

Chapter 7

General discussion and conclusions





Figure 91: *“Although I’m small mum...I’m not without persuasive power.”*

A medium pouch-infant playing, its mother, and in the background a female with a diminutive pouch-infant poking its head outside the pouch. The three photographs were taken in close temporal sequence.

7.1 Rearing schedules: implications of the pouch and comparisons with eutherian species

The mother-young relationship of eastern grey kangaroos in this study could be divided into four distinct phases, based upon the young’s stage of development: the pouch-neonate phase, the pouch-infant phase, the young-at-foot (YAF) phase, and the subadult phase. In this study I have been principally concerned with the pouch-infant and YAF phases.

Through much of this thesis I compared the period of permanent emergence in the kangaroo with birth in the ungulate. Both are critical times in the mother-young relationship, as there is a high probability of the young dying and this probability can be affected by mother-young behaviour. The mother tends to isolate herself from her conspecifics (see

section 4.6.2 for a discussion of the reasons). The young have to learn to identify their mother, monitor her movements, and respond appropriately. In some macropodoid species e.g. red-necked wallaby (Johnson, 1985) the young 'hides' upon permanently emerging from the pouch, just as do neonates of some ungulate species (see Lent, 1974). In the eastern grey kangaroo, the young learns to follow its mother around her home range, just as do the neonates of other ungulate species (*ibid.*). However, the recently permanently-emerged young is unlike an ungulate neonate in that it has had opportunities over several months to explore its environment, and to develop its signalling with and response to its mother as well as its co-ordination when allowed out of the pouch.

The mother-offspring relationship in the pouch-infant phase has some of the characteristics also found in the relationship of very young ungulates and primates with their mothers. However, it is this early phase in the young's development which includes characteristics of the mother-young relationship unique to rearing a young with a pouch (see table 104).

In the following subsections I discuss these similarities and differences in relation to the adaptiveness of rearing schedules from three perspectives: play, differences between the sexes, and rates of change in the roles of mother and young in the relationship.

7.1.1 Play schedules

The pouch-infant phase can be described as the 'play phase'. The mother kangaroo provides a pouch-infant with a warm pouch, virtually all its nutrition (Dove *et al.*, 1987; Janssens and Ternouth, 1987), and transports it around her home-range. In this population of kangaroos, pouch-infants were estimated to spend 5% to 10% of the daytime in play. This is comparable to that found in eutherian species (Fagen, 1981).

Regardless of whether or not the metabolic cost of play is small compared to an individual's total daily energy expenditure as was found for cats (<10%, Martin, 1984), an individual's activity budget may be under considerable time-constraints (Dunbar and Sherman, 1984). Consequently, the time and energy apportioned to play should be the result of the individual optimising the advantages it gains from play against the immediate costs of play and the benefit that could be derived from other activities (see subsection 5.2.4, and Fagen, 1981).

If Fagen's (1981, 1977, 1976) hypotheses on the ontogenic scheduling of play are correct, then it is appropriate that young kangaroos began playing at their first available opportunity in life, and played less as they developed toward adulthood, but especially played less

Table 104:

Different to behaviours previously observed in ungulate and primate species.

1. *the mother determined, at least proximately, the times and durations of the disruption to her activity schedule which occurred while her infant was out of the pouch (sections 5.2, 5.4, and 6.2).*
 2. *the pouch-infant was strongly oriented toward the pouch and frequently attempted re-entry (sections 5.2, 6.2, 6.3, and 6.5).*
 3. *pouch-infants were carried around their mothers' home range (though note primate mothers carry their young) and spend much time inside a warm pouch (sections 5.2 and 6.5).*
 4. *pouch-infants appeared to have only a tenuous idea of spatial relations and the identity of their mother (sections 6.4 and 6.5).*
 5. *pouch-infant daughters probably spent more time playing than pouch-infant sons (sections 5.2 and 5.5).*
 6. *social play was confined to mother-young play rather than including play between similar-aged peers, though this latter form of social play probably occurs between subadults (and possibly adult males according to Croft, 1983) (sections 6.7 and 6.8).*
 7. *when danger threatens, the pouch-infant dives for the pouch (section 6.2).*
 8. *isolation of mother and young from conspecifics during permanent emergence is not as complete as is the isolation of some ungulate mothers and neonates (sections 4.2 and 4.3).*
 9. *the behaviour of the young and its relationship with its mother changed suddenly and considerably during the brief phase of permanent emergence (sections 5.2, 5.3, 6.3, 6.5, 6.6, and 6.7).*
 10. *YAF spent very little time in play (sections 5.2 and 6.7).*
 11. *mothers actively play with their YAF (section 6.7).*
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(table continued)

Similar to behaviours previously observed in ungulate and primate species.

1. *mothers rarely terminated contact or sucking bouts of their pouch-infants (section 6.3). This is similar to mothers of very young ungulates.*
 2. *mothers were vigilant of their pouch-infant's movements (section 6.5).*
 3. *pouch-infants spent a proportion of their day in play that was similar to that reported for many eutherian species (section 5.2).*
 4. *young kangaroos began to play at their first available opportunity in life and tended to play less as they matured (section 5.2).*
 5. *pouch-infants were responsible for most of the changes in the distance between them and their mothers (section 6.5).*
 6. *pouch-infants changed their activity state more frequently than did their mothers, while in the active-behaviour mode (section 5.3).*
 7. *pouch-infants had activity-state sequences that were much less structured than those of adult females (section 5.4).*
 8. *pouch-infants spent little time grazing and instead spent most of their time resting (inside the pouch), or playing or sucking (outside the pouch) (section 5.2).*
 9. *pouch-infant sons played more 'roughly' than daughters; pouch-infant daughters were more likely to play in the other play-style, 'approach-avoid' (sections 5.2, 6.5 and 6.7).*
 10. *there was a high risk of mortality for young on permanent emergence. This risk can be compared to the high risk of mortality for many ungulate neonates. There were many characteristics of permanent emergence which might have caused the young to be particularly vulnerable to separation; these characteristics were similar in nature to those which might have caused neonatal ungulates to be highly vulnerable to separation and predation (see sections 3.5, 4.6, and 6.10).*
 11. *mother and young tended to be found less often with others and range over a smaller than usual area while the young was permanently emerging (sections 4.2 and 4.3). Their behaviour at this time could be compared to that of mother ungulates around the time of their young's birth.*
 12. *YAF follow their mothers around her home range (sections 4.2, 4.4, and 6.4).*
 13. *subadults are attracted to other subadults (section 4.3).*
 14. *sons and daughters behaved differently in many respects (see table 105).*
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during periods with a high risk of mortality, e.g. permanent emergence and the small YAF phase. Specifically, Fagen argued that play may act to train physiological responses, and may possibly affect the growth and development of an individual's muscles. The effects of training muscles early in life may have long term and perhaps idiosyncratic consequences for the manner in which an individual's body responds to physical exertion later in life. "Once growth ceases, exercise is less effective and is therefore more costly in terms of time and energy; in adulthood, exercise will often occur in a functional context; moreover, training of some physiological functions in adulthood appears to be impossible. For these reasons alone, young animals should play." (Fagen 1976, p197)

Play is often described as involving exaggerated or unstructured activity sequences; certainly the behaviour of individuals in 'play' is not similar to that of the adults around and is very conspicuous. Hence, play may increase an individual's risk of predation (Fagen, 1981; Jarman, 1974). Play may also reduce an individual's ability to monitor the environment. In section 6.4 I suggested that a YAF has a greater responsibility in monitoring its mother's movements and following her around her home range than have pouch-infants. Consequently, play may involve a risk for a YAF of becoming separated from its mother, and may be better confined to the pouch infant phase rather than being included in the YAF phase as well.

However, older YAF played more frequently than newly emerged YAF (PEP young and small YAF). According to Fagen (1980), although play may generally tend to decrease in frequency through an individual's life, bimodal age schedules for play can be selected for. This is likely when the cost of play temporarily increases during a particular period of the young's development. As a consequence, during this period the time spent by an individual in play may be temporarily reduced. The risk of mortality was very much higher for a newly emerged kangaroo young than it was for a pouch-infant or large YAF. It is possible that the lack of play in newly emerged YAF might have been related to their comparatively high risk of mortality; this risk might be increased further if newly emerged YAF had played as much as did the young of the other phases.

The relatively early ontogenic timing of play may have been responsible for the lack of play observed between kangaroo young and individuals other than the mother. The individuals of this species are social, and may be expected to gain from social play (if current theory is correct: see Fagen, 1981, Cheney, 1977, Baldwin and Baldwin, 1973). However, in eutherian species social play frequently does not appear until the young is well

developed, unless the young has siblings with which it can play (Altmann, 1980; Renouf and Lawson, 1986; Baldwin and Baldwin, 1974, 1978; Carson and Wood-Gush, 1983; Wilson, 1974a and b). I did not describe activity budgets or activity-state sequences for subadults. I believe from my field observations of this class that social play may be an important component of their behaviour. Support for this conclusion awaits quantification of their behaviour, but I did find that subadults were attracted to other subadults.

I would add, that assuming it is important to individuals to train their muscle responses while growing (as suggested by Fagen, 1976), kangaroo males might train their muscles through much of their life since they continue to grow (Jarman, 1983). It is also possible that kangaroo males may afford to delay some of the training of their muscles to specific fighting responses until a later age than is typical for ungulate or primate young. Thus, the typical 'rough and tumble' *social* play of young males might occur later in a kangaroo male's ontogeny, but for a longer part of his lifespan than in an ungulate or primate male's ontogeny. Croft (1983) suggests that fights observed in red kangaroo adult males share many of the properties ascribed to play fighting.

There are several possible reasons for a pouch-infant not to play socially with conspecifics other than its mother. Firstly, I believe that these young had a very tenuous idea of spatial relations and their mother's position within the environment. They appeared to rely on her maintaining her position in order to return to her after a 'play excursion'; and also were most likely to consider themselves 'lost' after interacting with another kangaroo (section 6.3). Secondly, pouch-infants were extremely oriented toward the pouch, and dashed toward it at the slightest call or postural invitation by the mother. In this fashion both mother and young may reduce the chance of their separation and the risk of mortality when danger threatened. Thirdly, social play may involve a risk of injury to the participants. There would possibly be less risk involved by playing with close relatives who are of a similar physical build (see also Cheney, 1978a and b). However, in an aseasonal environment there is less likelihood of there being a close relative of the same age present.

In general, the mother is a low-risk play-partner if she obliges. However, mothers also have constrained time budgets and may not have the same priorities for their investment as the young (see section 1.2, Trivers, 1978). Mother eastern grey kangaroos did play with their young, to a degree. There are two possible interpretations of this. Young who practised contact play may have had an advantage over their peers who did not, and young who practised it with individuals other than the mother were more likely to be lost. Thus, it

was adaptive for the mother to play with her young. Alternatively, contact play may be advantageous to the young and may also have been used by the young to manipulate the mother. As long as play between mother and young was not significantly disadvantageous to the mother, and by avoiding playing with the young she was less likely to maximise the number of her genes in the future generations, then mother-young contact play would probably be selected for. This latter argument is derived from mother-young conflict theory (see Trivers, 1978; and Parker and Macnair, 1979).

Overall, I would stress that kangaroos cannot be considered any less playful than the typical eutherian young. Most previous researchers have failed to study the young's behaviour during the pouch-infant phase, which is when young in this study were observed to spend much time in play. The strong mother-young relationship found in kangaroo young and the lack of 'play interactions' with others need not reflect a 'primitive' or 'less complex' social behaviour, as other researchers have implied (e.g. Eisenberg, 1981, Kaufmann, 1974, Caughley, 1962). Social interactions with individuals other than the mother occur in the subadult class, though I have not quantified them. Further, there are adaptive reasons for pouch-infants not to play with individuals other than the mother, for PEP young not to play, and for YAF to play only a little.

Lastly, I would caution against inferring that pouch-infants do not socially interact. Pouch-infants do initiate interactions with other kangaroos in their vicinity. They do this in a subtle manner by directing their 'play hopping' routes in close proximity to the others. I discuss this further in the next subsection.

7.1.2 Differences in rearing schedules according to the sex of the young

Sons and daughters have very different life-histories, hence it may be adaptive for them to behave differently when young. Eutherian males are often reported as spending more time in 'rough and tumble' play, or playing in total more than female young (Fagen, 1981; Sachs and Harris, 1978; Poirer and Smith, 1974; Arnold and Trillmich, 1985; Duncan, *et al.*, 1984). Further, in quite a few species the male young are reported as sucking more frequently than female young (Trillmich, 1986; Reiter, *et al.*, 1978; Lee and Moss, 1986; Clutton-Brock *et al.*, 1982b). Sons may spend less time in close association with their mother than daughters (Berman, 1982a and b; Missakian, 1974; Guinness *et al.*, 1979). There can be differences, too, between sons and daughters, in the types of social interactions they have with others (Simonds, 1974).

Table 105:

Behavioural differences of sons and daughters found in this study

1. *pouch-infant sons suck more frequently when out of the pouch than daughters. This difference was not apparent for YAF (section 5.2).*
 2. *pouch-infant sons played more frequently in the 'rough and tumble' style than did pouch-infant daughters (section 6.7).*
 3. *pouch-infant sons spent proportionally less time when outside the pouch in play than daughters (section 5.2).*
 4. *pouch-infant sons spent more time in contact with their mother than did pouch-infant daughters; while pouch-infant daughters spent more time greater than 2m from their mother (sections 6.5 and 6.7).*
 5. *pouch-infant sons initiated interactions with others excluding the mother, less often than did the pouch-infant daughters (section 6.8).*
 6. *pouch-infant sons' activity-state sequences were less structured than were those of daughters (section 5.4).*
 7. *pouch-infant sons changed their activity state less often than did pouch-infant daughters: possibly this occurred as a function of the sons sucking more often for longer durations than the daughters (sections 5.2 and 5.3).*
 8. *large YAF sons spent more time further than 10m from their mothers than did large YAF daughters (section 6.5).*
 9. *large YAF sons initiated contact with their mothers more frequently than did daughters; while large YAF daughters initiated more moves to further than 2m from their mother than did large YAF sons (section 6.5).*
 10. *small YAF sons tended to rest more than small YAF daughters (section 5.2).*
 11. *large YAF sons tended to graze more than large YAF daughters (section 5.2).*
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This study found these differences in the behaviour of the sexes also occurred in eastern grey kangaroo young (see table 105). The principal exception was that YAF sons were not found to suck from their mothers more than YAF daughters.

The behavioural differences of sons and daughters might have arisen from inherent factors, or from mothers rearing sons and daughters in a different manner (Lee, 1984a). According to current theory on parental investment in the sexes, the optimum *quantity* of investment given to individual young may differ for a parent according to the sex of the young when the life-histories of sons and daughters are different and sons' and daughters' expected lifetime-reproductive-success is differently affected by the investment they received (see section 1.3). However, not only might the theoretically optimum quantity differ, but also the theoretically optimum manner in which investment is distributed through a young's ontogeny may differ with the sex of the young. For example, in sexually dimorphic species sons may benefit from 'extra' nutrition, while daughters may benefit more from 'extra' maternal intervention in agonistic disputes with others. Thus, selection may operate to favour parents who rear sons and daughters in different (but adaptive) manners.

However in this study very few of the differences in the behaviour of sons and daughters appeared related directly to differences in the manner in which mothers reared them (see chapter 6 and summary table 106). The mother's behaviour probably was more affected by her young's behaviour than vice versa. Mothers of sons had a more disrupted pattern in their activity-state sequences and a greater rate of contact-state change when the pouch-infant was out of the pouch than mothers of daughters. Pouch-infant sons were more likely to 'play-fight' with and suck from their mother than were daughters. By these behaviours, they might have disrupted their mothers' behaviour to a greater extent. The mothers were unlikely to have caused the difference in the infant's behaviour, since mothers did not actively 'play-fight' their sons more than their daughters. Further, mothers tended to initiate more of their infant daughters' than sons' sucking bouts.

Nor did mothers appear responsible for the tendency of their small and medium pouch-infant daughters to spend more time than pouch-infant sons when out of the pouch at distances greater than 2 metres from their mother (section 6.5). In fact mothers of daughters were likely to take a more active role in maintaining a close spatial association with their infant than were mothers with sons.

It is possible that I missed subtle behavioural differences between mothers of sons and daughters. But overall I will tentatively conclude that much of the difference in the 'quality'

Table 106:

Differences in the mothers' production of sons and daughters

1. *mothers produced more sons (section 3.7).*
 2. *the inter-PEP interval prior to a son's permanent emergence (i.e. approximately indicates the duration of his pouch-life) was significantly more variable than it was for daughters. Further this interval appeared to vary significantly in relation to the time of year and according to whether the previous young was reared to weaning or lost for sons, but not for daughters (section 3.6).*
 3. *sons were likely to be produced after the production of a male sibling and daughters after the production of a female sibling (section 3.7).*
 4. *more sons tended to permanently emerge at the end of the offpeak season and beginning of the peak season than daughters (section 3.7).*
 5. *more sons than daughters were conceived following several months of relatively high rainfall and possibly during the months of the year when the females tended to be in better condition than they were at other times of the year. More daughters than sons were conceived (relative to the population average offspring sex ratio) during the year when the females were probably in quite poor condition (see sections 3.5, 3.7 and 3.9).*
 6. *Northern mothers produced more sons than Southern mothers (section 3.7).*
 7. *a mother's rate of weaning young was positively correlated with the proportion of daughters to sons that she produced (section 3.7).*
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(table continued)

Differences in the mothers' rearing of sons and daughters

1. *mothers were more active while in contact with their medium pouch-infant sons than daughters (section 6.7).*
 2. *but, mothers tended to contact pouch-infant daughters than sons, in total more frequently while they were out of the pouch (section 6.5).*
 3. *mothers initiated a slightly smaller percentage of their pouch-infant sons' than daughters' 'sucking' bouts (section 6.3).*
 4. *mothers may move at a slower rate when with small YAF daughters than small YAF sons (section 6.5).*
 5. *mothers groomed their small YAF daughters more than passively touching them, while they groomed their small YAF sons as much as they passively touched them (section 6.7).*
 6. *mothers were more likely to move away from their YAF sons, while they were more likely to move toward their YAF daughters (section 6.5).*
 7. *mothers weaned sons more aggressively than daughters (section 6.9).*
 8. *mothers were particularly less gregarious during the permanent emergence of an offpeak son (section 4.3).*
 9. *mothers tended to remain less gregarious following a daughter's permanent emergence for a longer period than for a son (section 4.3).*
 10. *mothers of pouch-infant sons had more disrupted activity sequences than those of pouch-infant daughters (section 5.4).*
 11. *mothers and subadult daughters had trip-home-ranges which overlapped to a greater extent than did those of mothers and subadult sons (section 4.2).*
 12. *mothers and subadult daughters associated with each other to a greater extent than did mothers and subadult sons (section 4.3).*
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of the relationships of mothers and sons and of mothers and daughters appears a function of the differences in the behaviour of the young rather than of the mother. By 'quality' of the relationship, I mean the differing roles of the mother and young in their behavioural relationship, and not aspects of the mother's behaviour which do not directly affect her interaction with her young.

Assuming the above conclusion is valid and the young is in part responsible for the form the relationship takes, there are interesting implications for parental-investment theory. For example, since activity budgets of young may vary between environments (e.g. time spent in play, Baldwin and Baldwin, 1973), the form of the mother-young relationship may vary between environments. I discuss this further in relation to parent-offspring conflict in section 7.2.

In general, it is understandable that the behaviour of sons and daughters will be subject to different selection pressures if it is adaptive for them to behave differently. The mothers' behaviour may be selected for according to their response to the behaviour of their young. However, this conclusion does not preclude the possibility that the processes of natural selection may favour reproductive tactics of mothers which emphasise different types of maternal care for sons and daughters, beyond responding to the behaviour of their young. Such differences in reproductive tactics may not necessarily be reflected in the 'social aspects' of the mother-young relationship. At least, this appeared to be the case in the mother-young relationships studied in this population of kangaroos. I believe that the few differences I found in the behaviour of mothers of different sexed young did reflect different tactics for rearing sons and daughters. I discuss this further in section 7.3. It would be worthwhile studying the form of the mother-young relationship in a population where individual male young are invested in preweaning more intensely than daughters (see section 7.4). One consequence of a difference in the intensity of preweaning investment between the sexes might be that the the social relationships of mothers and sons and of mothers and daughters differ to a greater extent than was found for this population.

7.1.3 Rates of change in the mother-young relationship

The mother-young relationship in the kangaroos at Wallaby Creek was characterised by long periods of relative stasis in form, i.e. the pouch-infant phase and the YAF phase, which were terminated by brief periods of abrupt change, i.e. permanent emergence and weaning.

In part, the abruptness of the change in the mother-young relationship between the pouch-infant and the YAF phases may be a consequence of rearing a young with the aid of a pouch (see also Russell, 1973). A pouch-infant probably relies upon the mother to detect potentially threatening circumstances and respond appropriately. The mother determines the time and duration of her infant's exit from the pouch. However, since mothers did not appear to be able forcibly to cause the young to enter the pouch, the time of pouch-entry was dictated by the mother purely because the infant virtually always was willing to enter the pouch. This strong orientation to the pouch by the infant was dramatically reduced on permanent emergence when the mother started, continually but gently, to move away when the infant attempted to poke its head into the pouch. In this manner the young appeared to be rapidly trained to poke its head into the pouch to suck only for a few discrete bouts per day and not enter.

It is likely that a more gradual training of the young to reduce its orientation to the pouch would increase the probability of separation of mother and infant. By increasing her rejection of the infant, a mother may increase its independence of her (see Hinde and Spencer-Booth, 1971, 1967). In turn, an increase in the level of independence may reduce the infant's ability to detect and respond to its mother's pouch-entry posture, especially since a pouch-infant spends much of its time in play.

The proportion of time the infant spent out of the pouch also increased abruptly around the time of permanent emergence from less than 30% to 100%. When an infant is out of the pouch the mother's activities are quite disrupted and very different from the typical pattern of adult females (chapter 5). Hence, it may not be adaptive for mothers to allow their infants out of the pouch for a longer proportion of the day, unless the infant simultaneously becomes a less disruptive influence on her activity schedule (chapter 6). The behaviour of infants rapidly changed from predominantly play and sucking to a quite adult-like structure and activity schedule during permanent emergence.

However, I doubt that the abrupt transitions I observed in the mother-young relationship of eastern grey kangaroos occur purely as a function of the unique mode of rearing young via a pouch. Certainly, the more commonly reported pattern in the mother-young relationship of mammals is one in which the mother increasingly terminates a greater proportion of the young's attempts at contact or to suck and the young simultaneously becomes increasingly responsible for maintaining their close spatial association (Hinde and Spencer-Booth, 1971, 1967; see section 6.3). However, there are a few studies of eutherian mothers and young

which describe the onset of weaning as very abrupt, with the prior form of the relationship being relatively static e.g. desert bighorn sheep (Berger, 1979a), some ponies and horses (Tyler, 1972; Duncan *et al.*, 1984), and the common seal (Wilson, 1974a). In these latter species the young was commonly responsible for terminating sucking, just as I found for the young kangaroo. This pattern in the mother-young relationship is not necessarily a species-specific characteristic, as mountain bighorn sheep (Berger, 1979a) were reared to the more gradual weaning pattern and were considered weaned at a later age than desert bighorn sheep.

In section 6.10 I proposed that permanent emergence may not always be marked by an abrupt transition in the behaviour of the young eastern grey kangaroo. It is possible that in an environment where an infant plays much less frequently, the mother's activities are much less disrupted when her infant is out of the pouch. Further, an infant who seldom plays may take a greater responsibility for monitoring its mother's behaviour and position in the environment. Consequently, a mother may be more likely to steadily increase the proportion of time her young spends out of the pouch as it approaches permanent emergence in a manner such that there is no abrupt transition between the pouch-life phase and the YAF phase.

I suggest that some local environmental factor may influence the rate at which mothers wean young, possibly the rate at which they invest in young, and, for kangaroos, the abruptness of permanent emergence. As yet there is little information to determine what this environmental factor might be. There may be several types of circumstances in which it is most adaptive for mothers to rear young intensely for the duration of the young's dependent life, but to reduce the duration of this period.

At Wallaby Creek the mothers appeared to be following the strategy of rearing as many young as possible (see section 7.3). Weaning a young in a gradual manner may increase the duration of the young's dependant life.

Perhaps in unpredictable or aseasonal environments mothers may emphasise rearing young at a high rate but shorten the period of the young's dependency. In seasonal and predictable environments mothers may adjust the rate at which they invest in young to the seasonal conditions; a long but less intense schedule of parental investment may 'benefit' the young to a greater extent than a short intense schedule or it may be a less costly schedule for a mother with a long lifespan. I discuss strategies for maternal investment further in section 7.4.

7.2 Parent-offspring conflict?

The mother appeared at least proximately, responsible for initiating the changes in the relationship. Variation in the duration of the phases was significantly related to at least one of the following: the season in which the young was reared, whether the mother had reared a previous young to weaning, whether or not the mother produced peak season young only, and the mother's 'age'. However it is probable that the young had some influence on the changing form of the relationship as I have concluded in section 7.1.3. Both mother and young were responsible for maintaining their association, though the roles of each were quite different. These roles changed through the ontogeny of the relationship for both in a manner which was related to the sex of the young.

Thus, the quality and duration of the mother-young relationship was not merely determined by the mother (see section 6.10 for a discussion of the mother-young 'bond').

As Trivers (1978) and others have noted, both mother and young stand to 'gain' from the relationship; but the theoretically optimum form of the relationship may differ between the two (see section 1.2). Parker and Macnair (1979) suggested that a mother becomes open to manipulation by her young when she risks 'more' (I infer: risks not maximising her genetic contribution to future generations) by not attending to behavioural signals from her young. This is likely to occur when mothers rear young in a variable environment and the quality of their young is not predictable from the level of investment which the young received (*ibid.*).

At Wallaby Creek, mothers were rearing young in variable environmental conditions. The probability of a young's survival varied considerably between years. Moreover, there was some evidence that parent-offspring conflict was a potential part of the relationship (sections 6.5 and 6.10). A son was likely to be more persistent in his attempts to put his head into the pouch during his permanent emergence if the mother was terminating his pouch-life relatively early.

However, conflict need not be obvious, as manipulation of one partner by the other can be subtle (Altmann, 1980). If a mother's activity budget is constrained (Dunbar and Sharman, 1984; Altmann, 1980), or rather the optimum schedule for apportioning her activity directly into reproduction versus self-maintenance is sharply defined, then young may influence the mother's behaviour by interrupting her activities. In this manner the young may manipulate the mother toward a compromise (see Parker and MacNair, 1979).

Kangaroo mothers at Wallaby Creek did appear to be finely balancing the amount of time that they spent in each of four major activity-state categories (chapter 5). It should be noted that my data spanned the daylight hours only. As a mother's young aged she varied the amount of time she spent in surveying by using time that would otherwise be spent in resting. The proportion of time a mother spent feeding appeared to be maintained at a constant level in spite of an increasing disruption to her activities which occurred as her young approached permanent emergence. I suggest that kangaroo young have the potential to influence their mother's activities by the degree to which they disrupt her activities when they are out of the pouch.

The next step for future studies exploring parent-offspring conflict, is to study relationships between the young's behaviour and the probability of the mother altering her behaviour. For example, can young increase the probability of their entry into the pouch by consistently 'hassling' the mother? Alternatively, can young increase the time spent out of the pouch by changing their activity patterns when out of the pouch or by their level of activity when inside the pouch? In particular since sons may be more variably invested in than daughters, are sons more likely to dispute the amount of investment they are receiving and can they influence the mother? Overall, how much of the pattern of a mother's rearing behaviour is reliant upon her young's immediate behaviour patterns?

7.3 The females' general strategy for reproduction

7.3.1 Rates of maternal investment

The average female eastern grey kangaroo at Wallaby Creek produced young at a rate of 1 per 47 weeks. Since most matings involved females with small pouch-young, it was inferred that the majority of females were reproducing according to the delayed blastocyst cycle (see Poole and Catling, 1974). Females typically conceived young while a third to one half way through rearing a pouch-young and would wean their YAF (if not previously lost) about this time. The birth of a young occurred just following the previous young's permanent emergence. The female eastern grey kangaroos could not have produced young at a faster rate unless they reduced the duration of their young's pouch-lives. Indeed, the females of this population were particularly fecund once they had commenced breeding; and YAF were weaned at quite an early age in comparison with other populations of eastern grey kangaroos (section 6.10) (though note that these other populations were either captive or the measurements of YAF age assumed a growth rate for wild young similar to that of captive young).

Sixty-two percent of the young known to have been produced did not survive to weaning. Most of these young were lost in the month following their permanent emergence. However, mothers typically conceived and gave birth to the next young before their current young had passed through the period when the risk of death was high. Hence, unless the mother eastern grey kangaroo aborted the rearing of a young (about a third of the way through its pouch-life), she could not delay further direct investment in reproduction upon rearing one young to weaning; eutherian mothers are reported as commonly employing the tactic of increasing the interval between reproductive attempts upon having reared a young to weaning compared to when they do not rear this previous young to weaning (Clutton-Brock *et al.*, 1982b; Altmann *et al.*, 1978; van Schaik and van Noordwijk, 1985). In sum, most females in the Wallaby Creek study population maintained a high rate of reproduction regardless of their immediate past reproductive history.

In contrast, females tended to commence their reproductive life at a late age as compared to other populations of eastern grey kangaroos.

Overall, since the population did not increase over the four study years, and was not regulated by humans, the type of life-history described above is probably indicative of a level of interfemale competition comparatively high for this species (see Stearns, 1976). Thus selection for the optimum reproductive strategy should be relatively strong. Accordingly, I will assume that the reproductive tactics of the average female in this population maximised the probability of her contributing genes to future generations, given the local conditions.

This strategy should balance the quality of the offspring she rears (i.e. the quality as related to the probability of the offspring reproducing 'successfully'), with the quantity of offspring she produces in her lifetime (see chapter 1; Gadgil and Bossert, 1970; Smith and Fretwell, 1974). Since the rate of rearing young to weaning could not have been greatly increased, I can only assume that the expected lifetime-reproductive-success of a mother was maximised by producing as many young as possible, rather than investing in young over a longer period. Perhaps the 'quality' of each young was either loosely related to the young's expected lifetime-reproductive-success or else the young's probability of survival was not greatly predictable from the amount of maternal investment it received.

I doubt that the average young received a level of investment which maximised the 'benefit' it could derive. I suggest this because there were several elements of female reproductive tactics which, in combination, were consistent with females preferring to invest in reproduction via 'quantity' rather than the 'quality' of the young they produced. These

were:

1. females tended to shorten a young's pouch-life if it was an offpeak son following a son who was reared to weaning;
2. the next young reared after a son who was reared to weaning was more likely to be lost (nonsignificant tendency);
3. sons who were lost had a significantly shorter pouch-life duration than sons who were reared to weaning;
4. during the middle part of the study the females were estimated to be in particularly poor condition, yet the majority of females still reproduced continually;
5. further, during this period most young died;
6. and this increased permanent loss of young was correlated to the females being less likely to retrieve their young when separated from them.

There was one other factor which may have influenced the females to produce young at a high rate rather than invest in each young over a longer period. Females could reproduce aseasonally. In a seasonal environment where the mothers cannot increase their rate of reproduction above one young per year, mothers who are in above-average condition may be more likely to increase their investment in their current young upon a small increment in the young's expected fitness (see section 1.3). In an aseasonal environment mothers may have a higher probability of maximising their genetic contribution to future generations by using this 'extra' investment to maximise their rate of reproduction.

However, a few females at Wallaby Creek did produce young to one seasonal schedule.

7.3.2 Seasonal effects on reproduction

Despite the females' typical tactic of reproducing 1.1 young per year, there were some general seasonal effects on reproduction. More young permanently emerged during the period July to December (mid winter to mid summer: peak young) than during the period January to June (offpeak young). Conception was not so seasonally timed (see section 3.4). Hence, the seasonal peak was likely to be related to an adaptive seasonal timing of the stages of the young's development, rather than related to seasonal constraints on courting activity.

Table 107:

Differences in the production of offpeak and peak young which in combination support the view that offpeak young cost more to rear than peak young

1. *the mothers who did produce offpeak young tended to produce fewer consecutive offpeak young than consecutive peak young (section 3.6).*
2. *mothers of offpeak young tended to be in physically poorer condition while with a newly emerged YAF than this class of mothers with peak young (mothers could expect to be in their poorest condition while with a newly emerged YAF) (section 3.3).*
3. *mothers tended to give their offpeak young much shorter pouch-lives, especially if the young followed a sibling who was reared to weaning, than they gave peak young (section 3.6).*
4. *sons who were lost before being weaned were more likely to have had a short pouch-life than were those who were weaned (section 3.5).*
5. *offpeak young were more likely to die than peak young of the same mothers (section 3.5).*
6. *there appeared to be seasonal effects on the activity budgets of both mothers and young. For example, in winter, but not summer, mothers with PEP young slightly increased the percentage of time they spent feeding during the day, and reduced the percentage of time they spent in rest (section 5.2).*

Differences in the rearing of peak and offpeak young

1. *both offpeak sons and daughters had longer pouch-infant phases than did peak sons and daughters (section 3.6).*
 2. *mothers of offpeak young, particularly sons, who were permanently emerging were less gregarious than those of peak young (section 4.3).*
 3. *offpeak sons tended to disperse at an earlier age than peak sons (section 4.2).*
 4. *mothers who produced only peak young were less likely to reduce their ranging area at permanent emergence than mothers who were observed to produce both peak and offpeak young (section 4.2).*
-

Some mothers did not produce offpeak young. Old mothers and primiparae were particularly likely to produce only peak young.

It is likely that offpeak young were more costly to rear than peak young for the combination of factors I outline in table 107. However, I found only a few differences in the manners in which peak and offpeak young were reared (see table 107). These few exceptions might have contributed toward the relatively high cost of rearing an offpeak young.

It is worth noting that offpeak sons may have been more costly to rear than offpeak daughters since sons affected their mothers' next reproductive attempt to a greater extent than daughters (see section 3.8). Daughters were reared to a consistent schedule regardless of the season. The seasonally related differences in sons' pouch-life durations appeared to arise from offpeak sons being more affected than peak sons by whether or not the mother had just reared a son to weaning.

Whenever possible, mothers may rear offpeak young so that they *receive* levels of investment very similar to those given to peak young. That is peak and offpeak young may gain a similar 'benefit' from the parental-investment given to them, though their *cost* to mothers may differ. However, it appears that mothers are less likely (to afford?) to rear an offpeak young to the average schedule if they have just reared a son to weaning.

Conversely, offpeak sons dispersed at an earlier age than peak sons of the same mothers and an interpretation of this is that there may be some advantage to mothers in producing offpeak sons, even if their cost to mothers are greater and their probability of surviving to weaning are lower than are those for peak sons (see section 4.2 for more detailed discussion). Such a difference between peak and offpeak young in their life-histories might significantly influence mothers' reproductive tactics.

It would be interesting to investigate the proximate mechanisms of whether a female breeds seasonally or aseasonally. It may be related to the two reproductive modes (presence or absence of a delayed blastocyst) and the determining mechanisms.

7.3.3 Maternal investment in sons versus daughters

In other populations of sexually dimorphic large mammals such as red deer (Clutton-Brock *et al.*, 1982b, 1986) and elephant seals (Reiter *et al.*, 1978), the mothers have been reported as investing preweaning more intensely in individual sons than daughters. This has been theoretically explained by Trivers and Willard (1973); I briefly outline their explanation below.

When the expected lifetime reproductive success of the males is significantly more variable than it is for the females, a mother can expect on average that a son will be less likely to reproduce than a daughter. However, if a son becomes an 'alpha male' he is likely to

contribute genes to a larger number of weaned offspring than the greatest number of weaned offspring any sister could expect to rear. Thus, if the following apply:

1. the condition of the young after the parental-investment period is correlated with the condition of the mother during the parental-investment period,
2. differences in the physical condition of young at the end of the parental-investment period endure into their adult life, and
3. sons' expected lifetime-reproductive success is positively correlated to their physical condition;

a mother who is in good condition should preferentially conceive and intensely invest in a son, and a mother who is in poor condition should preferentially conceive and invest less intensely in a daughter. However, the relative cost of the sons and daughters to the respective mothers may be equivalent. Thus the total cost of rearing sons to the mothers of a population would be equal to the total cost of rearing daughters (see chapter 1).

I was not able to test whether these three assumptions were valid in the Wallaby Creek population of kangaroos. However, the estimated lifetime-reproductive-success of males was significantly more variable than for females (section 3.3). As Trivers and Willard (*ibid.*) predicted, mothers appeared to be more likely to conceive sons during that period of the year when they were in good condition (section 3.7). Further, more sons than daughters tended to have their YAF phase timed to span the spring-summer period of pasture growth. The preweaning cost of the average son to a mother was either equivalent to, or only slightly greater than that of the average daughter as there was a nonsignificant trend for more young to be lost following a son than daughter (section 3.5).

However, though maternal investment in some sons may have been intense and spread over a long period, other sons were given quite short pouch-life durations (see section 3.8). On average the durations of the pouch-young and YAF stages for sons were not obviously greater than for daughters; rather, they were just more variable for sons than daughters. Nor was frequency of sucking (an often used indicator of differences in maternal investment between the sexes) significantly different for YAF sons and daughters. The few differences in the manner mothers reared sons and daughters are summarised in table 106. It was not possible to infer from these differences that mothers were consistently likely to invest more intensely in sons than daughters. For some forms of investment daughters appeared to be more intensely invested in than sons.

Basically, a mother's strategy for determining whether to invest in an individual son or daughter did not appear to be related in a *simple function* to her condition, as predicted by Trivers and Willard (1973) (see also the next subsection)! A mother may have tended to conceive a son when in good condition. However, the preferential production of daughters was significantly correlated to a high rate of rearing young to weaning. Thus it is possible that mothers who were likely to rear a young to weaning may have preferentially produced daughters. Although, it should be noted that this relationship might also have arisen because there was a tendency, though nonsignificant, for daughters to be more likely to survive to weaning. Since daughters appear to affect and be affected by their mothers' reproductive history less than sons, a mother might have a higher rate of rearing young to weaning because she had produced more daughters (fortuitously?). Nevertheless, there was also a significant tendency for the 'younger' mothers and South mothers of the study population to produce more daughters than other mothers. These former two groups of mothers were in better-than-average or at least not in poorer condition than others (section 3.2). Therefore mothers were not simply preferentially producing daughters when in poor condition and sons when in good condition. Perhaps, as Altmann (1980) has suggested, mothers may have preferentially conceived daughters when they were likely to influence their daughters' more than their sons' expected lifetime-reproductive-success. I discuss this aspect further in section 7.4.

Overall, there were very few differences in the amount of 'investment' received by sons and daughters that could be interpreted as demonstrating more intense investment in individual sons than daughters (by mothers who were in better than average condition).

However, the mothers of the study population produced and reared to weaning significantly more sons than daughters. Thus mothers invested in total more in sons than daughters prior to their weaning by emphasising the *quantity* of sons they produced, instead of increasing the *quality* of an individual son by investing intensely in him.

A number of authors (e.g. Dittus, 1979; Clark, 1978; Clutton-Brock, *et al.*, 1982b) have suggested that maternal investment in many mammalian species may involve a greater postweaning investment in daughters. There is some evidence (Clutton-Brock *et al.*, 1982b; Johnson, 1985) that the greater natal philopatry of daughters in red deer and red-necked wallabies may penalise mothers by reducing their future reproductive success. Assuming that in the eastern grey kangaroo, daughters similarly exact a postweaning investment from their mothers, the total investment of the mothers in the Wallaby Creek study population

may be balanced between the sexes as Fisher (1930) has predicted (see chapter 1).

However, the exciting implication of the very male-biased offspring sex ratio in this population of eastern grey kangaroos is that mothers have the option of investing differently in the sexes by 'manipulating' the relative quantity versus quality of sons and daughters. The offspring sex ratio is not immutably fixed at parity with individual sons and daughters being equally costly to their mothers.

At Wallaby Creek, on average, mothers produced more sons rather than investing in individual sons intensely or over a longer period. In contrast, red deer and elephant seals are reported as investing in individual sons to a greater extent preweaning than daughters, but produce as many daughters as sons (Clutton-Brock *et al.*, 1982b; Reiter *et al.*, 1978). In what circumstances should either option be followed?

I have mentioned that Trivers and Willard (1973) suggested that maternal investment may be greater in individual sons providing certain terms apply. Perhaps in the population of eastern grey kangaroos at Wallaby Creek one of Trivers and Willard's (1973) assumptions (see above) was violated. In section 7.3.1 I suggested that mothers were, in general, maximising the number of young they produced rather than increasing the 'quality' of individual young. I assume that either there was a weak relationship between any 'further' level of maternal investment given to a young and its expected lifetime-reproductive-success, or that the probability of a young surviving to reproduce was not greatly predictable from the level of maternal investment given.

However, mothers did invest intensely in some sons. I have inferred from *indirect* evidence that the condition of a son at the end of the parental investment period may influence his expected lifetime-reproductive-success. If this is a valid assumption then the quantity of investment a mother gives to her son might significantly influence his expected lifetime-reproductive-success (see table 108). However, even if a mother could invest intensely in a son and thereby significantly increase the probability of his becoming an alpha male, it would not necessarily follow that he would produce many young who would be reared to weaning. Most of the young sired by an alpha male belong to an annual cohort, and the proportion of young surviving from any one annual cohort varied greatly between cohorts. In particular, the variation was unlikely to have been related to any characteristic of the alpha male. Thus, while the males who sire many weaned young may tend to have been sons who were given a higher than average level of maternal investment, the reverse relationship may be quite weak.

Table 108:

Indirect evidence supporting the claim that lifetime reproductive success of sons might be related to their condition at dispersal or at the end of the parental investment period

1. *investment in sons was more variable than it was for daughters. This was inferred from the:*
 - a) *more variable duration of the inter-PEP interval prior to sons' permanent emergence than daughters' permanent emergence (section 3.6).*
 - b) *a son was more likely to affect the duration of the inter-PEP interval following his permanent emergence (the next young's pouch-life duration) and the probability of the next young surviving to weaning (sections 3.5 and 3.6).*
 - c) *a son was more likely to be affected by whether the previous young was reared to weaning (section 3.6).*
 2. *old mothers tended to produce more sons (section 3.7). According to current theory (see section 1.3) older mothers' should be more likely to invest intensely in individual young than younger mothers who should maximise their probability of contributing genes to future generations by rearing young at a higher rate. Older mothers sons dispersed at a younger age than the sons of younger mothers. I believe that early dispersers were probably in better condition than late dispersers, but see chapter 4 for my arguments.*
 3. *mothers tended to conceive more sons following heavy rainfall and typically during the months of the year when they were in relatively good condition. Fewer sons were conceived during the year following weather which was quite atypical and probably stressful for the kangaroos. The females appeared to be in relatively poor condition during that year (sections 3.3, 3.5, 3.7, and 3.8).*
 4. *more sons tended to emerge permanently at the onset of the peak season (section 3.7). Their YAF phase was timed to span the spring-summer growth of pasture. A high early growth rate may be more important to sons than daughters.*
 - i *captive studies by Poole et al. (1982) have found a differential growth rate between sons and daughters following permanent emergence.*
 - ii *large YAF sons tended to spend more time grazing than large YAF daughters (section 5.2).*
 - iii *small YAF sons rested more than small YAF daughters (section 5.2).*
 5. *sons dispersed at a range of ages. The age of a son's dispersal was related to the 'type' of mother he had, the mother's 'age', and the season of his permanent emergence; his age of dispersal was not related to his level of association with his mother or with his male subadult peers (section 4.2).*
-

Does it then follow that mothers should produce 'many cheap' sons rather than 'fewer expensive' sons? Producing many sons reduces the variance of sons' expected lifetime reproductive success. Individual mothers may increase the probability of rearing a son who will be 'successful' by producing many sons. This tactic is adaptive only if 'cheap' sons have a close to average chance of being 'successful'.

There are a variety of circumstances when the probability of a son's survival may be only weakly correlated to the amount of maternal investment given or specifically to his condition at the end of the parental-investment period.

1. types of maternal care which increase the young's probability of survival need not simultaneously act to increase the physical condition of the young. The isolation of mother and young from conspecifics may reduce the probability of a young being separated from its mother or predated, but also be related to a greater loss of physical condition of the mother. The mother may spend less time resting or feeding, in order to survey for predators. Since a mother is presumed to have a limited amount of resources to invest directly in a young at any one time (see section 1.3), the mother might have a range of options as to the manner in which she invests in the young, ranging from maximising its probability of survival but not condition, to vice versa. In strongly sexually dimorphic species I would expect mothers to rear the heavier sex (sons) in a manner which would emphasise increasing their growth or condition at the expense of reducing their probability of survival, but rear the other sex (daughters) emphasising their survival rather than growth or physical condition. I believe that the mothers at Wallaby Creek probably were following the tactics outlined above (see section 4.6). However, this requires substantiation by further research.
2. in an unpredictable environment, the probability of a young's survival might not be closely related to the cost of the young to the mother. This may have applied to the Wallaby Creek population, as there was a high inter-year variation in the mortality of young.
3. there may be seasonal effects on the probability of a young's survival which do not affect the young's physical condition in the same manner. For example, most young in the study population were lost just subsequent to their permanent emergence and were particularly likely to be lost if they permanently emerged during the offpeak season. However, assuming that a son who emerged in the late offpeak season did survive, he

may be in better condition at the end of the parental investment period because his YAF and subadult phases were timed to coincide with the spring-summer growth of pasture, as compared to a late peak son whose YAF and subadult phases were timed to coincide with the poor autumn-winter pasture. The above argument assumes that young permanently emerge in a similar condition regardless of the season, or that any disadvantage in condition of offpeak sons on permanent emergence is offset by the longterm advantage. In the study population offpeak sons dispersed earlier than peak sons of the same mothers, but offpeak young were more likely to die. I have interpreted an early age of dispersal as being consistent with the subadult/small adult being in better than average condition (see chapter 4 and table 108).

4. specifically, in the study population there was such a high mortality of young concentrated in the month subsequent to permanent emergence that the mother's investment in any young was on average unlikely to have a 'return'. Although young which survived tended to have permanently emerged following a longer inter-PEP interval than those who were lost, the difference was not significant. Further the variance for surviving young was significantly greater than for lost young (section 3.5). Consequently, mothers were unlikely to be able reliably to 'predict' from the duration of a young's pouch-life (the interval between the permanent-emergences of the previous young and the current young) whether or not their young would survive past PEP to weaning.

In sum, the relationship between a young's probability of surviving to weaning and the amount of maternal investment it received above some threshold level, could be quite weak. Further, indirect evidence points to this relationship being weak for the Wallaby Creek population. At the same time, from indirect evidence it would appear that a son's expected lifetime-reproductive-success might be related to their condition at dispersal or at the end of the parental investment period. If this is a valid assumption, then in turn this may mean that the amount of preweaning maternal-investment he received if he survived affects his condition and ultimately his lifetime-reproductive-success. This correlation between reproductive success and preweaning maternal investment might be expected to be stronger for a son than a daughter (summary table 108). Using these propositions and conclusions from previous sections in this chapter, I have interpreted the mothers' reproductive tactics for producing and rearing sons and daughters in the following manner.

- a) the mother's priority is to maximise the number of young produced. This spreads

her investment in reproduction over a larger number of individuals each with a low probability of surviving; survival is weakly related to the cost of the young. Mothers typically initiate investment in young prior to 'knowing' whether they will have invested heavily in rearing the previous young to weaning (see section 7.3.1). This may have implications for the sex of consecutive young (see c)). Further, it may explain why the inter-PEP intervals following rearing a young to weaning were not longer than average as reported for several eutherian species. Typically mother kangaroos have already committed investment in the next young and while they should not commit the Concorde fallacy (Dawkins and Carlisle 1976; Sargent and Gross, 1985) by 'throwing good investment after bad', a strategy of rearing a 'low cost' son who may still survive to reproduce can be adaptive.

- b) whenever possible mothers should invest intensely in sons, but preferably in an opportunistic manner that does not reduce their reproductive rate. For example, during that time of the year when the mothers were in good condition, or when the young they conceived would permanently emerge in the late-offpeak or early-peak season, mothers tended to rear sons. Seasonal timing for a son was possibly important to a son's early growth rate.

Apart from an 'opportunistic' advantage which a son may have from the seasonal timing of his developmental stages, early maternal-investment in sons may also affect their age of dispersal. Sons tended to disperse at an early age if their mother was old or a seasonal breeder. These mothers were likely to have given their sons a long pouch-life. I have interpreted the investment given to sons in these circumstances as being greater than average (see chapters 3 and 4 and summary table 108).

- c) mothers tended to produce offspring of the same sex consecutively. This may be an adaptive strategy as mothers could variably invest in sons according to their condition, which was in part a function of whether or not they had reared an older son to weaning. In this manner mothers could maintain their reproductive rate. They could be described as 'hedging their bets' by investing in sons by *quantity* primarily, but for some sons via *quality*. Overall, the more sons a mother produces the more likely that at least one may survive to reproduce. This tactic may not be relevant for daughters as I explain below.
- d) a daughter's condition at the end of the parental investment period might not be as

strongly correlated to her expected lifetime-reproductive-success as it might be for sons. Daughters appeared to be reared in a more consistent manner (sections 3.8 and 4.6). A weaker relationship between parental-investment received and expected lifetime-reproductive-success is commonly assumed for the sex (females in this study population) with the lower variance in reproductive success (e.g. red deer Clutton-Brock *et al.*, 1982b). However, a daughter's value to a mother may be that her probability of reproducing is greater than that of a son. If it is important for females to maintain a high rate of reproduction as I have proposed for the study population, it will probably be important to commence reproduction as soon as is practicable. Thus daughters should be given a level of investment which enables them to reach a weight to reproduce (Millar, 1977) as early as possible and maximises their probability of survival. Any preweaning investment above this may not significantly increase a daughter's expected lifetime-reproductive-success. Daughters were reared in a consistent manner in this population; they affected a mother's next reproductive attempt less and in turn were affected by her previous reproductive history less than sons (section 3.6). Consequently, mothers may have best ensured that they reared daughters to a consistent schedule by producing them consecutively.

The type of maternal care given to daughters appeared to emphasise increasing the daughter's probability of survival, rather than her size. Mothers were more active in maintaining their association with their daughters than sons (sections 6.3 and 6.5), and mothers tended to remain isolated from their conspecifics following a daughter's permanent emergence for a longer period than they did for sons (section 4.3). Further, more daughters than sons emerged in the middle of the peak season. Peak young were more likely to survive than offpeak young.

In this study daughters were not significantly more likely to survive than sons, but there was a trend in that direction. The very heavy mortality of young which occurred in the middle of my study may have obscured any typical difference in mortality of the sexes. This deserves further study.

In addition to a consistent preweaning investment in daughters, a mother may reduce the age at which her daughter commences reproduction, and increase her daughter's probability of rearing young to weaning, if she shares the local resources with her daughter or provides a less competitive social environment. Thus daughters may

exact a postweaning investment from the mother. I discuss this further in the next section.

7.4 Differences between females in their reproductive tactics

Although I did not find that the females differed significantly in their rate of rearing young to weaning, I do not feel able to state this as a conclusion. This is because the data set from which I estimated the range of females' expected lifetime-reproductive-success was based on a maximum of four years' observations per female. This data set was quite small for testing for deviations from a 'normal' dispersion.

Furthermore, the females differed according to whether they reproduced aseasonally or seasonally. And though these tactics appeared related to a female's age, it is possible that a long-term study would find for example, that the age at which females changed tactics was significant in affecting their lifetime reproductive rate and the total number of young they reared to weaning.

In this section I briefly propose a set of age-related reproductive tactics for the female eastern grey kangaroos, discuss the potential importance of matriline, and then discuss a possible relationship between females' access to resources and their reproductive tactics. This latter topic has implications for the reproductive strategies of females in other environments. In general, this section makes more proposals for the direction of future research than absolute conclusions.

7.4.1 Age-related effects on reproduction

The age of a female appeared to influence her general reproductive tactics and her rate of rearing offspring to weaning. However, as the age of a female was measured by an indirect index, based on subjectively assessing a female's physical appearance, I emphasise that I can only *propose* possible age-related tactics.

I summarise the 'age'-related characteristics of females found in this study in table 109.

Although females were no more or less likely to rear an individual offspring to weaning as they aged, the rate at which they reared offspring to weaning significantly decreased with age. Offspring of 'older' mothers appeared to have longer pouch-lives than the offspring of 'younger' mothers. This is in accord with current theory (see section 1.3.1), which states

Table 109: ‘Age’-related characteristics of females in this study. Note that the age of a female was estimated from a subjective assessment of her physical appearance. Consequently the relationships found in this study which involve this ‘age’ index are tentative and require substantiation.

‘Age’:	young (NOT v. young)	mature young- & old- mature	old old & v. old	section
rate of weaning young	higher	moderate	lower	3.3
mean inter-PEP interval	shorter	short	longer	3.3
proportion of all young weaned	same	same	same	3.5
general physical condition	good	moderate	poor	3.3
condition during PEP	poor	poor	poor	3.3
seasonal timing of PEP	peak	aseasonal	peak	3.4
sex of offspring (rel. to pop.)	females	either	males	3.7
mean subgroup size	smaller	larger	smaller	4.3
trip-home-range size	smaller	larger	smaller	4.2
mean annual home-range size	larger	larger	smaller	4.2
proportion of interactions won	fewer	more	more	4.5
number of interactions	more	fewer	fewer	4.5
age of sons’ dispersal	older	older(peak) younger(offpeak)	younger	4.2

that as older females are less likely to survive to reproduce again they should invest in a current offspring at a greater cost to themselves. The mother's future expectations of rearing offspring to weaning decrease as the probability of her continued survival decreases over time. Since the probability of an offspring surviving is quite low, as a mother ages her expectations for further reproduction more closely approach her offspring's expected lifetime-reproductive-success.

'Old' females preferentially produced sons. This too is in accord with the above mentioned theory (see section 1.3 and 7.3); sons may 'benefit' more than daughters from an above-average preweaning investment. There was some indirect indication from my data that sons of the 'old' females were invested in more preweaning than were the sons of 'younger' mothers. They dispersed at a significantly earlier age and tended to follow longer inter-PEP intervals (had longer pouch-lives) than those of 'younger' mothers.

'Old' females timed their offspring's permanent emergence to the peak season. Peak offspring were more likely to survive than offpeak offspring, and these former offspring also might be less costly to produce (see table 108). I infer that 'old' females would have risked fewer offspring surviving had they reproduced aseasonally or maintained the high rate of reproduction of 'younger' females. 'Old' females also tended to be less gregarious than other females. This could have improved the probability of their offspring surviving (see section 4.6).

Since the 'older' females averaged a poorer condition than the other females, they may have been less able to invest at an intense rate in offspring, though they could invest in an offspring over a long time span. Thus 'old' females may time the very costly stages, i.e. those around permanent emergence, to the peak season to maximise the 'benefit' directly derived by the offspring from the rate of investment given. In this manner 'old' females may maximise the probability of their offspring surviving.

Assuming the above holds true, there may be a strong relationship between when a female changes reproductive tactics as she ages and her probability of rearing offpeak offspring to weaning. This deserves further study as it has implications for understanding how females maximise their genetic contribution to future generations.

'Young' females averaged a high rate of production of offspring. However, they began reproduction at a relatively late age, with a peak-season offspring. Reproduction was probably more 'costly' to these females than to the mature females, who similarly reproduced continually, as the 'young' females tended to lose relatively more condition (section 3.3).

I doubt that the heavy cost of reproducing for these females was necessarily correlated to 'extra benefit' gained by the offspring, i.e. 'benefit' above the average 'benefit' gained by its peers. 'Young' females' sons tended to disperse at a late age. In section 4.6 I suggested that a late dispersal age appeared more consistent with a low rather than high level of parental investment. Moreover, late dispersers were not likely to be gaining 'extra' investment directly from their mothers since the sons' age of dispersal was not significantly related to their level of association with their mothers. Finally, the offspring of 'young' females were as likely to die as other females' offspring, even though they permanently emerged in the peak season. A peak-season timing should have meant that these offspring were less likely to die, if they received a level of investment similar to that received by the offspring of the 'mature' mothers, who reproduced aseasonally.

The apparent heavy cost to these 'young' mothers of reproducing might have been related to their physical immaturity or their social position within the female social organisation. 'Young' females tended to be harassed by others to a greater than average extent. In addition or perhaps consequently, 'young' females became less gregarious for a longer duration around the time of their offspring's permanent emergence than did other females. If this reduction in gregariousness is associated with an increase in a mother's time spent surveying (section 5.2, Southwell, 1981; Jarman, 1987), then these mothers may be likely to lose condition because they would spend less time feeding or more likely according to my data, they would spend less time resting (section 5.2).

'Young' females tended to produce more daughters than the other females in this population. Though, as I have mentioned above, this is in accord with current theory of investment differences in sons and daughters, it is worth noting that individual daughters were estimated to affect their mother's subsequent reproductive attempt to a lesser extent than sons. Consequently, since 'Young' mothers may be maximising the number of offspring they produce, rather than the 'quality' of those offspring, it is appropriate that they produce daughters rather than sons. In addition, both mother and daughter born early in the mother's life, might gain later by forming a 'feeding coalition' whereby they have the advantage of feeding in a group but not the disadvantage of harassment by others (Dunbar, 1984). However, this proposal requires further research.

The 'mature' females also tended to maximise the number rather than quality of offspring they produced, and many of these females reproduced aseasonally. This may be the prime period in a female's reproductive life. These females tended to seclude themselves

around their offspring's permanent emergence for a shorter period than did the 'younger' or 'older' females (chapter 4). They were most likely to be following the typical strategy of reproduction outlined in the previous sections: that of reproducing offspring at a high rate, preferentially producing sons when in good condition, but daughters when either in poor condition or when they have access to consistently high quality pasture, generally producing more sons than in daughters, and investing in those sons more intensely preweaning than daughters in an opportunistic manner.

One particularly interesting question to research further is: do mothers preferentially conceive daughters when young and sons when old, because

- a) it is adaptive for older females to invest in offspring at a greater cost to themselves; or because
- b) it is adaptive for females to invest in daughters when young, so that both may benefit by reproducing in each other's company.

7.4.2 The possible importance of matriline

Johnson (1986b) has suggested that the tendency of mammalian males rather than the females to disperse might be related to a different effect of dispersal on the age of first reproduction between the sexes. Eastern grey kangaroo males are unlikely to begin reproduction until 8 years or older (Jarman, *pers. comm.*). Therefore any temporary set-backs to growth or maturation caused by dispersal may not significantly increase the age at which they commence reproduction. Conversely, a relatively early commencement of reproduction might significantly affect a daughter's lifetime reproductive success, at least in the study population, because an important part of a female's reproductive strategy appeared to be maximising the number of offspring produced.

Dispersal may reduce a daughter's physical condition or be costly by taking up valuable time which otherwise would be directly involved in reproduction. A daughter who dispersed may be subject to severe harassment by older, non-related adult females. Harassment of 'Young' females is readily apparent even within the 'local sets' of females. Young females who are commencing reproduction tend to be less gregarious than the middle-aged females. Assuming that relatives are more tolerant of each other and that aggregating in groups is advantageous, either to a female's general activity schedule or by reducing her probability of being predated, it may be that daughters who aggregate with close relatives commence

reproduction earlier, rear higher 'quality' young, are less likely to die at an early age, or in general rear a greater proportion of the young to weaning (see van Noordwijk and van Schaik, 1987).

It was beyond the scope of this thesis to compare lifetime-reproductive-success of females who dispersed compared to those that did not. Nor was I able to compare the reproductive success of females without to those with several close relatives. These are complex topics. For example, matriline may have a depressive effect on the individual members' success in reproduction (Clutton-Brock *et al.*, 1982a and b; Johnson, 1985), while increasing the inclusive fitness of the respective gene-line in general. Overall, because

1. no females migrated into the study site and few females emigrated;
2. mothers and daughters tended to maintain a preference for each other's company into the adult life of daughters;
3. females were organised into 'socially' defined 'sets'; and
4. females had preferential associates which were not necessarily their closest geographically sited neighbour nor even the closest neighbour who was reproductively synchronised nor a female of a similar 'age';

it is possible only to propose that it is adaptive for daughters to remain in their natal home range and associate with close relatives. Long-term research is required to substantiate my suggestion that sharing her home range with close relatives may influence a female's age of first reproduction, and the ages at which she changes reproductive tactics.

7.4.3 Differences between females in their production of sons and daughters

In section 3.8 I concluded that some mothers appeared to be preferentially conceiving daughters for a reason other than that they were in poorer than average condition, and the simplest explanation which would fit my observations was that females who had consistent access to high quality pasture may tend to produce more daughters. This proposal requires substantiation by further research.

However, the advantage of preferentially producing daughters could be related to the greater probability of a daughter reproducing compared to a son (an estimated 22% of daughters produced breed, 7% of sons produced breed, and 3% of sons produced become

alpha males). Further, assuming that females differed in their access to the local resources and that daughters inherited their mothers' local resources or her ease of access to them, then mothers might have the potential to influence their daughters' expected lifetime success to a greater extent than their sons' expectations.

There was a low probability (38%) of any young produced surviving to weaning age. However a mother might maximise the probability of every young she produced surviving to weaning by producing daughters rather than sons. Daughters were less likely to affect the probability of the following young surviving. Moreover, if the daughters survived to weaning there was a higher chance they would reproduce than for sons, especially if the mother could influence her daughters' reproductive expectations. Sons' expected lifetime-reproductive-success appeared unlikely to exceed daughters' expectations unless he became an alpha male; and even alpha males could expect to contribute an extremely variable number of gene-bearing progeny to the future generations (Appendix A). Overall, a mother would appear to have a better probability of contributing genes to future generations through the production of daughters, if both she and her daughters have an above-average chance of reproducing 'young who will reproduce' (see also Armitage, 1987).

Alternatively, mothers with access to resources of high and consistent quality may be able to invest preweaning in individual sons at an intense rate, while simultaneously maintaining a high rate of reproduction. They may invest in daughters postweaning and be more likely than the other mothers of the population to produce the sexes in a 1:1 ratio.

Overall, much more research is required in this very exciting field, as it is abundantly clear from the tactics of the Wallaby Creek females that individuals do have options of preferentially rearing one sex and can vary the schedules to which they rear young. I have been unable to determine whether the females balanced investment between the sexes according to their individual condition or whether they were also able to assess their condition relative to their peers' condition and alter their tactics accordingly.

7.4.4 Implications of females' flexibility of reproductive tactics

Eastern grey kangaroo females in other populations are probably following different reproductive tactics to that of the average female in the study population. I suggest this because, according to Johnson and Jarman (1983) offspring sex ratios vary between populations in a relationship with the local average rainfall. The offspring sex-ratio is male-biased in areas with either of the extremes in average annual rainfall, and is slightly biased toward female

offspring in areas of moderate rainfall. Therefore, assuming, as Fisher's (1930) hypothesis proposes, the mothers of a population invest in total equally in sons and daughters, mothers in populations with offspring sex ratio biased to females may be investing in each son more intensely than in each daughter: while since more sons are produced in this study's population the converse should be true.

Clutton-Brock *et al.* (1986) have suggested that for red deer what may be selected for in each population could be a similar set of rules for determining optimum rearing schedules for sons and daughters, according to the environmental constraints on reproduction and a female's physical condition, or the degree to which her condition fluctuates. Since this study has shown how flexible females can be in their reproductive tactics, it may be used to predict the tactics employed by females in other populations.

Emlen *et al.* (1987) has provided theoretical evidence that in avian species in which sons help with rearing subsequent clutches, the male-biased sex ratios of offspring may be the result rather than the cause of the 'help' given by sons. If this finding is valid, it is possible that in mammalian species in which there is postweaning investment in daughters, a more intense preweaning investment in sons than daughters or male-biased offspring sex ratios also may be a result rather than a cause of the postweaning investment.

I will assume that in most populations of eastern grey kangaroos sons disperse while daughters are philopatric and exact a post-weaning cost from their mothers. In order to balance investment between the sexes, mothers may either increase the preweaning investment given to sons or increase the relative number of sons produced. According to Trivers and Willard (1973) mothers might be expected to invest more intensely preweaning in individual sons than daughters, when such an investment is strongly correlated to an increase in the son's expected lifetime-reproductive-success. If this relationship is weak, mothers could balance investment between the sexes by producing more sons than daughters and invest preweaning in individuals of either sex equally.

However, it is important to realise that it may not be possible for mothers to rear young in a manner which maximises both the probability of a young's survival and its physical condition at the end of the parental-care period (section 7.3). Further, mothers may emphasise these aspects differently for sons and daughters.

When the probability of a son's survival and his physical condition are weakly correlated, their relationship with his expected lifetime-reproductive-success may be quite different. In some circumstances, the probability of a son surviving may not be strongly correlated to the

level of maternal investment given, despite a relationship between a son's expected lifetime-reproductive-success and the level of maternal investment he received. In this case mothers might 'hedge their bets' by producing more sons than daughters, but intensely invest in sons in an opportunistic manner.

However, there are environmental constraints on the production and rearing of young. The maximum rate at which mothers can rear young may be influenced by the nature of the environmental fluctuations.

Mothers rearing young in a strongly seasonal environment might spread investment in individuals over a longer period than mothers in an aseasonal environment (see section 1.3). In a seasonal environment, the rate of rearing young is typically fixed at 1 or less per year. Mothers in above-average condition do not have the option of investing in more young than others. Consequently, these mothers may preferentially produce the sex which will benefit most from 'extra' preweaning investment. If this sex is sons, then the offspring sex-ratio may approach parity.

In an unpredictable environment, such as that in semi-arid areas of Australia, or a highly productive but unpredictable environment, such as this study site, where the rate of reproduction or the probability of the survival of young is highly correlated to environmental fluctuations, the mother's best tactic may be to invest in as many offspring as possible (for the arid environment when conditions are favourable), rather than investing intensely in each young at a cost to maximising the rate at which young are produced. Young should be reared intensely and over as short a period as possible. Mothers may rear more sons than daughters as, on average, preweaning investment in individuals of either sex may be equal. However, this strategy does not preclude preweaning investment in sons being given intensely in an opportunistic manner, if the physical condition of sons at the end of the parental-investment period (which occurs on dispersal) is more strongly correlated to their lifetime reproductive success than it is for daughters.

Overall, I suggest that there are two potential factors which may influence whether it is more adaptive for a mother to invest in sons by producing them in 'quantity' or by increasing the 'quality' of each reared:

1. the relationship between the probability of a son reproducing 'successfully' and the level of maternal investment he received; and
2. the seasonal nature or predictable nature of the environment.

These two factors may be inter-related. Further research is required to disentangle the relative importance of these factors for mothers' rearing tactics.

Finally there are several implications of commencing with the assumption that a greater postweaning-investment in the nondispersing sex is almost inevitable. One is that, as daughters are less likely to disperse in many mammalian species, there is less likely to be highly biased offspring sex-ratios favouring daughters. Reviews of offspring sex-ratios have often noted the rarity of female-biased sex ratios in mammalian populations (Clutton-Brock and Albon, 1982; Trivers and Willard, 1973). Secondly, it may not be necessary for sons to have a more variable lifetime-reproductive-success in order for it to be adaptive for mothers to invest in more of them than daughters. Thirdly, as I mentioned in the previous subsection, mothers may differ in their production of the sexes according to their ability to invest [in their daughters] after weaning, not just their ability to invest intensely [in sons] preweaning.

In conclusion, if the strategies of mothers of other mammalian species are as flexible as I believe is the strategy of mother eastern grey kangaroos, then in order to understand the factors which influence females' reproductive tactics, long-term studies which measure a wide range of life-history variables, as well as describing the variation in individuals' behaviour, are obligatory. For example, as the 'quality' of offspring need not be highly correlated to the probability that they will survive, studies which relate offspring reproductive success to the parents' tactics are required.



Figure 92: "...and this is the tail-end mum?" A very small pouch-infant under its mother.