF sons were significantly less likely to exhibit 'play fight' contact states (20%) than were medium pouch-infant sons (45.7%) ($G = 16.601$, $df = 1$, $p < 0.05$). However, the frequency of 'play fight' states relative to 'passive' states increased again, moderately (35%) but significantly, for large YAF sons ($G = 5.039$, $df = 1$, $p < 0.05$).

Daughters also reduced the relative frequency of their 'play fight' states to 'passive' states as they became small YAF (19%) from the medium pouch-infants (28%). However, the difference was not significant ($G = 2.833$, $df = 1$, $p > 0.05$), as the daughters did not 'play fight' much as pouch-infants. The daughters then increased significantly the relative frequency of their 'play fight' states as they became large YAF (31%) ($G = 3.886$, $df = 1$, $p < 0.05$). Thus, both small YAF sons and daughters not only played less frequently than

pouch-infants (section 5.2), and were in contact much less often with their mothers than pouch-infants, but they were also in 'passive' contact rather than actively 'play fighting' with their mother. There was no significant difference between sons and daughters in the relative frequency of their 'passive' versus 'play fight' contact states as small or large YAF (small YAF $G = 0.040$, $df = 1$, $p > 0.05$; large YAF $G = 0.399$, $df = 1$, $p > 0.05$).

The mothers were observed to exhibit the same types of contact states as their young (table 96), excepting the 'jump on' state, but far less frequently. They also exhibited the half pouch-entry posture during some contact bouts with pouch-infants, and were never observed to cuff, grab, lean-over, or high-stand while in a contact bout with pouch-infants. These latter states were observed only in mothers with YAF. Contact states of mothers of pouch-infant sons were more likely to be the allogroom state (79%) than it was for daughters (68%), but the difference was not significant ($G = 3.778$, $df = 1$, $p > 0.1$). As the young became a YAF, the mother was more likely to return the young's 'play fight' activity-states with similar states.

Therefore, I divided the mothers' contact states into three categories: allogrooming, 'passive but non-allogrooming', and 'play fight'. The percentages of these states relative to each other are presented in table 96. The mothers of sons significantly altered the relative frequency of states in these three categories as their young grew from medium pouch-infants to become a small YAF ($G = 20.817$, $df = 2$, $p < 0.001$). The mothers groomed small YAF sons relatively less compared to the other two categories. The relative frequencies of these three types of states did not differ significantly between mothers of medium pouch-infant daughters and mothers of small YAF daughters ($G = 1.160$, $df = 2$, $p > 0.05$).

As both sexes of small YAF became large YAF, the mother was significantly more likely to exhibit 'play fight' contact-states (mothers of sons, $G = 7.491$, $df = 2$, $p < 0.05$; mothers of daughters, $G = 14.948$, $df = 2$, $p < 0.001$). It appears that mothers were allogrooming their small YAF daughters rather than passively touching them to a significantly greater degree than the mothers of small YAF sons ($G = 9.862$, $df = 2$, $p < 0.01$). However, this difference between the mothers of different sexed YAF disappears as the YAF ages ($G = 3.668$, $df = 2$, $p > 0.05$).

Pouch-infant sons were in contact with their mothers for a greater proportion of the time than were pouch-infant daughters (section 6.5). Thus, the relative frequencies of the types of contact states that the mothers were exhibiting should be put in a context of how active the mothers of sons were in contacting per contact minute, compared to the mothers

Table 97: *The frequencies and rates of mothers' contact states (per contact minute) for mothers of sons and daughters analysed by the time since PEP.*

	months from PEP:					
	PEP	1	2	3	4	≥5
<i>mothers of sons:</i>						
<i>contacts</i>	11	20	17	17	18	26
<i>duration</i>	29.3'	23.2'	6.3'	43.3'	26.3'	27.7'
<i>contact/c min.</i>	0.375	0.861	1.895	0.392	0.685	0.938
<i>mothers of daughters:</i>						
<i>contacts</i>	3	9	5	1	13	63
<i>duration</i>	19.5'	3.9'	41.1'	3.3'	1.4'	3.6'
<i>contact/c min.</i>	0.003	2.398	1.291	—	1.378	3.563

of daughters. This analysis differs from that of whether the mother or young initiated or terminated a whole contact bout.

Young might be responsible for initiating most of the contact bouts, whether they are male or female, while the mothers might differ in how active they were in a contact bout depending on the sex of their young. I was able to compare the individual contact-state rates of mothers of medium pouch-infant sons and of daughters, but not for mothers of YAF. Their contact rates were too low, so I combined them into categories according to the month post permanent-emergence of their YAF.

Mothers of pouch-infant sons tended to have a higher rate of contact states per contact minute ($N=7$, mean=1.195c/min, SE=0.247) than mothers of pouch-infant daughters ($N=7$, mean=0.729c/min, SE=0.372, MWU test $U=11.38$, $p < 0.1$). The rates for the combined mothers according to the age of their YAF were still quite variable and not obviously related to their YAF's age (table 97). Thus, if there was a difference between mothers of sons and mothers of daughters further data are needed to substantiate it. The combined contact rate for all mothers of YAF sons was 0.858 contacts/contact minute and for mothers of YAF daughters it was 1.705 contacts/contact minute.

In summary, pouch-infant sons were more likely than pouch-infant daughters, to 'play fight' with their mother, rather than 'passively' contacting their mother. Hence, pouch-infant sons might well have been expending as much energy 'playing' as were pouch-infant daughters, because the sons were playing in the 'rough and tumble' style rather than the 'approach-withdrawal' style (Fagen, 1976). Further work on the metabolic expense of the different styles of play in eastern grey kangaroos is required before it is possible to conclude

that either sex is investing more in 'play' behaviour than the other. Indeed sons could have been sucking more in order to invest more absolutely in play, just as male foals are thought to be doing (Duncan *et al.*, 1984). Play can be energetically costly, according to Fagen and George (1977).

Mothers of pouch-infants did not actively play fight with their young. However if the young was a son, these mothers tended to make a greater number of active contacts during a contact bout, compared to the rate at which they contacted daughters. Further, contrary to my prediction in the introduction to this section, they did not enter the allogrooming state compared to other contact-states more frequently with pouch-infant daughters than with sons. However, mothers of small YAF daughters were more likely to groom their daughters when in contact with them than were mothers of small YAF sons.

When the young becomes a small YAF, not only is the time it spends in 'play' absolutely reduced (chapter 5), but it also contacts its mother in a more 'passive' manner rather than 'play fighting' her. However, both sons and daughters increase the relative frequency of their contacts in the 'play fight' style as they become large YAF. The mother, too, begins to 'play fight' with her young in a more active manner once her young is a large YAF.

Overall, it is becoming quite clear that it is not possible to look at one type of maternal investment only, e.g. suckling (Trillmich, 1986), in young mammals, and conclude that the mothers are investing more in a son than a daughter prior to weaning. Mothers appear to rear sons and daughters to different schedules.

6.8 Interactions between young and others

In the ungulate literature there is frequent mention of adult females being quite aggressive toward young other than their own, while adult male ungulates are reported as being quite tolerant of young (Espmark, 1969; Tyler, 1972). One commonly invoked explanation (Lent, 1974) is that this increased antagonism of females toward strange young helps ensure that the female invests her time and energy in her own young only, and perhaps helps maintain the bond between herself and her own young.

In some of the primate literature there are also descriptions of the aggression of adult females toward foreign young, but as more researchers in this field have been emphasising the importance of matriline relations and inter-female competition, authors such as Silk and Boyd, (1983) (see also Altmann, 1980; Clark, 1978; Hrdy, 1977; Hunte and Horrocks, 1987)

Table 98: Frequencies of the types of interactions between young and adult males and adult females.

	low intensity				moderate intensity		high intensity	
	passive nose stretch	aggressive paw	cuff at	growl	jump cuff	growl paw-wave	jump growl	cuff growl chase
	1	2	3	4	5	6	7	8
from females to:								
sons	16	7	12	26	30	3	11	4
(%)	(18)	(low intensity 51%)			(moderate intensity 15%)		(high intensity 17%)	
daughters	15	6	8	27	30	5	13	6
(%)	(17)	(low intensity 46%)			(moderate intensity 17%)		(high intensity 21%)	
from males to:								
sons/daughters	26	1	2	2	4	0	0	0
(%)	(74)	(low intensity 14%)			(moderate intensity 17%)		(high intensity 0%)	

have suggested that it arises because it is in the interests of individual adult females to reduce competition by others for the environmental resources necessary for their successful reproduction. That is, females may actively try to lower the fitness of nonrelated young, especially female young, who might eventually become reproductive competitors.

However, other authors, (Berman, 1982a,b; Cheney, 1978a,b; Kurland, 1977; Handen and Rodman, 1980) have emphasised the importance of nonagonistic interactions between female relatives as a means of increasing an individual female's access to important resources via affiliative relationships. Accordingly, female infants should initiate and spend more time interacting with adult females who are either high ranking or close kin, and who may aid the infant in her progress toward successful reproduction; in comparison, male infants, who will disperse, may interact less with the adult females in their natal group, at least, until they become interested in courting. Clutton-Brock *et al.* (1982b) for red deer and Johnson (1985) for red-necked wallabies have shown that the size of a female's matriline does appear important in influencing her reproductive success.

In chapter 4 I suggested that the eastern grey kangaroo females may have preferential associates, who are possibly close female relatives. Although confirmation of this awaits further long-term research, if the presence of female relatives does affect a female kangaroo's reproductive success, young female kangaroos might initiate interactions more frequently with the local adult females than young male kangaroos. Alternatively, if there is a high level of inter-female competition, rather than tolerance between related females, adult females

Table 99: Percentage of types of interactions of females with young, according to the reproductive class of the female.

interaction females with:	passive	aggressive			total count
		low intensity	moderate intensity	high intensity	
no PY:	28%	33%	23%	18%	40
small PY:	4%	58%	9%	29%	55
pouch infant: PEP young or small YAF:	7%	56%	15%	22%	41
large YAF:	3%	10%	0%	0%	13

G test:
female class (PY, PEP young or small YAF) × interaction intensity (nil or low, moderate or high)
 $G = 1.858$, $df = 1$, *ns*

might initiate more aggressive interactions with nondaughter female young than they do with male young. If adult females' interactions with young other than their own are affected only by the female ensuring that she does not invest in those young, and simultaneously maintaining the bond with her own young, then there should be no significant difference in the frequency and types of female-young interactions according to the sex of the young.

I categorised the 'young-other' interactions into 8 types (table 98), but basically all except for type 1 were agonistic interactions. Of all of the interactions I observed between adult males and young, 26% (9/35) involved the male behaving aggressively toward the young, while of all the interactions between adult females and young, 84% (150/179) involved the female behaving aggressively toward the young. The difference is significant ($G = 43.641$, $df = 1$, $p < 0.001$). Thus adult female kangaroos are exceptionally aggressive to young other than their own, but why?

The adult females were being equally aggressive toward male and female young (table 98, $G = 0.818$, $df = 3$, $p > 0.05$). However, whether they had a pouch-infant or a YAF, rather than no or a small pouch-young, made no difference to their aggression (table 99). Moreover, pouch-infants were initiating most of their interactions (table 100); and among the medium pouch-infants, females appeared to be initiating relatively more interactions than males (when the proportion of the two sexes of young in the population was taken into account table 101).

Table 100: *Frequencies of interactions initiated by the young towards others and by others toward the young.*

class of young	young initiated		other initiated	
	mal: young	f. male young	male young	female young
<i>pouch-infant:</i>				
observed	48(83%)	51(83%)	10(17%)	12(17%)
expected	63	42		
<i>PEP young:</i>				
observed	23(62%)	21(72%)	14(38%)	8(28%)
expected	25	19		
<i>small YAF:</i>				
observed	24(75%)	11(58%)	8(25%)	11(42%)
expected	22	17		
<i>large YAF:</i>				
observed	17(50%)	11(50%)	17(50%)	18(50%)
expected	20	15		

Table 101: *Tests comparing initiation frequencies of interactions between the sexes of young and between the classes of young. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.*

comparison	test statistic	df	probability
<i>initiation by pouch infant</i>			
male young vs female young:	$\chi^2 = 9.552$	1	< 0.01*
<i>initiation by male young</i>			
PEP vs small YAF vs pouch-infants:	$G = 3.670$	1	< 0.1†
<i>initiation by female young</i>			
PEP vs small YAF vs large YAF:	$G = 3.140$	1	< 0.1†
<i>initiation by pouch infant</i>			
PEP vs small YAF vs pouch-infants:	$G = 4.795$	1	< 0.05*
<i>initiation by female young</i>			
PEP vs small YAF vs large YAF:	$G = 2.149$	1	> 0.1ns

Table 102: *Rates of young's interactions with others analysed according to the initiator.*

class	N	no. interactions		rate of initiations (no./hr)		
		initiated		time(hr)	initiated	
		young	other			young
<i>medium pouch infants:</i>						
<i>male young</i>	7	5	1	2.9	1.72	0.34
<i>female young</i>	7	13	0	2.9	4.54	0
<i>large pouch infants:</i>						
<i>male young</i>	4	8	1	2.4	3.39	0.42
<i>female young</i>	4	5	0	1.5	3.25	0
<i>very large pouch infants:</i>						
<i>male young</i>	7	2	1	10.0	0.20	0.1
<i>female young</i>	6	5	2	3.23	1.55	0.62
<i>PEP young:</i>						
<i>male young</i>	3	2	5	3.87	1.29	1.29
<i>female young</i>	3	5	1	4.27	0.25	0.25
<i>small YAF:</i>						
<i>male young</i>	13	2	7	11.6	0.60	0.60
<i>female young</i>	12	4	5	15.1	0.33	0.33
<i>large YAF:</i>						
<i>male young</i>	12	6	1	11.4	0.09	0.09
<i>female young</i>	11	1	1	9.57	0.10	0.10

To substantiate this I looked at a sample of 7 male and 7 female medium pouch-infants and combined the data for individuals of each sex to calculate a rough index of the number of interactions per hour which medium pouch-infants of each sex initiated. The male young initiated 1.7 interactions per hour (5/2.9), while the female young initiated 4.5 (13/2.8) interactions per hour. This difference between male and female young was not maintained as they aged. The rate at which small and large YAF male young initiated interactions was 0.6 (N=13, 7/11.6) and 0.1 (N=12, 1/11.4) interactions per hour respectively; the rate at which small and large YAF female young initiated interactions was 0.3 (N=12, 5/15.1) and 0.1 (N=11, 1/9.6) interactions per hour respectively (table 102). From these figures it also appears that YAF might be initiating fewer interactions as they age (table 102). Other classes were initiating, proportionally and possibly absolutely, more of the YAFs' interactions compared to the medium pouch-infants' interactions (tables 100, 101, and 102).

It is unlikely that any of the three hypotheses alone explains interactions between young and others. The inter-female competition hypothesis does not account for the pouch-infant's initiation of the majority of their interactions. Adult females initiated very few interactions

with the young when they were rather vulnerable pouch-infants, thus the females could not have been actively seeking to reduce the fitness of other mothers' young. However, as females compared to males were particularly aggressive towards young, some may have acted opportunistically when the young initiated the interaction. The hypothesis suggesting that females interact aggressively with foreign young to avoid investing accidentally in them is inadequate as the most aggressive females should have been those with young, and this was not necessarily so.

Although the matriline hypothesis does not explain why others were initiating aggressive interactions with YAF, it might explain why the female medium pouch-infants initiated more interactions than male pouch-infants. There was a wide gradation in the form of the interactions from passive to extremely agonistic. I am unsure whether the adult females reacted in a consistent manner toward particular young. But, if they did, it is possible that a female pouch-infant, in spite of receiving many threats when initiating interactions, might be exploring her social environment, which is the one she will eventually breed in. In this manner the daughter may determine which of her mother's peers are tolerant of her presence. This exploration might best occur while the young is a pouch-infant who can retreat toward the safety of a pouch, or has time to explore. The interactions between YAF and others are more consistent with an inter-female competition hypothesis, as, even though the females were not more aggressive to female young, they were initiating relatively more of the interactions. Adult females are in general aggressive towards individuals smaller than themselves (section 4.5), but again it is possible that they act differentially toward those individuals. I believe that this topic deserves further investigation.

6.9 Changes in interactions around weaning

The onset of weaning of the eastern grey kangaroo young at Wallaby Creek is rather abrupt and concentrated (section 6.3). Prior to this time the mother consistently terminates about 20% of her young's suckling bouts. Mothers were observed to be aggressive toward their young during and after weaning, but almost never before weaning. As for other-young interactions, there appeared to be 7 forms of mother-subadult agonistic interactions (table 103), which involved one or a combination of the following behavioural actions by the mother: cuff at/paw at, growl, jump at, and chase.

Daughters were remaining in their mothers' home range and associating with their

Table 103: Mothers' types of interactions with sons and daughters following weaning.

	low intensity				moderate intensity		high intensity		total
	passive nose stretch	aggressive paw	cuff at	growl	jump cuff wave	growl paw- growl	jump- cuff chase	jump-cuff growl	
	1	2	3	4	5	6	7	8	
to sons	2	7	7	56	0	15	8	3	98
	2%		LI=71%			MI=15%		HI=11%	
to daughters	1	5	7	32	0	6	0	0	54
	2%		LI=81%			MI=17%		HI=0%	

G test:
sons/daughters with low/moderate/high intensity
 $G=10.161$, $df=2$, $p < 0.01^*$

mothers more than were subadult sons; this difference might be related to the mothers behaving differently toward their sons and daughters. Mothers moved away from their large YAF sons more than their large YAF daughters (section 6.5). Were mothers more aggressive toward their subadult sons than towards their subadult daughters?

I observed 149 instances of mother-subadult agonism and 96 were directed toward sons, while 53 were toward daughters. However, as there were more subadult sons in the population, it is more appropriate to consider the average number of agonistic interactions per subadult. The 13 subadult males I observed consistently were seen to receive on average average 7.4 acts of maternal aggression; the 11 daughters were seen to receive an average of 4.8 acts of maternal aggression. A statistical test is not valid because the individuals were observed for different durations, since males dispersed and daughters remained in their mothers' home range. However, I could test for a difference in the intensity of aggression in mother-son and mother-daughter interactions.

A single cuff at, or paw-wave at, or growl, was considered a low-intensity aggressive act. A paired combination of single acts, such as a jump at and cuff or a growl and paw-wave, was considered a moderate-intensity aggressive action; while a combination of all 3 acts, with or without a chase involved, was considered a high-intensity aggressive action. Sons received significantly more high-intensity aggressive action by the mother than did daughters who were receiving more of the low-intensity aggressive actions from their mothers (table 103, $G=10.161$, $df=2$, $p < 0.01$).

Thus mothers appear to be more aggressive to their sons, during and after weaning, than to their daughters.

6.10 Discussion

6.10.1 Mother-young social relations

Social relations between mother and young have previously often been referred to by discussing the mother-young 'bond' (see Hinde, 1979). However I believe the word 'bond' (as others i.e. Lynch *et al.*, unpubl manuscript) have suggested) can be rather misleading when referring to the association of a mother and young. I believe that the relationship between the eastern grey kangaroo mother and her young is more likely to be a result of a combination of the young's developmental schedule, adapted towards maximising its lifetime reproductive success, and the mother's rearing schedule, which is adapted towards maximising her lifetime reproductive success. There does not appear to be one universal thread that ties the mother and young together, and gradually weakens or breaks suddenly as weaning approaches.

The responsibility for the spatial relations between kangaroo mother and young is shared by both, but is exercised in quite different fashions. Further, the 'roles' each assumes in the relationship vary as the young ages, and according to the sex of the young.

In one way the mother-young relationship in the eastern grey kangaroo is unlike those previously described for eutherian species. The young exhibits two quite distinct ontogenetic phases of behaviour, after first leaving the pouch: the pouch-infant phase, and the YAF phase.

As a pouch-infant, the young typically spends less than 30% of its time out of the pouch. But when out, its behaviour state is usually different from its mother's state; 80% of its time spent out of the pouch is divided between 'sucking' and solitary or social play. The pouch-infant frequently changes its spatial position, and initiates more interactions with others than does a YAF.

On permanent emergence the young's behaviour dramatically alters, so that within a fortnight the young is predominantly in the same behaviour state as its mother, and moves to and from her at about the same rate as she moves to and from it. As a YAF ages there is a slight increase in the frequency of play fighting with its mother, and a slight increase in the percent of its time spent at a distance from the mother. Otherwise, a YAF's behaviour changes little until weaning.

Why should there be such a distinct difference between the behaviour of pouch-infants and YAF? And what does it mean to the mother-young relationship?

Although a pouch-infant frequently alters its position in relation to the mother, it appears to rely on the mother maintaining her spatial position (sections 6.4 and 6.5) in order to

identify which kangaroo in the group to return to. A pouch-infant more easily loses its mother's location after interacting with others, or by following other kangaroos when these kangaroos move, as compared to YAF. YAF are more likely to become separated by not following their mothers.

Thus, it is understandable that mothers of pouch-infants out of the pouch significantly reduce their rate of movement, and spend a greater proportion of their time surveying, especially when the infant is more than 10m away, than they typically do while the young is in the pouch. When the pouch-infant is threatened, the mother assumes a pouch-entry posture and may call to the infant. If necessary, the mother may move to the threatened infant. Consequently, while a mother may not be directly responsible for her infant's location in the environment when it is out of the pouch, the mother definitely plays a significant role in maintaining the association. In addition, the mother is primarily responsible for the times of the young's exit and entry into the pouch (section 6.2).

It is easy to see that the mother could be in control of her infant's exit from the pouch, via the control of her pouch-opening muscles. However, in order for her to determine a young's entry into the pouch, she relies on the young being constantly willing to enter. I have not yet seen a mother pick up a young and forcibly push it into the pouch; I doubt they are capable of doing so. From my observations in the field, the young appear to be constantly attempting to re-enter the pouch, and they readily do so upon the mother assuming a pouch-entry posture (section 6.2). I suggest that this form of relationship is well adapted to conditions where there are predators or other dangers to the infant and mother. The infant may rely on the mother's experience in identifying potential dangers, and the mother has some flexibility in determining the extent and timing of the disruption to her activities, which occurs when her young is out of the pouch (chapter 5).

The active responsibility the mother kangaroo takes in maintaining the relationship with her pouch-infant resembles the frequently greater responsibility of eutherian mothers in the early phases of their relationship with their young. For example, mother primates are often observed to restrain their very young infants from moving off them (Altmann, 1980; Simpson, *et al.*, 1986); pony mares will remain in close proximity to their young foals when the foals are lying down (Crowell-Davis, 1986; Tyler, 1972); and mother southern right whales maintain a high approach rate toward their very young calves (Taber and Thomas, 1982). The principle differences appear to be that the eastern grey kangaroo mother has some control over the times when her young may disrupt her behaviour; and

the responsibility in maintaining the association shifts gradually toward many eutherian young, while for eastern grey kangaroo young it occurs rapidly at permanent emergence.

However, why is permanent emergence so rapid and sudden? Perhaps, in order to initiate a reduction in the young's orientation to the pouch, the mother, as she does at permanent emergence, would have to reject a greater proportion of the infant's contacts than she ordinarily does, and in doing so would risk the infant not entering the pouch when danger threatened. Hinde and Spencer-Booth (1971, 1967) have shown that an increase in maternal rejections of infant rhesus monkeys is correlated with an increase in the infant's independence. Further, if the infant remains out of the pouch for too long a period, the mother may have to increase her surveillance behaviour until it encroached upon valuable feeding time (section 5.2).

However, if the pouch-infant concurrently altered its activities toward surveying more and playing less as it slowly approached permanent emergence, then a more gradual transition toward the YAF stage might result. That is, the pouch-infant's behaviour might have a less disruptive effect on the mother's activity schedule, with the consequence that the mother might allow or even keep the infant out of the pouch for a greater proportion of the day.

Since the amount of time spent in play by a young has been found to be related to its nutritional state (Fagen, 1981; Berger, 1979b; Lee, 1984b), it is possible that pouch-exit schedules may vary between environments according to the nutritional state of the young. Experimental work in this area may elucidate some of the influences on the nature of the mother-pouch-infant relationship. If the offspring is in control of the amount it plays while out of the pouch, it may influence the type of relationship it has with its mother. Consequently, there is the potential for parent-offspring conflict and manipulation. Alternatively, if the rate at which the infant develops is fixed (e.g. the development of its capacity to identify the mother and identify its spatial location in the environment as it moves), then the onset of permanent emergence may remain abrupt.

I believe that the developmental schedule of the young is probably not fixed and prohibitive of a gradual permanent-emergence, because the duration of the pouch-life varied between infants considerably (section 3.6).

The duration of a young's pouch-life may affect the probability of the young's survival and be related to the physical condition of the young at the end of the parental investment period. For example, as a male's size appears to be important to his success in achieving

matings (Jarman and Southwell, 1986), and as according to Poole *et al.* (1982) the growth rates of young slow down as the young becomes a YAF. Sons who were given longer pouch-life durations might have a greater expectation of reproductive success than sons who were given short pouch-life durations.

Thus, I would expect that if there was conflict in the mother-young relationship, it would be particularly prominent during the stage of permanent emergence. In section 6.5 I found that mothers were more likely to terminate more of a son's contacts if that son was permanently emerging at a relatively early age. I have interpreted this as meaning that behavioural conflict was more intense the earlier the mother terminated a son's pouch-life.

Further research in this area could describe some interesting patterns in the mother-young relationship. For example, if daughters are more uniformly reared than sons, is there less conflict in the mother-daughter, as compared to mother-son, relationship? Also, can sons increase the duration of their pouch-life by manipulation of their mothers?

After permanent emergence, the YAF, whose behaviour is then far more adult-like, becomes more responsible for following the mother around her home range. The mother is as likely to retrieve a 'lost' YAF as she is a 'lost' pouch-infant, but she is much more likely to move away from a YAF. It is probable that YAF have to maintain a vigil on their mother's movements. I believe that YAF are likely to be separated from their mothers at least once, and this in itself may increase the YAF's tendency to be responsible for maintaining the association (Hinde and Davies, 1972). However, in general the mother-young relationship changes little until the rather abrupt onset of weaning.

Parent-offspring conflict may be prominent in the relationship at weaning as well as at permanent emergence. Mothers can be quite aggressive toward their young when weaning them. There is variation in the duration of the YAF stage, although not as much as there was in the duration of 'pouch-life' (see section 3.6). In addition, the typical duration of 6 months at Wallaby Creek is rather shorter than the 8 or more months reported for other captive and field populations (Kirkpatrick, 1965c; Poole, 1973 and 1975). Some mothers were reproducing aseasonally. Thus it may have been more adaptive for these mothers to maintain a high rate of producing young, and to invest in each young minimally. However, if the expected reproductive success of a young was positively correlated to the duration of its YAF phase, then young may seek to increase the duration of this phase. I discuss schedules of weaning and parental investment further in chapter 7.

Overall, the mother-young social relationship has many levels to it, with parent-offspring

conflict being quite a plausible component, as there is considerable variation in the manner in which young are reared. I discuss further variations in the relationship in the next sections.

6.10.2 Mothers and sons versus daughters

The social relationship of a mother and a daughter may differ from that of a mother and a son not just because males and females have different life histories and consequently may behave differently as young, but also because the mother may rear them in different manners. It is difficult to disentangle the mother's from the young's responsibility in defining the relationship, as the form of their relations at any point in time is affected by their past histories (Hinde and Spencer-Booth, 1967, 1971; Hinde, 1976). However, by comparing some of the gross patterns in the development of the relationship of mothers and sons with those of mothers and daughters, it is possible to describe areas in which the mother or young appear more influential.

Differences in reproductive strategies are rarely divided into clear-cut dichotomies (Caro and Bateson 1986), but rather tend to range through a continuum between the extremes. This is probably all the more relevant for the maternal rearing strategies of eastern grey kangaroo females, since the durations of the different stages in the mother-young relationship varied considerably (section 3.6), and more so for sons than for daughters. Hence, sons were not reared to one schedule and daughters another. Unfortunately, as I did not have enough data to investigate intrasexual variation in the mother-young relationship, my discussion refers to the average relationship rather than the typical relationship, or the extremes to which it can develop. However, if sons receive more investment than daughters could expect prior to weaning, are sons more 'demanding' than daughters? Do sons and daughters 'demand' different types of care from the mother? Or does the mother alone define the different rearing schedules for sons and daughters?

First, the differences in the mother-young relationship between sons and daughters are as follows:

1. pouch-infant sons 'suck' more frequently, and are in contact with their mothers for longer bouts and in total a greater percentage of their time than are pouch-infant daughters, although their contact rate with their mother is similar or slightly lower;
2. pouch-infant sons engage in more 'play fight' states than daughters, who tend to

- groom or paw their mothers;
3. small and medium pouch-infant daughters spend more time further from their mothers than sons of the same classes;
 4. pouch-infant daughters initiate more interactions with others than do sons;
 5. mothers were more active while in contact with their medium pouch-infant sons, than with their daughters;
 6. mothers initiated a slightly greater percentage of their pouch-infant daughters' 'sucking' bouts than of their sons' bouts;
 7. large YAF sons spend more time away from their mothers than do the daughters;
 8. but as compared to sons, large YAF daughters initiated more moves to beyond 2m from their mothers instead of initiating contact;
 9. mothers seemed to be moving at a slower rate when with small YAF daughters than when with small YAF sons;
 10. mothers were more likely to move toward YAF daughters than YAF sons, and they were more likely to move away from their sons;
 11. mothers passively touched their small YAF sons as much as grooming them, but they groomed their small YAF daughters more than passively touching them; and
 12. mothers wean sons more aggressively than daughters.

The differences observed between pouch-infant sons and daughters seemed to arise from the infants themselves, as the mothers' behaviour differed little. The two exceptions where mothers behaved differently (5 and 6), should not have caused the differences in the son and daughter pouch-infants' behaviour. Once the young had permanently emerged they had very similar suckling patterns (chapter 5). Despite male pouch-infants maintaining a higher 'sucking' frequency, the mothers of sons did not terminate any higher proportion of their 'sucking' bouts during permanent emergence.

However, subsequent to permanent emergence, mothers were more likely to leave sons than daughters, and in this manner may have kept their sons sucking at a rate similar to that of daughters. YAF sons were still more likely than daughters to initiate contact with

their mothers rather than move away from them. So perhaps sons were more demanding than were daughters to suck from their mothers; but they were not necessarily allowed to suckle more as YAF. The increased leaving by mothers of their sons possibly caused the sons to spend more time further from their mother than daughters.

In general, mothers of YAF daughters sought to maintain their association to a greater degree than mothers of sons, and this could have affected or reflected the long-term differences in the mothers' greater association with daughters subsequent to weaning.

On permanent emergence, the difference between the frequency of 'play fighting' of sons and daughters disappeared. In general, play fighting was reduced in frequency, while the young was a YAF as compared to a pouch-infant. But, as my data set was likewise reduced, this may have meant that any difference between sons' and daughters' 'play fighting' was not apparent. In the field I observed some male YAF to have quite intense if infrequent 'play fights' with their mothers, while daughters' 'play fights' seemed less elaborate.

Thus, the principle differences between sons and daughters were that pouch-infant sons 'sucked' more, played more roughly and less frequently, and as YAF they spent increasingly more time at a distance from their mother. Daughters spent more time in solitary hopping and investigation play, as well as initiating interactions with others when on their excursions from their mothers. These differences are consistent with findings in eutherian species (see review by Fagen, 1981).

Current theories suggest that these differences arise because rough play is important to males, who will be competing with each other for mates, especially in such a sexually dimorphic, polygynous species as the eastern grey kangaroo (see Fagen, 1981). The greater association of a daughter with her mother might be related to an increased reproductive success of daughters who breed within a matrilineal social group (Clutton-Brock *et al.*, 1982b; Johnson, 1985).

It is possible that the early interaction of daughters with others in their environment is also important to daughters in allowing them to establish relationships or determine who are more tolerant of them (see Cheney, 1977). Sons will eventually disperse. Consequently interacting with the local adult females and males may have a smaller effect on their expected lifetime reproductive success, at least until they become subadults.

Overall, sons and daughters themselves appeared more responsible for the different quality of their relationship with their mother, with one exception: mothers were likely to be more active in maintaining an association with their daughters than with their sons.

Mothers appear more responsible for the quantity of the investment they put into a son or a daughter. I have not described the quantitative differences between pairs of mothers and sons or between mother-daughter pairs in their relationships, but they are likely to be considerable. A few daughters had a rather weak association post-weaning with their mothers, and some sons spent more time in close proximity to their mothers and had much longer sucking bouts than was typical for sons. It would be well worth-while investigating the causes of these individual differences and outcomes.

6.10.3 Seasonal differences in the mother-young relationship

Presumably, some females produced peak-season young only because they were unlikely to rear offpeak-season young to weaning (sections 3.4 and 3.5). Those females who did produce offpeak-season young may have had greater feeding constraints on their activity schedules (section 5.2) or energetic restrictions on their interactions with their young.

However, I did not find significant differences between seasons in the percentage of suckling bouts terminated by the young rather than the mother (section 6.3), or in whether or not the mother was likely to retrieve the young when it became separated from her (section 6.4), or in the mothers' rates of movement (section 6.5) when their pouch-infant was in or out of the pouch. Nor were there seasonal differences in the degree of co-ordination between mother and young (section 6.6). There were no obvious seasonal differences even when I controlled for the mother's continuity of breeding.

There was a weak correlation between the percentage of young disappearing in a three month block and the likelihood of the mother actively retrieving her young after becoming separated (rather than the young being responsible for finding the mother) (section 6.4). If, as I suggested in section 3.5, the large loss of young which occurred during the middle of my study was related to the mothers' condition being particularly poor (and a concurrent increase in dingoes), then the mothers also may have been less able to expend energy, time and the risk in searching for temporarily lost young. Thus, temporarily lost young may have been more likely to become permanently lost.

At Wallaby Creek seasonal factors did not obviously affect the mother-young relationship. This might be because either the between-year differences overwhelmed the within-year differences, or females who could not invest in an offpeak young to the typical schedule did not make an attempt. I discuss investment schedules more fully in the next chapter.