

## **Chapter 3**

# **Female reproductive ecology**



Figure 9: *Time flies ... "I'm sure I fitted in here somehow mum?"*

A young at the beginning of the permanent emergence phase, poking its head in the pouch.

### 3.1 Introduction

According to current theory (Williams, 1966a; Dawkins, 1976) females compete with each other to contribute a greater share of the next generation's gene pool. But only recently have investigations shown that females as well as males may have a quite variable level of success in rearing young and that they too may use a variety of reproductive strategies (Wasser, 1983; Clutton-Brock *et al.*, 1986). Different maternal rearing strategies may be related to inherent differences between the mothers. Among others, inherent differences may be based upon rank-related access to the local resources (Silk *et al.*, 1981), age (Clutton-Brock *et al.*, 1982b), or physical condition (Verme, 1983).

A female's rearing strategy may also vary according to her young's expected life-history. Not all young produced have a similar probability of reproducing. Some young may be more likely to die than others. Alternatively, they may be less likely to gain condition at the same rate as others per unit of maternal investment. If their condition at the end of parental investment is correlated with their expected lifetime reproductive success, those young who gain condition at a slower rate may be more costly to rear or have a reduced expected lifetime reproductive success. Young produced during a period when many other young were produced and survived may also have a reduced expectancy of reproductive success compared to young produced during a period when relatively few young survived. The different life-histories of young may be a function of, for example, the season in which they are reared (Werren and Charnov, 1978), local environmental fluctuations, or their sex (Trivers and Willard, 1973). In general, if a young's expected lifetime reproductive success varies in a predictable manner with its life-history, and the form of this life-history can, in turn, be predicted by the mother, then it may be adaptive for the mother to invest in each young variably according to its expected life-history (see chapter 1).

With the foregoing in mind, in this chapter I develop an ecological perspective of maternal rearing strategies for the female eastern grey kangaroos at Wallaby Creek. The first half of the chapter outlines the general pattern of reproductive schedules and the average rate of rearing young to weaning. The second half discusses some variations which occur in the rearing schedules and proposes how and why some of these variations may arise.

## 3.2 The female reproductive classes and their duration

### 3.2.1 The female reproductive cycle

According to Poole and Catling (1974) and Kirkpatrick (1965c) there are two types of reproductive cycles found in eastern grey kangaroo females. Most females return to oestrus toward the end of their current young's occupation of the pouch, at about 297 days (Kirkpatrick, 1965c) to about 320 days (Poole, 1975) after birth or within days upon the loss of their pouch-young. These females may cycle into oestrus several times before conceiving (cycle=45.6days, Poole and Catling, 1974). Poole (1975) found gestation to be on average 36.4 days. As young may continue to be suckled more than 227 days after permanently emerging from the pouch (PEP) (*ibid.*), a mother may conceive, give birth, and suckle a pouch-young while also suckling a young-at-foot (YAF) on a different teat.

However, some females (Poole and Catling, 1974; Kirkpatrick, 1965c; Clarke and Poole, 1967) return to oestrus somewhere between 112 and 243 days after a birth; that is, in the middle rather than toward the end of the pouch-life of the *current young*. These young which are conceived prior to the permanent emergence from the pouch of the *current young*, remain as dormant blastocysts until about 2 weeks before the *current young* does permanently emerge. At this time the blastocyst begins to develop into a foetus. This foetus develops in utero until its birth approximately 2 weeks following permanent emergence of its older sibling (*ibid.*). Consequently, the interval between permanent emergence from the pouch of the previous young and the permanent emergence of new young, represents the latter's pouch-life duration plus about 2 weeks. This mode is referred to later as the delayed blastocyst cycle.

In fig. 10 I have schematically outlined the relative timing of fundamental events in the female eastern grey kangaroo's reproductive cycle at Wallaby Creek (please note that in this section I am concerned to present a general description of the timing of reproductive events and the reader is referred to section 3.6 for the variation involved). However, as I did not catch and examine the females, I have used the results from the above mentioned studies to make inferences about the females' physiological condition. It was possible for me to estimate the duration of time a female spent in the reproductive classes (as outlined in section 2.3.3) to the nearest week.

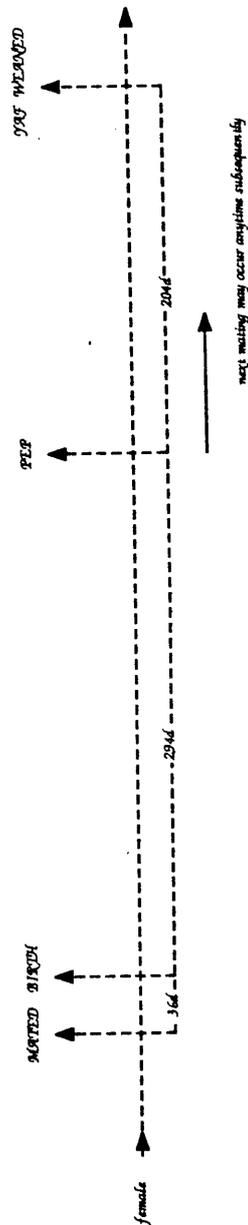
At Wallaby Creek females may breed throughout the year, although there is a seasonal peak with most young permanently emerging in late winter and spring (section 3.4). Of all matings and intense courtships seen by the field researchers at Wallaby Creek during the period from April 1982 to March 1986, 74% (48/65) involved females with small pouch-young; these young will emerge permanently on average 18.6 weeks (SE 0.54, N=37) after their mother's mating. The other 26% (17/61) of matings or intense courtships involved

Figure 10: The two modes of reproductive cycles:

- A. The cycle without a delayed blastocyst.
- B. The cycle with a delayed blastocyst.

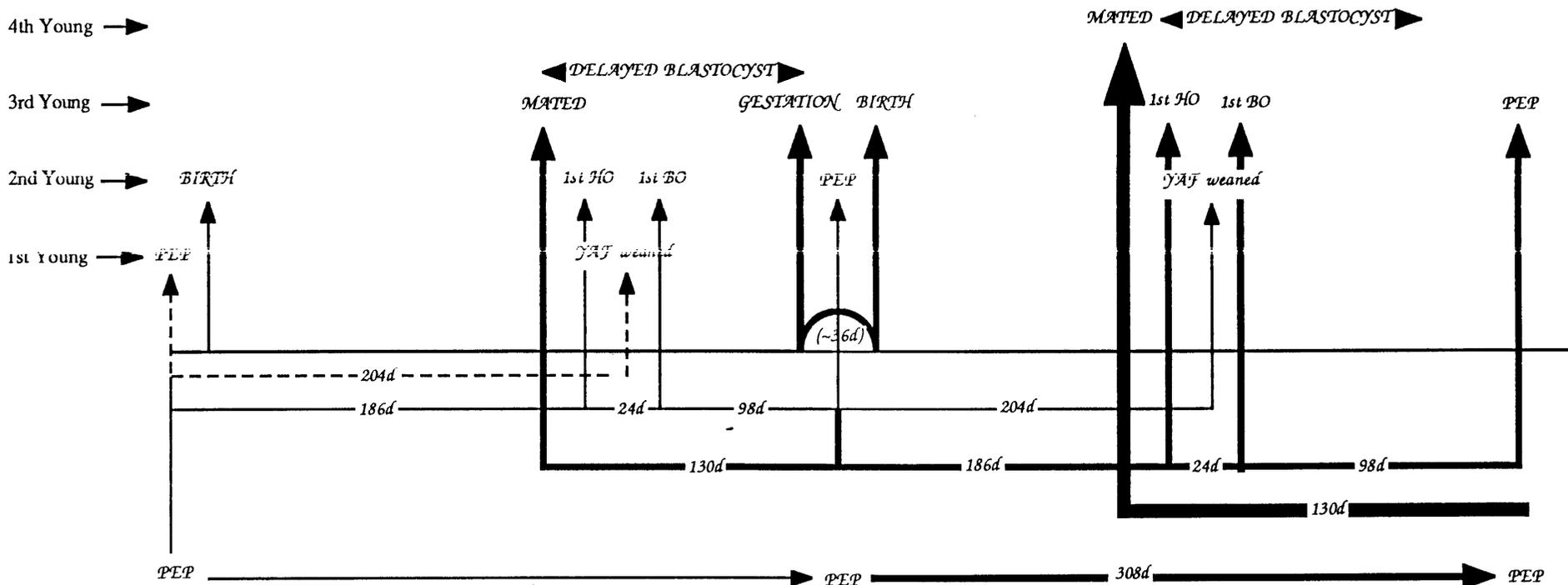
The duration of intervals between events are means from data gathered in this study, with the exception of gestation (the 36 days is taken from Poole (1975)). Units are days (d). HO means head out of the pouch for the 1st time. BO means whole body comes out of the pouch for the first time. The sequence of events depicted in the A reproductive mode for a single young may be repeated for the next young anytime following the permanent emergence (PEP) of the current young. The sequence of events (e.g. mating/conception, birth, 1st head out, 1st body out, PEP, weaning) always overlap with mating/conception of the next young occurring about 1/2 to 2/3 of the way through the current young's pouch-life.

A: Reproductive Modes: cycle without delayed blastocyst



2 young - identified by: - - - - - 1st  
 - - - - - 2nd - same cycle as for 1st, may or may not overlap 1st's YMY phase,  
 never overlaps 1st's pouch infant stage

*B: Reproductive Modes: delayed blastocyst cycle*



inter-PEP interval  
est. mean = 308 days  
est. range = (245 to 336)

4 young - indicated by: - - - - - = 1st  
 \_\_\_\_\_ = 2nd  
 \_\_\_\_\_ = 3rd  
 \_\_\_\_\_ = 4th

1cm = 30 days

females without any pouch-young bulge, and included 3 nulliparae. The previous young of these 'without pouch-young' females may have permanently emerged from the pouch (PEP) any time greater than 1 week previously. No females were observed to be mated while with a medium or large pouch-infant (see section 2.3, for description of classes).

About the time when a female with a small pouch-young is mated, her current young is typically just beginning to poke its head from the pouch. This first protrusion from the pouch takes place on average 26.6 weeks (186 days) since the last young permanently emerged from the pouch. From this point on, for the next 17 weeks (122 days) on average (see table 8), the young (now a pouch-infant, see section 2.3) gradually increases the time it spends protruding or temporarily emerging from the pouch, until its own permanent emergence at 285 to 294 days old (see chapters 5 and 6).

Following permanent emergence, young at Wallaby Creek were observed to continue to be suckled by the mother, on average for the next 29.1 weeks (SE 0.51, N=55). These young-at-foot (YAF) are weaned around the time when the mother's next young is beginning to poke its head from the pouch, and the mother is most likely to be mated.

I have plotted the mean ages of first head out, first complete exit and permanent emergence found for the Wallaby Creek young onto the weight-by-age curve of Poole *et al.* to highlight the developmental changes which occur in the young (fig. 11).

The average inter-permanent-emergence interval (inter-PEP interval) for the females was 47.4 weeks (SE 0.78, N=113) (and by averaging each female's average inter-PEP interval 47.1 (SE 0.97, N=50)).

Overall, the percentage of matings/intense courtships which involved females with small pouch-young was exceptionally high compared to previous studies (Kirkpatrick, 1965c; Poole, 1973, 1975,) which reported less than 30% of female eastern grey kangaroos in the field to be carrying dormant blastocysts (i.e. females who would have been mated while with a small pouch-young). Most young at Wallaby Creek conceived in the middle of their previous sibling's pouch-life are born about 2 weeks after the previous young permanently emerges, emerge fully from the pouch for the first time about 30 weeks of age, and are weaned prior to the next sibling's first emergence from the pouch. I discuss the question of whether females were typically conceiving and rearing young to permanent emergence via the delayed blastocyst cycle further in the next section.

The age for first emergence from the pouch reported here, 30 weeks, is the earliest age of any reported in the literature. Kirkpatrick (1965c) stated an age of 35 weeks and Poole

Table 8: The mean duration of female reproductive classes. I was able to estimate the duration of time a female spent in a reproductive class to the nearest week. When I calculated mean durations of these classes I have taken the result to one decimal place. However the means below have been converted into days spent in a class. I did this to make my results easily compared to other researchers' results (see text). Brief descriptions of pouch-young stages are included.

female reproductive class		duration of each class (days)		
		sample size	mean	SE
	prev. young PEPed		0	
7&8	no/small pouch-young	70	186	
9	diminutive pouch-infant	70	26	0.5
10	small pouch-infant	70	16	0.4
11	small pouch-infant	70	20	0.6
12	medium pouch-infant	70	20	0.7
13	large pouch-infant	70	17	0.6
14	very large pouch-infant	70	14	0.4
15	young permanently-emerging from the pouch (PEP)	70	9	0.4
	<b>total</b>		308	
16	small YAF		84	
17	large YAF no/small pouch-young		120	
	<b>total</b>	55	204	3.6

The stage of development of the pouch-young as it corresponds with the mother's reproductive class.

class 9	first poking head from the pouch
class 10	first exits from the pouch
class 11	beginning to move around the mother when out of the pouch
class 12	
to	becoming increasingly co-ordinated
class 14	
class 15	most of the time is spent out of the pouch. also beginning to physically fill out

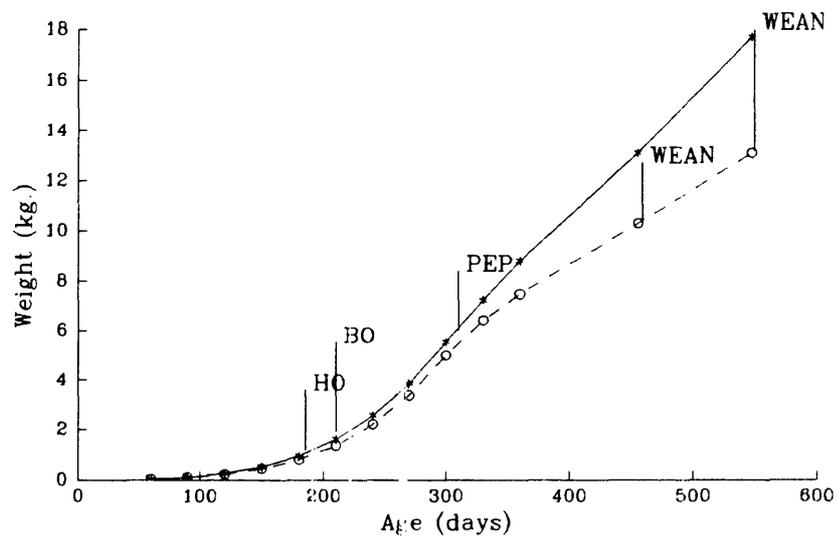


Figure 11: *The weight-by-age curve for young taken from Poole et al. (1982). The sexes are plotted separately: males — continuous line, and females — broken line. The estimated timing of the following events are pointed to on the curve: HO — 1st time young has head out of the pouch, BO — 1st time young fully leaves the pouch, PEP — when the young permanently emerges from the pouch, and WEAN — the young is weaned sometime between the two ages. The timing of these events were determined from averages of the young's ages calculated from data from the study population.*

(1975) mentions a range from 35 to 47 weeks, with an average of 40 weeks.

### 3.2.2 Estimating pouch-life duration

While the average inter-PEP interval was 47.4 weeks, it was extremely variable, ranging from 35 to 96 weeks. How much of this variation could be expected to represent a variation in true pouch-life duration, rather than variation in the delay of conception, or variation arising from the loss of a diminutive pouch-young. The loss of a diminutive pouch-young would extend the duration of the interval between two permanent emergences to include the pouch-life of the lost pouch-young and that of the young who next permanently emerged.

If the sample of observed matings/intense-courtships accurately reflected the proportion of conceptions for the population in general, which occurred in the middle of a pouch-life rather than after permanent emergence then 77% (48/62, note the 3 primiparae excluded) of inter-PEP intervals may represent the duration of a pouch-life plus 2 weeks. However, if some of the 23% of females who were mated/courted subsequent to a permanent emergence (i.e. with no pouch-young) conceived a young via the delayed blastocyst cycle, but then lost the blastocyst or pouch-young then, at minimum, 70% of inter-PEP intervals would represent a pouch-life duration plus 2 weeks.

It is unlikely that all of the females mated when in the 'no-pouch-young class' had previously conceived during the 'with small-pouch-young class' but then lost the young. I suggest this because females may enter lactational anoestrus, according to Poole (1973, 1975), for the full duration of a young's pouch-life, or even longer. Most previous field work (Kirkpatrick, 1965c; Poole, 1973; Jaremovic, 1984; Southwell, 1981; Kavanagh, 1977) emphasise either that only a small proportion of females have delayed blastocysts or that most of the females were breeding within a seasonal peak. A seasonal peak in breeding is less likely to arise if most females are breeding continuously, one young every 10.5 months (Poole, 1975), via the delayed-blastocyst cycle. Thus, to account for the particularly long inter-PEP intervals, the elongation of anoestrus is as likely as, or even more likely than the loss of a young produced via the delayed-blastocyst cycle.

Moreover, at Wallaby Creek the elongation of the anoestrus condition was more likely to explain the observation of very long inter-PEP intervals (see fig. 12 for frequency distribution) as very few females lost pouch-young, at least once a pouch bulge (age estimated at 2 months) was discernible. Also, 29% (4/14) of the matings/intense-courtships of females with no pouch-bulge involved a female whose last young permanently emerged more than

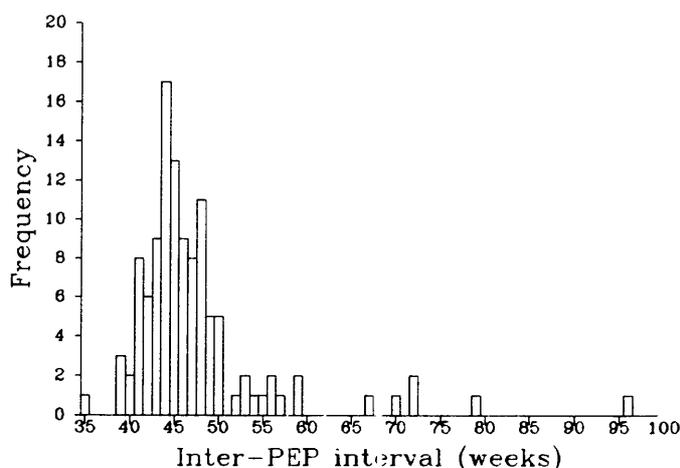


Figure 12: *The frequency distribution of inter-PEP intervals.*

11 weeks previously. These females cannot have come immediately into oestrus upon losing a pouch-young, as I should have been able to discern a pouch-bulge in the few weeks before such a loss. They could have lost a diminutive pouch-young and cycled several times before I observed their mating/intense-courting.

However, I believe that conception at Wallaby Creek is highly probable upon mating, as no females with medium or large pouch-infants were observed to be mated or intensely-courted. Also, only 1/65 of the observed matings/intense-courtings was of a female who was known to have been mated/intensely-courted less than 5 months previously. Further, the average interval between an observed mating/intense-courting of a female with no pouch bulge and the subsequent permanent emergence was 49.3 weeks ( $N=10$  SE 1.1 range 44--56). Thus most of these females probably did conceive, at this time, the young that was next observed to permanently emerge.

Was the sample of 65 matings/intense-courtings an accurate reflection of the general proportions of the types of matings that occurred in the Wallaby Creek population?

A female who was being courted was extremely conspicuous. They typically had a retinue of males of all sizes with them, and they moved far more frequently during the day of intense courting than females do at any other time (see Jarman and Southwell, 1986; Jarman, unpubl.). Subsequent to a mating, females had blood on their cloaca (pers

obs.) and were often still accompanied by the alpha male (most dominant male in the local population). Consequently, I would expect that for the duration of any field trip, at least 1 of the 3 field researchers would notice any courting that occurred.

As the population was monitored for approximately a third of the 4 year span within which the 65 observed matings/intense-courtings occurred, I estimate that probably about 130 matings were missed by our absence (total of 195 matings). An alternative estimate using the average number of breeding females in the population (47), the average inter-PEP interval (47 weeks), and assuming that females were typically conceiving upon a mating and were unlikely to lose diminutive pouch young, comes to 208 matings. This 2nd estimate is consistent with the first estimate of 195 matings. Thus, a sample size of 1/3 of the total matings should provide a fair representation of the types of matings which occurred in the population.

Therefore, I believe that at least 75% of the inter-PEP intervals at Wallaby Creek involved the young being conceived via the delayed-blastocyst cycle.

It is also possible to check this prediction roughly. The subtraction of 25% of the long inter-PEP intervals from the calculation of the mean inter-PEP interval should indicate pouch-life duration plus 2 weeks, because the birth of the young is expected to occur 2 weeks following a permanent emergence (Poole, 1975). This average interval should be equal to the average interval between observed matings of females with no pouch-young and the subsequent permanent-emergence of the conceived young minus 3 weeks. Gestation is 5 weeks in duration (Poole and Catling, 1974).

The average interval between a mating of a female without a pouch-young and the permanent emergence of the young was 49.4 weeks (SE 1.03 N=10). The average interval for the shortest 75% of inter-PEP intervals was 44.1 weeks (SE 0.28 N=83). As 49 weeks minus 3 weeks equals 46 weeks which is greater than the average inter-PEP interval of 44 weeks, for the predicted delayed-blastocyst-cycle intervals, it appears highly probable that most of the short intervals (35 weeks to 48 weeks) were derived from a delayed-blastocyst cycle.

The range estimated from the Wallaby Creek data, of 35 weeks to 48 weeks for an inter-PEP interval arising from a delayed blastocyst is quite consistent with the shortest and longest pouch-durations as reported by Poole (1975) and Kirkpatrick (1965c), 42 to 51 weeks.

Henceforth I use the inter-PEP interval as an index of pouch-life duration, where it is

Table 9: *Estimated age at first conception for 7 primiparae. The dates of these females' own permanent emergence were known. I added 11 months (as an estimate of pouch-life) to their 'age' from permanent emergence. Units are months.*

---

<b>primiparae</b>	<b>estimated age of first conception (months)</b> <i>that is minus 3 months from first observable signs of a pouch-bulge</i>
<i>Wattle</i>	36
<i>Zenith</i>	> 43
<i>Almond</i>	36
<i>Rowan</i>	33
<i>Tissan</i>	40
<i>Gambol</i>	45
<i>Cambric</i>	42
<hr/>	
<i>mean (SE)</i>	39.3 (1.8)

---

less than 49 weeks.

### 3.2.3 Ages of primiparae and reproductive rates

I was able to calculate the ages for 7 of the 9 primiparous females (table 9). The average age was 39.3 months (SE 1.79), and ranged between 33 and 45 months.

The females were commencing reproduction at an age which was twice that of the earliest age, 17 months, reported in the literature (Kirkpatrick, 1965c) and possibly relatively late compared to other populations of eastern grey kangaroos (table 10).

The females' reproductive rates could be determined from their mean inter-PEP intervals, the average of which was 47.1 weeks (SE 0.97, N=50). Hence, the average female produced one young every 10.9 months.

Most other eastern grey kangaroo populations are reported to have an average breeding rate of one young per year per female. Figures reported are: Pearse, 1981, approx. 1 per year; Poole, 1974 and 1983, approx. 1 per year; Kavanagh, 1977, approx. 1 per 11 months; Kirkpatrick, 1965c, approx. 1 per year; Kirkpatrick and McEvoy, 1966, less than 1 during a drought; Jaremovic, 1984, approx. 1 per year; Southwell, 1981, 1 per year, and less than 1 per year). Thus, the Wallaby Creek population appears to be unusually fecund, once females have begun breeding.

Table 10: Ages of first conception found in other populations. Units are months.

reference	age (months)		site
	mean	range	
<i>Kirkpatrick (1965)</i>	22	17-28	central south Queensland S.E. Queensland
<i>Poole (1973)</i>	24	20-60	Mt Hope, central N.S.W.
<i>Poole and Cahing (1974)</i>	22	19-46	captive studies
<i>Kavanagh (1977)</i>	36-44	28-72	north tablelands N.S.W.
<i>Pearce (1981)</i>	24?	13/16-36	Tasmania
<i>Poole (1984)</i>	-	< 20 -< 36	centre south N.S.W.
	-	< 20 -< 60	centre south Queensland
	-	< 20 -< 36	S.E. Queensland

### 3.3 Female reproductive history and non-behavioural characteristics

Lifetime reproductive success in polygynous mammals has been hypothesised to be much more variable for males than for females (Trivers, 1978; Bateman, 1948). There is evidence in some species to support this view (red deer, Clutton-Brock *et al.*, 1982b, 1986; northern elephant seals, LeBouef, 1974; rhesus monkeys, Meikle *et al.*, 1984; black-tailed prairie dog, Hoogland and Foltz, 1982). However, it is possible that there may not be a greater variation in male lifetime reproductive success than in females in all populations of polygynous species. This is because males may have a shorter reproductive lifespan, or an age-related reproductive success rate which tempers the extreme variation between males during any one season (see Clutton-Brock *et al.*, 1982b, and Dunbar, 1984).

In contrast, females may have a more variable lifetime reproductive success than has previously been supposed. For example, a female's rank may affect her reproductive rate and success in rearing young to weaning, and also her daughter's age of commencing reproduction and success in rearing young. If a female's rank relative to others in the population typically does not change greatly, then there might be considerable variation between the success of individual females and, in particular, matriline in rearing young to breeding adults (Silk *et al.*, 1981; Silk, 1983; Silk and Boyd, 1983; Wasser, 1983; Clutton-Brock *et al.*, 1986; Drickamer, 1974; Dittus, 1986).

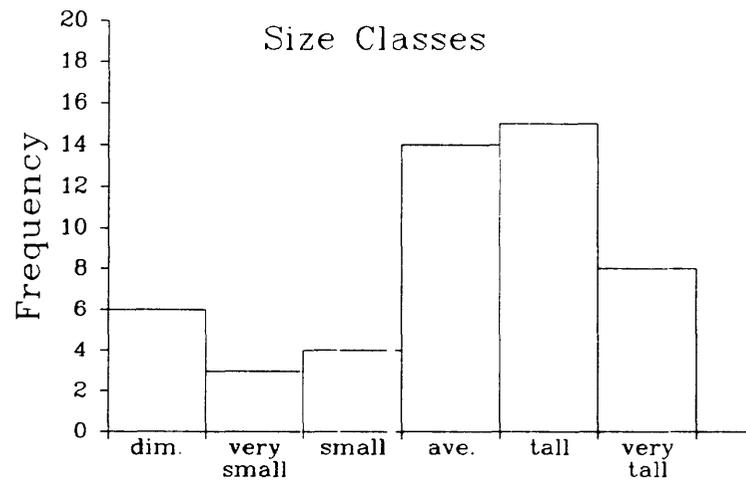


Figure 13: *Frequency distribution of females in 6 size categories: diminutive, very small, small, average, tall and very tall.*

Differential variation in reproductive success between the sexes is often cited when discussing parental investment strategies (Trivers and Willard, 1973; Trivers, 1978; Maynard-Smith, 1980; see Chapter 1). Consequently, I believe that it is important to estimate at least tentatively the variance for both sexes rather than assume a greater variance among males than among females of polygynous species.

In the following sections I discuss variation in the size, age, and condition of the females. Seasonal and class effects on the females' physical condition are also discussed. I then describe the variation between the females in rates of rearing young to weaning and suggest whether this variation was related to size, age, or physical condition. By offering these suggestions I hope to make a preliminary proposal concerning whether the females' success in rearing young to weaning is highly differentiated between individuals. In section 3.3.5 I compare the females' and males' variations in estimated lifetime reproductive success.

### 3.3.1 Size and age variation

An index of hindleg height (method section 2.4) was used to place 50 adult females each in one of 6 size categories: diminutive, very small, small, average, tall, and very tall. The frequency distribution of the females in each size category is depicted in fig. 13.

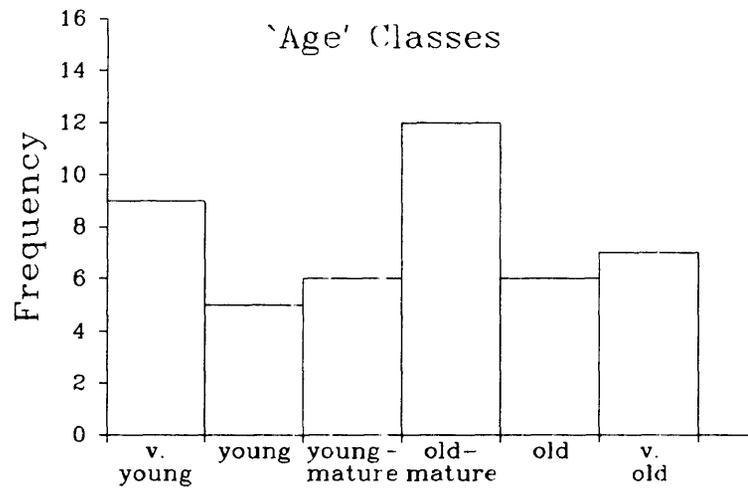


Figure 14: Frequency distribution of females in 6 'age' categories: very young, young, young-mature, old-mature, old, and very old.

The first 3 classes have fewer females than the 'Average' and 'Tall' categories. Perhaps, as would be expected from an asymptotic growth curve (Poole *et al.*, 1982), females are passing rapidly through the three smaller categories, and more slowly through the latter three.

In order to estimate the females' relative ages without disturbing their behaviour by capture and dental examination, I devised an 'age' index based on a female's appearance for each of 6 variables (see section 2.4 for methods). The validity of this 'age' index rests on the assumption that as a female ages her fur becomes greyer, and may be lost, and her skin baggier. Thus, this index can be viewed as only a tentative estimation of a female's age in relation to the rest of the females.

Fig. 14 depicts the frequency distribution of the number of adult females in each of the 6 categories into which I collapsed the raw 'age index': very young, young, young-mature, old-mature, old, and very old. The raw values ranged between 0 and 100, young to old, and reflect the average score a female obtained over the 6 categories, converted to a percentage of the maximum score.

If this index was a fair reflection of the females' relative ages, then it should be correlated to the size index. 'Age' and size were significantly correlated ( $R^2=0.516$ ,  $p<0.0001$ ,  $\text{size}=0.06(\text{age})+0.66$ ). Further, the 'age' index was significantly correlated to the condition

index (section 3.3.3), but size was not. A female's condition should be correlated to her appearance, but 'age' is the most likely attribute to link a female's appearance to her size, while 'size' is not correlated to her physical condition.

From this point, I will continue as if the 'age index' is a valid estimation of a female's age relative to her peers. But I strongly emphasise that it remains a tentative estimate, and is used only to suggest relationships between age and other female attributes.

### 3.3.2 Estimated breeding life span

Twenty-seven breeding females disappeared or were known to have died during the study period from April 1982 to March 1986. Twenty were definitely rather grizzled in appearance, but I had assessed the age of only twelve prior to their disappearance. The population declined in size during most of the four study years (table 3). In 1982 there were 52 adult females, but by August 1985 there were 34. Consequently, some females may have disappeared at a younger age than would be expected. Recruitment of females also has been low. Eleven young females have survived to replace those 27 lost. No females migrated into the study site.

It is difficult to make an estimate of adult female turnover because of the discrepancy between loss and recruitment. According to Pearce (1981) few female eastern grey kangaroos in Tasmania live beyond 12 years of age. Kirkpatrick (1965b) found some 16-year-old eastern grey kangaroo females who were breeding in Queensland.

The field research team at Wallaby Creek collects all skulls and carcasses they find. To date, P. Jarman has estimated the age of 13 skulls known to be female, using the molar progression technique (Kirkpatrick, 1965a and b). The average estimated age of these females at death was 9.5 years (SE 0.86, range 5 to 14).

At Wallaby Creek adult female mortality may be concentrated toward the older age classes. My age '6' category, which contained a slightly greater than average percent of females who disappeared/died, may include females greater than 11 years. According to the percentage of females who disappeared from each 'age' category (table 11), about 60% of females may disappear before they reach category 6. The 40% of skulls with the greatest molar indices were 11 or older.

Since the average age of my 7 known primiparous females was 3 years 4 months (table 9), I predict that the breeding life of a female in the studied population is on average 6 years, though the median is likely to be greater, perhaps 8.5 years.

Table 11: *Proportion of females who disappeared from each of the 6 'age' categories.*

age classes	no. of females	no. who disappeared within $1\frac{1}{2}$ years	% of that class
1 very young	9	1	11.1
2 young	5	0	0
3 young-mature	6	1	16.7
4 old-mature	12	3	25.0
5 old	6	2	33.3
6 very old	8	5	62.5
	46	12	

### 3.3.3 Female condition

Age, seasonal factors and a female's reproductive state are known to be related to a female's condition for a variety of mammalian species (Mitchell *et al.*, 1976; Clutton-Brock *et al.*, 1982a and b; Altmann, 1980 and 1983; Andersen, *et al.*, 1976; Caughley, 1962; Allen, 1984; Leader-Williams and Ricketts, 1981; Costa *et al.*, 1986; Johns *et al.*, 1983/4). Although the female kangaroos at Wallaby Creek are not restricted to a seasonal breeding regime, there is a peak in permanent emergence during the latter half of the year (section 3.4). One explanation of this peak is that, if there is one reproductive state which is more energetically expensive than the others, then some females may time their reproductive attempt according to a seasonal variation in their condition.

Caughley (1962) found that female grey kangaroos' kidney fat was significantly lower than the population average for females with a newly emerged YAF or a YAF and a very small pouch-young. This probably coincides with a peak in the female's metabolic input to lactation (*ibid.*; for tammars: Green, 1984; Dove *et al.*, 1987, and Janssens and Ternouth, 1987).

Studies on a variety of mammalian species have shown a positive correlation between nutrition and reproductive performance (e.g. Mitchell, 1973; Robinette *et al.*, 1973; Allen, 1984; Blaxter and Hamilton, 1980; Mitchell *et al.*, 1976; Newsome, 1966; Reimers, 1983; Scucchi, 1984; van Schaik and van Noordwijk, 1985). Consequently, if a significant proportion of the Wallaby Creek females' condition cannot be explained by seasonal factors or according to reproductive state, then this inter-individual difference in condition may be correlated to the female's rate of rearing young; to weaning.

M. Jones, for P. Jarman, and I have both independently assessed the condition of the

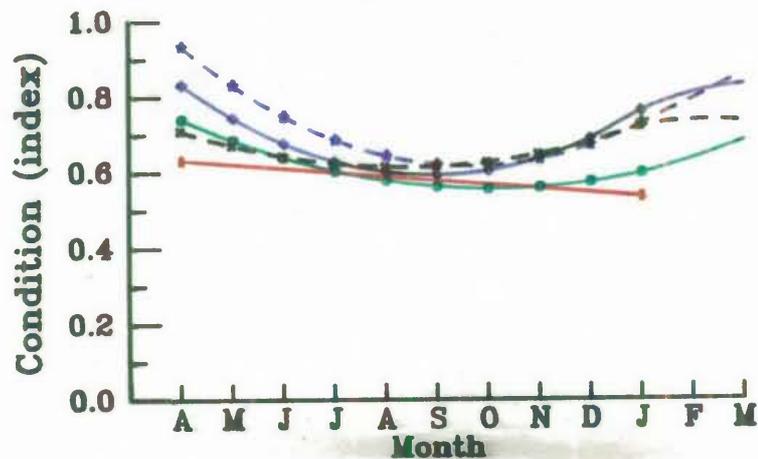


Figure 15: Best-fit equations describing the relationship between female condition and month of the year for various classes of females. The classes represented are: with small PY – black dashed line, with medium PY – blue continuous line, with large PY – blue dashed line, with PEP young or small YAF – red continuous line, and with large YAF – green continuous line. A condition value of 0 is very poor and a value of 1 is very good.

females by subjectively rating their appearance on a number of characteristics, which were averaged to provide an index of how well covered a female's skeleton is with fat and muscle (see section 2.4). I measured the females' condition twice, once in October 1984 and once in March 1985. M. Jones then continued an assessment schedule on a monthly basis. Unfortunately, we used slightly different systems, which made combining our data not feasible. Thus I have used the data M. Jones collected between June 1985 and March 1986, to describe the seasonal trends and mine to support those trends and show the relationship between condition and non-seasonal variables.

Best-fit equations for the seasonal variation in condition of the females are depicted in fig. 15. The classes of females: with small pouch-young (class 8), with diminutive to medium pouch-infants (classes 9-12), with large pouch-infants (classes 13&14), with PEP young or small YAF (classes 15 and 16), and with large YAF (Class 18), were separately analysed for seasonal trends in condition. Although a considerable amount of the variation was explained by month of the year, a greater proportion was explained by inter-female variation (table 12). It appears that most females are in their poorest condition in late

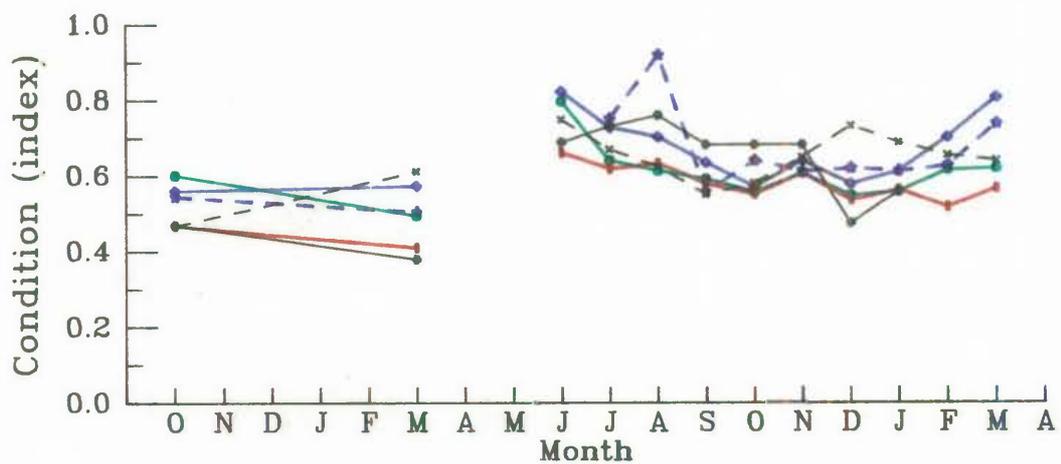


Figure 16: The mean monthly values of female condition for various female classes. The classes represented are: with no PY - black continuous line, with small PY - black dashed line, with medium PY - blue continuous line, with large PY - blue dashed line, with PEP young or small YAF - red continuous line, and with large YAF - green continuous line. A condition value of 0 is very poor and a value of 1 is very good.

Table 12: *Variation in females' physical condition explained by month of the year, and individual females for the various classes of females.*

class	% significantly explained by		% unexplained	df
	individuals	month of year		
<i>small PY:</i> <i>(8 &amp; 9)</i>	77.8	7.0	14.6	81
<i>medium PY:</i> <i>(10-12)</i>	59.8	38.5	2.2	60
<i>large PY:</i> <i>(13 &amp; 14)</i>	42.0	30.8	27.1	19
<i>PEP/small YAF:</i> <i>(15 &amp; 16)</i>	81.2	11.3	7.5	68
<i>large YAF:</i> <i>(17 &amp; 18)</i>	77.3	14.1	8.5	61

spring. However, females with newly emerged YAF (classes 15&16) were likely to be in progressively poorer condition the later in summer that their young permanently emerged (see figs. 15 and 16).

The above-mentioned finding that inter-female variation was relatively great compared to any fluctuations in the condition of individual females was further supported by a significant correlation between a female's condition in October 1984 and March 1985 (paired t test  $N=32$ , correlation coefficient=0.381,  $p=0.032$ ).

Thus, I compared each female's condition when with a pouch-young and when with a newly-emerged YAF. Individual females were significantly likely to be in poorer condition when they had a newly emerged YAF, than when they had a small pouch-young (Wilcoxon matched paired tests:  $N=22$ ,  $T=35$ , 1-tail  $p<0.005$ ), or a medium pouch-young ( $N=25$ ,  $T=30.5$ , 1-tail  $p<0.005$ ) or a large pouch-young ( $N=15$ ,  $T=10.5$ , 1-tail  $p<0.01$ ).

In general, females with newly-emerged YAF averaged the lowest condition of all classes (fig. 16), except in some months when females with no young, small pouch-young or large YAF were in equally poor condition.

It is understandable that the lactational demands of a female suckling two compared to one young are likely to be greater, but why should females with no young be in poor condition? Perhaps these females were not breeding because they were in poor condition, or they had just lost a small YAF and had not yet regained condition. Most young are lost

around permanent emergence (section 3.5).

As most of the variation in condition was explained by differences between individuals rather than variation in the individuals' condition over seasons and reproductive classes, I considered whether particular female characteristics such as, size, 'age', and immediate reproductive history were significantly related to condition.

A significant relationship between size and condition existed only for the classes of females 'with small pouch-young' and 'with medium pouch-young' (table 13). In those, taller females tended to be in poorer condition.

A female's condition was significantly related to her 'age', in October 1984, and to a lesser extent in March 1985 (table 14). Class effects may have mediated the influence of 'age' on condition: the difference between the averages of each class' condition varied between these two months. A female's condition was significantly related to her 'age' when in one of the following classes: no pouch young, small pouch-young, small to medium pouch-infant, and large YAF plus small pouch-young (table 13). In all of these classes the younger females were in better condition than the older females. However, the younger females' condition varied over a wider range of values between classes than it did for the older females (fig. 17). There was no significant relationship between age and condition for the classes with large pouch-infant, and with small YAF. Females in the latter class were typically in poorer condition than other females, and this appears to occur regardless of a female's age.

In a variety of other mammalian species (Clutton-Brock *et al.*, 1982b; Altmann, 1980; Paul and Thommen, 1984; Drickamer, 1974; Mitchell *et al.*, 1976; van Schaik and van Noordwijk, 1985) rearing a young to weaning may be associated with a delay in the next reproductive attempt, a loss of condition by the female compared to her peers who lost their young, or an increased probability of losing the next young. Consequently, I predicted that female kangaroos who had reared their young to weaning might be in a poorer condition, than the other females, while rearing their next young. However, this variable did not explain a significant proportion of the variation in condition, even with age and month of the year as covariates (table 13). Indeed the averages tended to lie in the opposite direction (table 13). Perhaps the females who rear young to weaning have greater access to the local resources and can invest in young and maintain their condition to a greater extent than can the females who lost young.

Lastly, I tested for whether the North and South females differed in physical condition (see chapter 4 for female home-ranges). The South females averaged a significantly better

Table 13: Best-fit equations for size with condition, and for 'age' with condition. Also the variation in condition explained by class, 'age', month of year, and by whether or not the previous young was weaned are included. The  $R^2$  values and probabilities ( $p$ ) which relate to the equations and the mean ( $\bar{x}$ ), standard errors ( $SE$ ), and sample size ( $N$ ) of females' condition following having lost or weaned a young are presented. The equations of condition to size ( $S$ ) and 'age' ( $A$ ) are presented below each  $R^2$  and probability. Note that probabilities between 0.1 and 0.05 have a † next to them while those less than 0.05 have a \* placed next to them.

class	size		age		prev. young			
	$R^2$	$p$	$R^2$	$p$	$\bar{x}$	$N$	$\bar{x}$	$N$
7 (NPY)	0.247 0.72 - 0.02(S)	0.120 ns	0.514 0.75 - 0.03(A)	0.013, *	0.611 SE 0.030	(6)	0.556 (2)	
8 & 9 (SPY)	0.130 0.78 - 0.03(S)	0.055, †	0.429 0.84 - 0.05(A)	<0.001, *	0.66 SE 0.023	(20)	0.71 SE 0.079	(4)
10—12 (MPY)	0.224 0.81 - 0.03(S)	0.005, *	0.260 0.79 - 0.03(A)	0.002, *	0.66 SE 0.020	(20)	0.66 SE 0.035	(8)
13 & 14 (LPY)	0.148 0.80 - 0.04(S)	0.104, ns	0.111 0.74 - 0.02(A)	0.164, ns	0.63 SE 0.025	(11)	0.68 SE 0.052	(7)
15 & 16 (PEP/SYAF)	0.000 0.58 - 0.0005(S)	0.973, ns	0.029 0.62 - 0.01(A)	0.375, ns	0.56 SE 0.019	(19)	0.62 SE 0.028	(8)
17/18 (LYAF)	0.055 0.67 - 0.02(S)	0.294, ns	0.257 0.70 - 0.03(A)	0.016, *	0.59 SE 0.016	(13)	0.62 SE 0.041	(7)
	% variation explained by		probability		$R^2$			
class:	11.5		0.001					
prev. young (lost/weaned):	1.0		0.409					
class x prev. young:	6.1		0.355					
covariates								
age:	8.3		0.0002		-0.023			
month of year:	6.4		0.0008		-0.010			
error:	66.8							

**Table 14:** Females' condition related to 'age' and home-range site. Means, standard errors (SE) and results of Mann-Whitney U tests are presented. See text for calculation of a female's average relative condition. 'Age' has been collapsed into three equal categories. Probability values ( $p$ ) which lie between 0.1 and 0.05 are presented with a † and those which are less than 0.05 are presented with an \*.

'age'	October 1984			March 1985		
	sample size	mean	SI	sample size	mean	SE
young	8	0.63	0.036	6	0.58	0.041
mature	18	0.55	0.035	17	0.54	0.027
old	12	0.38	0.037	9	0.41	0.073
<b>home range site</b>						
North	10	0.43	0.038	9	0.42	0.036
South	20	0.54	0.031	15	0.57	0.031
<b>average relative condition with home-range site</b>						
North	9	0.99	0.027	<i>F test</i>	$F=1.04$	$p=0.891ns$
South	17	1.00	0.019	<i>t test</i>	$t=-0.50$	$p=0.624ns$ $df=24$
<b>Mann Whitney U tests</b>						
'age'	$z$	$p$		$z$	$p$	
young vs mature	-2.531	0.006*		-0.808	>0.1ns	
mature vs old	-3.156	0.001*		-1.593	0.055†	
young vs old	-3.397	0.0004*		-1.421	0.077†	
<b>home-range site</b>						
North vs South	-2.135	0.033*		-3.201	0.001*	

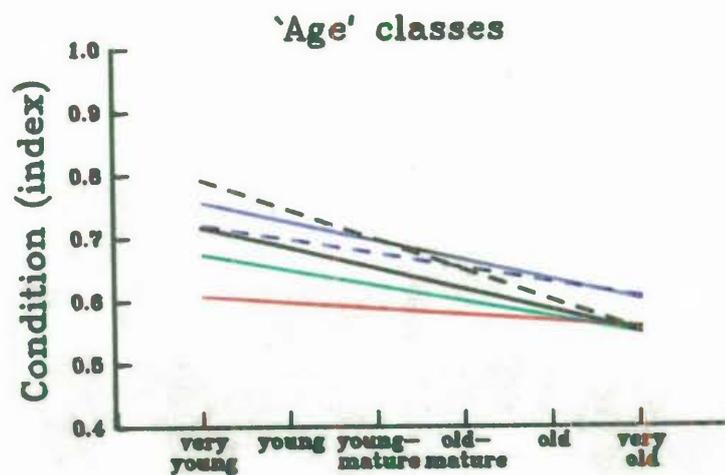


Figure 17: Best-fit equations for the relationship between a females's condition and her 'age' for the various clases of females. The classes represented are: with no PY - black continuous line, with small PY -black dashed line, with medium PY - blue continuous line, with large PY - blue dashed line, with PEP young or small YAF - red continuous line, with large YAF - green continuous line. A condition value of 0 is very poor and a value of 1 is very good.

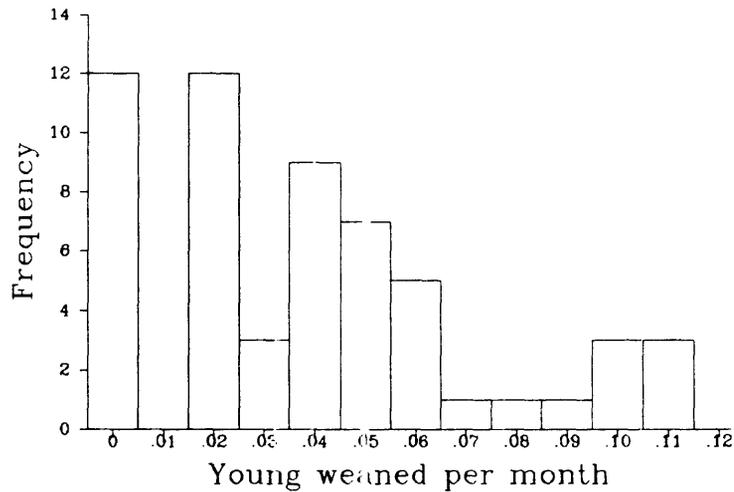


Figure 18: *Frequency distribution of the rates at which females were weaning young.*

rating on the condition index than the North females when using either of the condition values obtained in October 1984 or March 1986. However, these two ‘sets’ of females were not significantly different according to their average relative condition indices between June 1985 and March 1986 (this latter index is calculated by subtracting the ‘average’ female’s condition for a month from each female’s condition rating for that month and then averaging, for each female separately the monthly values obtained; see table 14). These tests are particularly relevant to the discussion in sections 3.7 and 3.8.

Overall, there was considerable variation in the females’ condition and most of it was explained by inter-individual variation rather than month or reproductive class; but these latter two factors did influence a female’s condition. The ‘age’ index explained some of the inter-individual variation, but there was still much variation unexplained (see table 13).

### 3.3.4 Variation in female reproductive success

My study has been too short to measure the females’ lifetime reproductive success, and thus be able to test whether females differed significantly in their lifetime reproductive success. However, I could test whether the females’ rates of rearing young over the time they were observed were significantly non-normally distributed, or significantly related to a characteristic such as age or size or average condition.

Table 15: Tests for a relationship between a female's rate of weaning young, and her size, 'age', condition, and home-range site. The females' raw 'age' index values were used; these values ranged between 25 (very young) and 95 (very old). A female's size refers to her categorisation in one of the 6 size classes; these ranged from diminutive - 1 to very tall - 6. A female's 'relative condition' each month was determined by subtracting the mean condition (calculated from all females that month) from the female's condition index value that month, and adding 1.0 to the result. An overall average value for each female was obtained from all of her monthly 'relative condition' values (her ARCond). RWY refers to the index rate of weaning young (number per month). Probability values of between 0.1 and 0.05 are presented with a † and those of less than 0.05 are presented with an \*.

	R <sup>2</sup>	Equation	probability	
			linear	quadratic
size	0.011	$RWY = 0.017 + 0.009(\text{size}) - 0.001(\text{size})^2$	0.798	0.751 ns
age	0.166	$RWY = 0.142 - 0.003(\text{age}) + 0.003 \times 10^{-2}(\text{age})^2$	0.023	0.032 *
ARcond	0.047	$RWY = 0.760 - 1.469(\text{ARcond}) + 0.740(\text{ARcond})^2$	0.343	0.334 ns
home-range site		RWY: mean, SE, (sample size)	test	p
North		0.024, 0.005 (13)	F=2.08	0.187 ns
South		0.041, 0.005 (25)	t=-1.97	0.057 †

Table 16: Percentage of young reared to weaning of those produced by Young, Mature, and Old females. The 6 'age' categories were collapsed into 3. Mean inter-PEP intervals for each of the three classes and the correlation between 'age' and mean inter-PEP interval are included.

'Age':	young	mature	old
	v. young & young	young- & old- mature	old & v. old
number weaned	10	23	18
(% weaned)	(48)	(33)	(39)
total produced	21	69	46
G test: G=1.464, df=2, ns			
average inter-PEP interval:			
mean	46.0	46.3	52.2
SE	1.19	0.98	2.90
sample size	5	18	13
Pearson correlation coefficient:			
'Age' to average inter-PEP interval = 0.333, N=36, p=0.024			

The frequency histogram of rates of weaning young for the females is depicted in figure 18. The average rate of weaning young was 0.037 young/month (SE 0.004, N=54) (i.e. 1 young per 27 months). The mode was 0. The median was 0.031 young/month. Despite this appearing atypical of a normal distribution, according to a Kolmogorov-Smirnov test, the frequencies were not significantly non-normally distributed (extrinsic factor, Sokal and Rohlf, 1969) ( $d_{max}=0.122$   $p>0.1$ ).

I tested for a relationship between the females' rate of rearing young to weaning and their size, 'age', home-range site and condition. The 'age' and home-range site of a female were significantly related to her rate of rearing young to weaning (table 15), while neither size nor condition were. South females had a greater rate of rearing young to weaning than North females. Younger females were more likely than older females to have a high rate of rearing young to weaning. As these younger females were not significantly more likely to rear any one of their young to weaning (see table 16), their greater rate of rearing young to weaning is probably based upon a greater rate of producing offspring. Indeed the 'younger' females had much shorter average inter-PEP intervals than the 'older' females (table 16).

An age-related difference in the weaning rate would not lead to lifetime inter-female differences. However, the test for departure from a normal distribution was based on a small sample size and there was a preponderance of females who did not rear any young to weaning. Further, condition might not be related in a simple linear relationship to rearing young to weaning (Clutton-Brock *et al.*, 1982a and b; Andersen *et al.*, 1976; Altmann, 1980). Therefore, further research may show that females differ in their lifetime reproductive success in a non-random manner.

### 3.3.5 Female versus male reproductive success

At Wallaby Creek, there has typically been one adult male, the alpha, who obtains an estimated 75% to 80% of all the possible matings per year (Jarman, pers comm.). The study population represents one fairly cohesive unit (see chapters 2 and 4). The alpha male is the largest in the population, and may easily displace other males from an oestrous female (Jarman and Southwell, 1986). However, a male's tenure of the alpha position has consistently averaged only one year; alpha males are probably 10 years of age (*ibid.*).

I have estimated the average and variance for the males' expected lifetime-reproductive-success (Appendix A) from the point of birth, using data on male mating success kindly given to me by P. Jarman, and data I collected on the young. A male born at Wallaby Creek

may expect, on average, to produce 0.64 young; will be reared to weaning, with a variance of 12.4 and a range from 0 to 33 young.

A female born at Wallaby Creek may expect, on average, to rear 0.95 young to weaning, with a variance of 4 and a range from 0 to 10 young (see Appendix A, for calculations). This estimated variance of female reproductive success is significantly smaller than the variance calculated for males (F test,  $F=3.146$ ,  $df_1=295$ ,  $df_2=197$ ,  $p<0.05$ ).

However, the frequency distribution of the expected number of young reared to weaning that a male will produce is highly skewed toward 0. Consequently, in appendix A I have also presented the estimated averages and variances of the number of young reared to weaning for males and females who produced at least one young. The difference between the variances of the sexes is still significant and even greater.

Thus, a mother eastern grey kangaroo at this site can expect that a son will be less likely to produce weaned young than a daughter (see also section 3.7 on sex ratios of young); but there is the possibility that, if a son does become an alpha male, he may far out-reproduce even the most productive of daughters. However, it is important to note that not all alpha males can expect to produce (many) young reared to weaning. This is because there is considerable between-year variation in the survival of young (see also section 3.5) and alpha males appear to hold tenure for one year only.

### **3.4 The timing of reproduction: conception , birth and permanent emergence**

#### **3.4.1 Seasonal variations in the timing of reproduction**

Investment schedules in young can be affected by the seasonal nature of an environment or the predictability of the weather (Berger, 1979a and b; Barash, 1974; Smith and Ivins, 1983; Andersen *et al.*, 1976; Ohsawa and Dunbar, 1984; Altmann, 1983, 1980; Franklin, 1983; van Schaik and van Noordwijk, 1985; see section 1.3).

In New South Wales and Queensland, the eastern grey kangaroo's reproduction is not seasonally restricted (Poole, 1983, 1973; Poole and Catling, 1974; Kirkpatrick, 1965a; Southwell, 1981; Kavanagh, 1977), although a peak in births usually occurs in summer, with the young permanently emerging in spring. Breeding becomes more seasonally restricted in the southern states of Tasmania and Victoria (Pearse, 1981; Jaremovic, 1984).

Seasonality in reproduction may be recorded according to one of a number of events in the reproductive cycle. The above authors used birth. However, my study was principally a behavioural study and I did not wish to capture and inspect pouches of the females, which would have been necessary to determine birth dates. Of the easily visible stages in reproduction, I could be most certain of the timing of the young's permanent emergence. At Wallaby Creek, I was able to determine within which fortnight every young permanently emerged from the pouch. This process lasts typically 9 days (section 3.2). In addition, this point in a young's life history is probably more relevant to the seasonal timing of parental-investment schedules, as it represents a turning point in the mother-young relationship (see chapter 6), as well as being the peak of lactation (Dove *et al.*, 1987).

However, conception also is an important point in reproduction, as the sex of the young is determined at this time. There is a growing body of literature on the possible influence of the relative timing of conception within the oestrus cycle and of the environmental conditions in which a female conceives, on the probability of a male versus a female being conceived (McShea and Madison, 1986; Pederson and Harper, 1984; Verme, 1985; Cockburn *et al.*, 1985; Bull, 1981; Verme and Ozoga, 1981; Mech, 1975; Clark *et al.*, 1986; Clutton-Brock *et al.*, 1984). I discuss secondary sex ratios in the eastern grey kangaroos in section 3.7. In this section I will discuss the seasonal timing of conception.

For each month from April 1982 to March 1986, I have calculated the percentage of females who had a young permanently emerge (fig 19). Young were observed to emerge permanently at all times of the year, but there were months when a particularly high percentage of the females had a young permanently emerge. As I was more interested in defining a set of months for which there was a greater probability of more of the females' young being timed to permanently emerge, rather than in defining the absolute timing of a peak season, I smoothed the curve by calculating 3-monthly rolling averages. There appeared to be a fairly consistent increase during the months July to December, which was confirmed by a significant relationship between month of the year and the percent of females with permanently-emerging young ( $R^2 = 0.248$ , % females with PEPyoung =  $-0.25 + 3.11(month) - 0.24(month)^2$ , quadratic  $p=0.006$ , linear  $p=.0005$ ). The averages for each month of the year, from January to December are as follows: 3.2, 3.5, 5.7, 4.2, 4.0, 4.5, 6.8, 13.6, 9.9, 13.5, 6.5, 10.7. From here on I refer to the months July through to December as 'peak' season months and the months January through to June as 'offpeak' season months.

Figure 19: Percentage of females with PEP young of the total females in the population. The fine continuous line represents % PEP young/female population for each month. The thick continuous line represents the mean % for that month of the year (calculated from the 4 years of the study). The fine broken line represents the 3-month rolling cumulative, average %

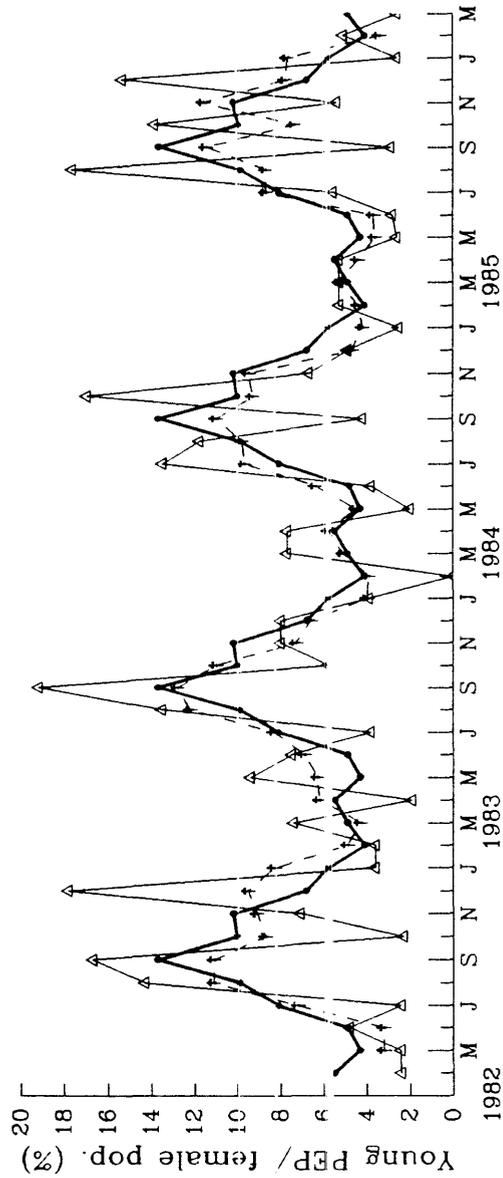
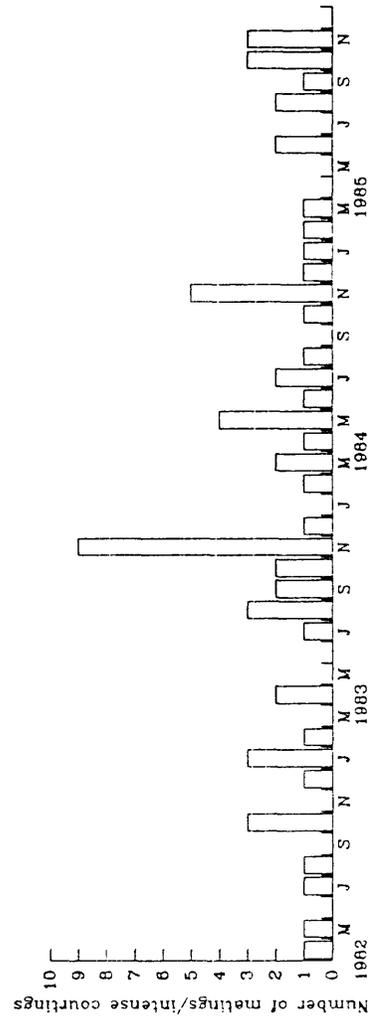
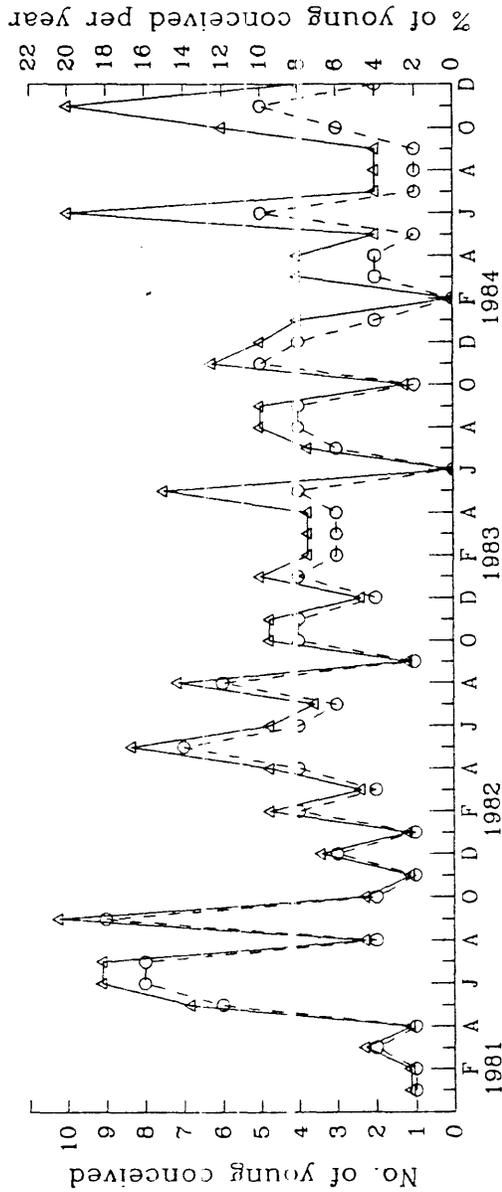


Figure 20: The estimated number of young conceived per month is represented by the broken line. The estimated percentage of young conceived per month of the total conceived per year is represented by the continuous line. The number of observed matings/intense courtings per month is represented by the bars.



I estimated the month of conception for young by assuming that, if the inter-PEP interval prior to its emergence was less than 49 weeks, it was conceived via the delayed-blastocyst cycle, 18 weeks prior to the previous young's permanent emergence (see section 3.2). This unfortunately neglects a standard error of 0.54 weeks (a range of 10—26 weeks). However, the observed variation was not seasonal (duration of oestrous to PEP to month of the year of oestrous:  $R^2=0.097$  linear probability = 0.269 quadratic probability = 0.161). Thus the mean I used in estimating conception dates should not have camouflaged any seasonality in conception dates. Young who permanently emerged after an inter-PEP interval greater than 48 weeks in duration were assumed to have been conceived 11.5 months previously (section 3.2). As I did not know the number of females present in the population during 1981 and for half of 1982, instead of estimating the percentage of females who conceived per month, I calculated the percentage of young conceived per month from the total conceived during that year.

Conception appears to be less seasonal than permanent emergence (fig. 20); it was not possible to fit a significant relationship for the estimated percentage of conceptions to the month of the year ( $R^2 = 0.066$  linear  $p=0.099$ , quadratic  $p=0.141$ ). In figure 20 I have included a graph of the dates of the observed intense courtships/matings. This plot further exemplifies the relatively aseasonal nature of mating and hence conceptions as compared to permanent emergence. However, please note that there was an overwhelmingly high number of matings/courtships in November 1983. This could be related to more females

delaying reproduction i.e. conceiving without a delayed blastocyst after the current young permanently emerged. The weather this year was atypical and probably stressful to the kangaroos (see sections 2.2 and 3.5). Hence further investigations may find that in some years more of the females are conceiving seasonally via the delayed blastocyst cycle.

Overall, if it is adaptive for females to time reproduction seasonally at least some of the time, at Wallaby Creek, then it is the timing of the young's development which is more likely to be affected by seasonal constraints, rather than the activity of courting and mating. From this I predict that the survival of the young or the mother, or the quality of their relationship should be affected by the seasonal timing of reproduction.

From this point on, when I refer to a 'peak' or 'offpeak' young, I mean one who permanently emerged in that season.

#### 3.4.2 Annual variations in the timing of reproduction

Timing of reproduction can be affected by periods of atypical weather. Eastern grey kangaroos are known to cease breeding during droughts (Southwell, 1981; Kirkpatrick and McEvoy, 1966). Poole (1973) has suggested that reproduction in kangaroos may be stimulated to recommence immediately upon breaking of the drought by a period of rain. In general, female eastern grey kangaroos may enter a prolonged period of anoestrus when stressed, with the consequence that when they recommence reproduction it will not be via the delayed-blastocyst cycle.

There was significantly more inter-year variation in the duration of the inter-PEP intervals, compared to within-year variation (table 17, as measured from the second PEP). In 1984 significantly fewer of the eastern grey kangaroo females were estimated to have conceived than in 1981, 1982, or 1983 (table 18). Also, from 1982 to 1984 there was an insignificant ( $G=1.680$ ,  $df=2$ ,  $p > 0.1$ ) decline of 12% in the proportion of conceptions that occurred via the delayed-blastocyst cycle (table 18).

Table 17: The mean duration of inter-PEP intervals for 4 12-month periods. The 12 month periods lie between April and March the following year. Results of an  $F$  test comparing between 'year' and within 'year' variation are given.

<b>inter-PEP</b>			
<b>interval:</b>	<i>sample</i>	<i>mean</i>	<i>SE</i>
<b>year</b>	<i>size</i>		
1982/1983	3	42.0	1.22
1983/1984	49	44.7	0.69
1984/1985	37	48.5	0.92
1985/1986	27	51.3	2.71

Variation between versus within year  
 $F$  test:  $F=4.066$ ,  $df=3$  & 103,  $p = 0.009$  \*

Table 18: Percentage of the females estimated to have conceived each year and of those the estimated percentage who conceived via the delayed blastocyst cycle (i.e. those with inter-PEP intervals less than 49 weeks). Results of tests comparing years are included.

<b>Year</b>	<b>females est. conceive/total</b>	<b>%</b>	<b>females est. conceive a delayed blastocyst /total (known inter-PEP)</b>	<b>%</b>
1981	44/53	83		
1982	42/52	81	35/41	85
1983	40/47	85	34/44	77
1984	25/37	68	19/26	73
<i>G tests between years</i>				
1981.1984	$df = 1, G = 2.872, ns$			
1982.1984	$df = 1, G = 2.004, ns$		$df = 1, G = 1.502, ns$	
1983.1984	$df = 1, G = 3.532, p < 0.1$		$df = 1, G = 0.154, ns$	
1982.1983.1984			$df = 2, G = 1.680, ns$	

Table 19: Percentage of females who had a young PEP in each of 4 12-month periods. The 12 month periods extended between April and March the following year for the 4 study years.

<b>period:</b>	<b>females with PEP young /total females</b>	<b>%</b>
<i>April-March</i>		
1982/1983	46/53	87
1983/1984	46/52	89
1984/1985	40/47	85
1985/1986	30/37	81

Thus, toward the latter half of 1983 and during 1984, at least some females were delaying the initiation of their next reproductive attempt. This was a time with a relatively high adult mortality (table 4) and followed a year with a quite atypical weather pattern (see section 2.2).

However, the percentage of females in the population who had a young emerge permanently from the pouch varied by less than 8% between years (table 19).

Thus the greater delay between consecutive reproductive attempts by the females in 1984 as compared to the previous 3 years was not related to more females temporarily ceasing to reproduce. The delay could have arisen from either of two causes. It could have been related to the females' tendency to time young to emerge permanently during the 'peak' season. Compared to the other years, in 1984 proportionally more females may have had to delay the production of their next young if it was to emerge permanently during the peak season. That is, proportionally more females in 1984, compared to 1982, may have had young emerge permanently at the beginning, rather than the middle or end, of the 'peak' season. Alternatively, the delay may have been related to environmentally induced stress, such as pasture deterioration, with the consequence that proportionally more females time their next young permanently emerge during to the peak season of 1985.

### 3.4.3 Individual females' timing of reproduction

The peak in permanent emergence might have arisen by three processes.

1. the duration of pouch-life may vary according to the season in which the young is produced. If peak young typically have longer pouch-lives than offpeak young, then mothers are more likely to produce consecutive peak young than consecutive offpeak young.
2. all females may follow a similar strategy of delaying some of their reproductive attempts in order that relatively more of their young emerge in the peak season than the offpeak season.
3. some of the females may have tended to delay consecutive reproductive attempts so that they produced only peak young, while other females may have reproduced without delaying so that they would eventually produce as many offpeak young as peak young.

Table 20: Percentage and number of females producing a young who PEPed in July or August. Data are given separately for each 12 month period between April and March (the following year) during the 4 study years. Included are averages of the inter-PEP intervals which followed a July or August PEP.

female type	1982/3	1983/4	1984/5	1985/6
'peak only'	1 (6%)	5 (.5%)	10 (48%)	6 (46%)
'offpeak also'	5 (18%)	4 (.5%)	4 (21%)	3 (18%)
duration of inter-PEP intervals following a July or August PEP				
'peak only':				
mean	59	50	66	
SE		7.92	7.94	
sample size	1	5	4	

Although the young who emerged in the peak season were more likely to follow an inter-PEP interval of greater duration than young who emerged in the offpeak season (see figs. 25 and 26), the amount of variation in the duration of inter-PEP intervals explained by the month of the year in which the second young emerged was 12.6% only ( $R^2 = 0.126$ ,  $\text{inter-PEP} = 20.67 - 1.18(\text{month}) + 0.08(\text{month})^2$ , linear  $p = 0.003$  quadratic  $p = 0.004$ ).

This study has been too short to be able to test whether there are 'types' of females who follow different reproductive tactics on a life-long basis, as suggested in 3). However, it is possible to make a conservative analysis of whether females were differentiated at least over a short term, according to a tendency to produce only peak young. A four-year study spans about half of the estimated breeding life of a typical female.

An analysis of the sequential timing of the permanent emergences of each female's young (Appendix B) revealed that significantly more females than expected had produced peak-season young only ( $\chi^2 = 2.858$   $df=1$ ,  $p < 0.1$ ). The average inter-PEP interval of the females who produced at least one offpeak young was 44.9 weeks (SE 1.1, N=28), which was significantly shorter (t test,  $t=3.185$ ,  $p < 0.01$ ) than the average interval of 50.6 weeks (SE 1.6, N=21) for females who were not observed to produce an offpeak young.

All 7 primiparae had a peak young. The average 'age' of the two types of females was not significantly different ('peak only' age index ave.=3.7 SE 0.45, N=20; 'offpeak also' ave. age index=3.9 SE 0.23, N=19; t test unpooled,  $t=0.39$ ,  $p > 0.1$ ), but the variances

were significant (F test  $F=4.06$ ,  $p=0.004$ ). Thus, females who were observed to produce at least one offpeak young tended to be middle-aged, while there was a greater probability of females who produced only peak young being old or primiparous.

If the females are differentiated according to their tendency to produce only peak young, was the 1985 high average-inter-PEP interval a result of more of the 'peak only' females delaying a subsequent reproductive attempt in order to avoid producing an offpeak young? The females most likely to delay conception to avoid producing an offpeak young are those with young who emerged in the months July or August. From 1982 to 1984 there was a steadily increasing proportion (table 20) of females producing young who emerged permanently in these months. However, the particularly long inter-PEP intervals in 1985 were not necessarily related to a 1984 July/August young. A greater proportion of the 'peak only' females had inter-PEP intervals greater than 48 weeks in 1985 (6/11) compared to 1983 (6/17); although the difference was not significant ( $G=0.396$ ,  $df=1$ ,  $p>0.1$ ). In general, the 1985 set of inter-PEP intervals included 5 of 32 which were outstandingly long (Appendix B), and 2 were determined from females who at some time had an offpeak young. In previous years only one inter-PEP interval had been longer than 55 weeks. One of the 'offpeak also' females who had an exceptionally long inter-PEP interval in 1985, had an offpeak or July/August young in 1984. All three of the 'peak only' females who had an exceptionally long inter-PEP interval in 1985 had a July-August young in 1984.

I believe that the 1985 extended inter-PEP intervals were possibly related to both an external factor, such as nutritional stress, and a fortuitous result of relatively more females delaying reproduction so that they could maintain a production of peak-season young.

It is worth noting that 42% (11/26) of the females who produced only peak young did not have an inter-PEP interval of greater than 48 weeks. Thus, some may have eventually produced offpeak young. Further, as 3 of the females who produced at least one offpeak young delayed reproduction during 1984 and consequently produced a peak young the subsequent year, females do not appear to be strictly differentiated into the two types on a life-long basis.

Overall, I suggest that, though females may tend toward either producing peak young consecutively (peak only females), or producing young approximately every 45 weeks (off-peak also females), this tendency does not appear to be fixed as a life-long tactic. These options could be implemented on an age-related basis, or be related to the condition of a female relative to her peers, as well as being mediated by environmental conditions and the

female's past reproductive history. I investigate the effect of a female's reproductive history on her tendency to produce only peak young in section 3.6. Although it would be interesting to look for the proximate mechanisms involved (possibly with respect to the presence or absence of a delayed blastocyst), this area is beyond the scope of this behavioural/ecological study.

For the purposes of investigating the relationships between females' reproductive tactics and other characteristics of the females, I have categorised the females according to whether they produced only peak young (peak only) or produced at least one offpeak young (offpeak also). Comparisons between females of the two 'types' will tend toward conservatively differentiating the females, as there may have been females who were categorised as producing only peak young who might later have produced an offpeak young.

### 3.5 The survival of young

Ungulate young appear to be particularly vulnerable to predation at birth (Byers and Byers, 1983; Clutton-Brock and Guinness, 1975; Jarman, 1976; Estes and Estes, 1979; Edwards, 1983; Millar, 1975; Bergerud, 1985; Bergerud *et al.*, 1983; Kruuk, 1975; Nowosad, 1975; Caughley, 1976). In primate young, the period immediately following birth is not always emphasised as having an outstandingly high mortality rate compared to the rest of the young's dependant life (Altmann, 1980; Dunbar, 1984; Dittus 1979,); and when mortality is exceptionally high in the first month of life, predation is not necessarily the prime cause (Paul and Thommen, 1984; Drickammer, 1974; Silk *et al.*, 1981).

In general, factors other than predation, such as the mother's physical condition, age, experience, reproductive history and social position, may influence mortality of young mammals through their dependent life (e.g. Arman *et al.*, 1978; Silk *et al.*, 1981; Silk and Boyd, 1983; Blaxter and Hamilton, 1980; Dittus, 1978; Johnson, 1985; Hrdy, 1977; Paul and Thommen, 1984; Simpson and Simpson, 1985; Drickammer, 1974; van Noordwijk and van Schaik, 1987). Also, the seasonal timing of the young's development and its sex can affect the overall probability and age-related probabilities of mortality (e.g. Clutton-Brock *et al.*, 1982b; Smith and Ivins, 1983; Nowosad, 1974; Thomas and DeMaster, 1983; Paul and Thommen, 1984; Dittus, 1979; Bergerud, 1971; Hamilton and Blaxter, 1980).

The developmental schedule of young kangaroos is quite different from that of the young ungulate. Ungulate young are quite precocious at birth. The young kangaroo is introduced to the external environment in a more gradual manner: it spends part of its later pouch-life making short excursions from the pouch (chapters 5 and 6). The young primate also is born in an altricial state and has a period of almost total dependence on its mother.

Consequently, the young kangaroo may have an extended period with an evenly distributed high risk of mortality, as reported for some primate young (Altmann, 1980; Dittus, 1979), rather than a brief period of heightened vulnerability to predation, as do many ungulate young (Estes and Estes, 1979; Lent, 1974).

In the following subsections I describe the age-related mortality rates of sons and daughters, and then discuss the possible influence of predation, environmental effects, and the mother's reproductive history on the survival of young.

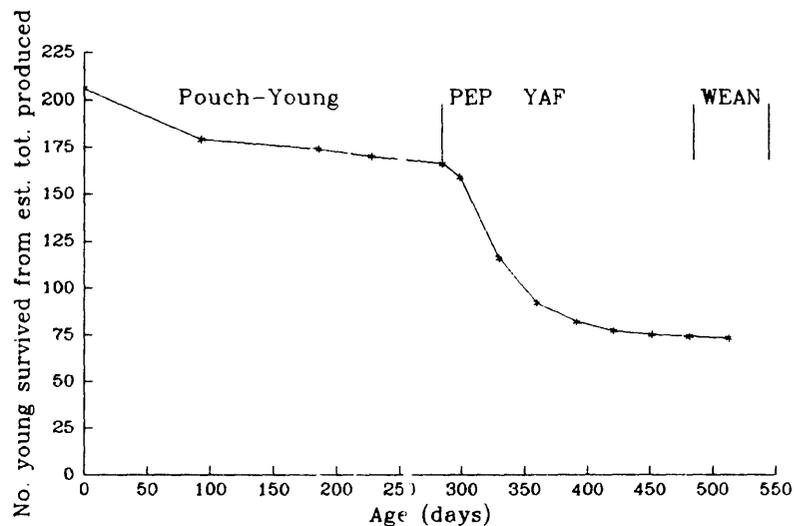


Figure 21: Curve depicting the rates of disappearance of young as they age.

### 3.5.1 Mortality of young related to their age and sex

At Wallaby Creek, of 190 young known to be produced during the four study years, 73 (38.4%) were reared to weaning. The age-related probability of a young disappearing is presented in appendix C. The rates of disappearance for each class of young can be seen in figure 21. It should be noted that in this figure I have included an estimated maximum number of neonates (27) that could have been lost prior to 2 months of age, but exclude (11) pouch-young 'lost' as a result of their mothers' disappearance. While I refer to the 'disappearance' or 'loss' of young, I infer death, as young were not observed to migrate into or out of the study population.

I was unable to discern whether a mother had a young in the pouch until a pouch

bulge appeared. In retrospect, this typically occurred when her young was 2 to 3 months of age (see section 3.2). However, I have estimated that at most there would have been 13% (27/206) of young disappearing as diminutive pouch-young, if all females who had an interval between permanent-emergences of more than 48 weeks, lost a pouch-young in the interim. I doubt that there was such a high rate of disappearance of small pouch-young, but see section 3.2 for my arguments.

Poole (1973) estimated a pouch-young mortality rate of 10% for pouch-young greater than 3 months of age in a wild population of eastern grey kangaroos in central New South Wales. My estimate for the Wallaby Creek population of 10% (20/approximately 206, see appendix C) is identical. Poole (1975) has also reported that the mortality of young born to a population of captive mothers was 17% during their pouch-life. Thus, if there was a similar percentage (7%) of pouch-young less than 3 months of age being lost at Wallaby Creek compared to the captive population, then about half of the 'greater than 48 week' inter-PEP intervals probably involved the loss of a diminutive pouch-young (i.e. 13 rather than 27 neonates lost).

Regardless of whether or not the percentage of diminutive pouch-young lost was close to the maximum estimated, the greatest rate of loss of young occurred on permanent emergence and in the subsequent two months (fig. 21). The rate of loss of older YAF returns to the rather low rate found for pouch-young.

I was able to sex 161 young, and of these 56% of males and 51% of females were lost before weaning. The difference was not significant ( $\chi^2 = 0.467$ ,  $df=1$ ,  $p=0.46$ ). The mean age at loss for both sons and daughters was a similar 1.1 months post-permanent-emergence (SE 0.12, N=54, SE 0.24, N=33, respectively). The medians were 1.0 and 0.5 months post-PEP for sons and daughters respectively. However, as I was unable to sex many of the pouch-young who disappeared, the average age of disappearance for sons and daughters is only comparable if they were equally likely to disappear as pouch-young. This is discussed further in section 3.7.

Overall, the age-related probability of the mortality of young resembles that for many ungulate young, where there is an outstandingly high risk immediately after birth (Estes and Estes, 1979; Lent, 1974), except that in kangaroos it occurs on or after permanent emergence.

Table 21: Number of young (pouch young and YAF) lost and weaned in each of the 4 consecutive 12-month periods between April 1982 to March 1986 inclusive. Probabilities of less than 0.05 are presented with an \*.

Year	lost	weaned	total
1982	17	29	46
1983	44	7	51
1984	38	8	46
1985	7	25	32
<i>G tests between years</i>			
1982,1983	$df = 1 \quad G = 26.558, p < 0.01*$		
1984,1985	$df = 1 \quad G = 30.147, p < 0.01*$		
<i>G test for independence</i>			
1982,1983			
1984&1985:	$df = 3, G = 57.193, p < 0.001*$		

### 3.5.2 Inter-year variation in mortality of young

Loss of young varied significantly between the years 1982 to 1985 (table 21). It is difficult to determine even the proximate cause of a young's disappearance, because that is what they did do — disappear!

The few carcasses that were found showed signs of predation, and researchers have seen dingoes chase the kangaroos and wallabies at Wallaby Creek and feed on carcasses. However, nutritional factors or disease may have predisposed the young to be vulnerable to predation.

Over the four years dingo activity has varied greatly (fig. 22), as measured by the number of sightings of dingoes per month. There was an outstandingly higher frequency of dingo sightings during the period from the end of 1983 to mid 1984. According to the local farmers (E. and J. Hayes, and Bell) the increase in the dingo population at this time was one of the worst in the region for 10 to 20 years. The farmers began intensively baiting and trapping for dingoes in 1984.

The number of dingo sightings per month over the four-year study period was significantly related to the proportion of young produced per month which disappeared (see fig. 22,  $R^2 = 0.095$ ,  $df=45$ , (% of young which disappeared from the total produced) =  $9.83 + 5.78(\text{no.dingoes}) - 0.56(\text{no.dingoes})^2$ , linear  $p=0.034$ , quadratic  $p=0.048$ ).

However, the increased loss of young in 1983 followed and lasted throughout a period of particularly atypical weather; in the beginning of 1983 the 'wet season' was very dry, and

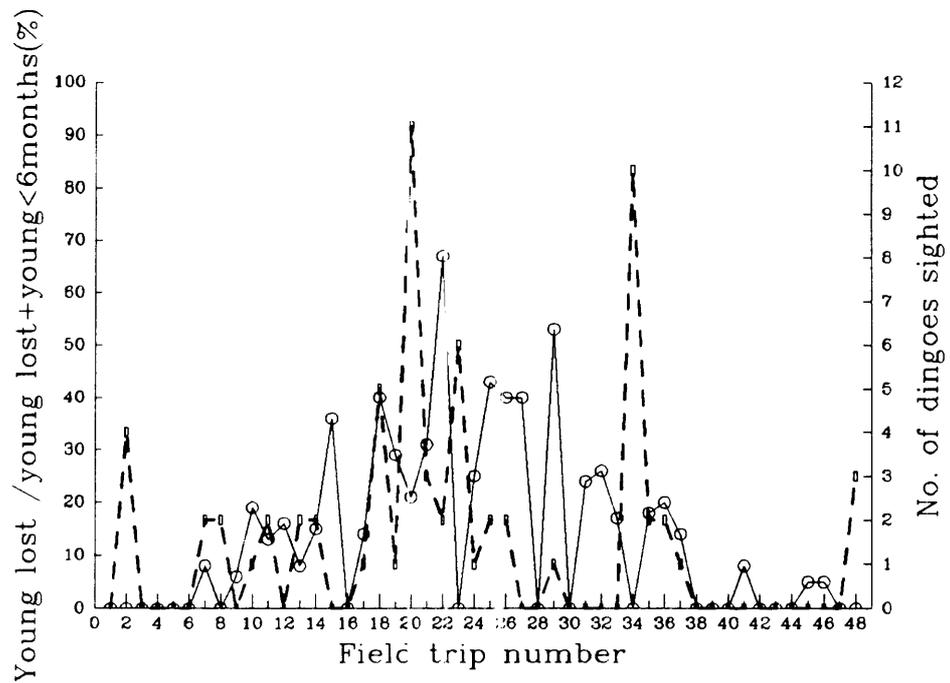


Figure 22: The number of dingo sightings per month and the proportion of young less than 6 months post-PEP who disappeared in each month. The broken line represents the dingo sightings and the continuous line represents the young lost.

Table 22: Number of young who were lost and who were weaned for young who PEPed in one of 4 'seasons' over the 4 study years. Also included are the numbers of young lost and weaned according to whether the young PEPed in the peak or offpeak season with a 'peak only' or 'offpeak also' mother. Only young who survived to at least within a month of PEP could be included, otherwise the dates of PEP could not be estimated. G tests comparing frequencies of lost and weaned young between seasons and/or types of mother are included. Probabilities of less than 0.05 have an \*.

PEP date	lost	weaned	total
April, May, June	35 (56%)	12 (44%)	27
July, Aug., Sept.	33 (57%)	25 (43%)	58
Oct., Nov., Dec.	31 (53%)	28 (47%)	59
Jan., Feb., March	15 (63%)	9 (36%)	24

G test for independence  
df = 3, G = 0.723, ns

mother X season	lost	weaned	total
'peak only', peak	45 (67%)	22 (33%)	67
'offpeak also', peak	17 (39%)	27 (61%)	44
'offpeak also', offpeak	34 (67%)	17 (33%)	51

G tests of independence:  
 'offpeak also' mothers: peak vs offpeak season  
 df = 1, G = 7.553, p < 0.01\*  
 peak season: 'peak only' vs 'offpeak also' mothers  
 df = 1, G = 8.825, p < 0.01\*  
 'offpeak also' vs 'peak only' mothers  
 df = 1, G = 3.962, p < 0.05\*

then the 'dry season' was quite wet (see section 2.2). Consequently, mothers and young may have been stressed either nutritionally or directly by inclement weather in 1983. The weather returned to a more typical pattern by 1984. However, many young were still disappearing during 1984. The continued loss of young could have been related to the females not having recovered from reproducing in the atypical year of 1983. This suggestion is supported by a high loss of adults in 1984 and early 1985 (section 2.3), even though dingo activity had been reduced. The population size reached its lowest level for the 4 year study period in July 1985.

Overall, while the pattern of disappearance of young coincides well with the change in dingo activity, it is not possible to discount the effect of the changing weather pattern, pasture quality, and maternal condition on the rate of loss of young (see also section 6.4).

### 3.5.3 Intra-year variation in the mortality of young

Although the total frequency of the disappearance of young did not follow a distinct

seasonal pattern (table 22), this analysis does not take into account the fact that some females were producing peak young only. If these females had an inherently different probability of rearing a young to weaning compared to females who tended to produce young regardless of the season, then there may be a seasonal effect on the probability of a female rearing a young to weaning.

Females who produced only peak season young did have a significantly lower rate of rearing young to weaning (0.30 young per year SE 0.048, N=19), as compared to females who produced at least one offpeak young (0.52 young per year SE 0.052, N=29; t test  $t=2.87$ ,  $df=46$ ,  $p=0.006$  see appendix A for calculation of rate of rearing young to weaning).

Thus, I divided young into one of three categories: emerged in the offpeak season, emerged in the peak season but with a mother who was known to have produced at least one offpeak young, and emerged in the peak season with a mother who was observed to produce only peak young. Significantly fewer offpeak young survived to weaning, as compared to peak young reared by the same set of mothers. Significantly fewer peak young reared by mothers who produced only peak young survived to weaning as compared to peak young from the mothers who reared both types of young (table 22).

Hence, an individual mother can expect to rear to weaning fewer of the young she produces who are timed to emerge in the offpeak season, as compared to those timed to emerge in the peak season. But the probability of a young being reared to weaning is also dependent on the type of mother.

#### **3.5.4 The effect of the previous young on the current young's probability of surviving to weaning**

For a number of mammalian species, the survival of a young has been found to be negatively related to the successful rearing of a previous young, or to the presence of an older sibling in the mother's home range. (e.g. see Johnson, 1985; Clutton-Brock *et al.*, 1982b; van Schaik and van Noordwijk, 1985; Silk, 1983; Silk and Boyd, 1983; Simpson and Simpson, 1985). In addition, this effect of the previous young can be dependent on the sex of that young (see above references). There are two currently discussed hypotheses for the depressive effect of older kin on a current young's probability of surviving. One is that there is a cost attached to the presence of kin in an individual's home range, which affects the survival of subsequently produced young (Clutton-Brock *et al.*, 1982a and b; Dittus, 1979; Johnson, 1985). The other is that the mothers who have just reared a young may be

**Table 23:** The percentages of young lost and of young weaned following siblings who were lost and weaned. Siblings are also categorised by sex. Results of G tests are included. Probabilities of between 0.1 and 0.05 are presented with a † and those of less than 0.05 are presented with an \*.

previous young	current young		
	lost	weaned	total
lost	42 (57%)	32 (43%)	74
weaned	36 (73%)	11 (27%)	41
G test for independence df = 1, G = 3.114, p < 0.1†			
previous young	current young		
	lost	weaned	total
<b>male:</b>			
lost	20 (57%)	15 (43%)	35
weaned	17 (77%)	5 (23%)	22
<b>female:</b>			
lost	13 (46%)	15 (54%)	28
weaned	9 (56%)	7 (44%)	16
G tests			
previous son: lost vs weaned df = 1, G = 2.485, ns			
previous daughter: lost vs weaned df = 1, G = 0.394, ns			
previous sibling: son vs female df = 1, G = 2.273, ns			
previous sibling weaned: son vs female df = 1, G = 1.885, ns			

Table 24: The mean duration of the inter-PEP interval prior to sons' and daughters' PEP for lost and weaned young separately. The units are weeks. *F* tests and *t* tests comparing lost and weaned young are included. Probabilities of between 0.1 and 0.05 are presented with † and those less than 0.05 are presented with an \*.

inter-PEP interval	lost	weaned	test	probability
sons				
sample size	40	22	$F=9.04$	$p < 0.001*$
mean	45.8	51.8	$t_{up}=1.94$	$p = 0.064†$
SE	0.75	3.04		$df=23.6$
daughters				
sample size	24	21	$F=1.42$	$p = 0.433ns$
mean	47.3	46.3	$t_p=0.53$	$p = 0.601ns$
SE	1.46	1.31		$df=43$

in poorer condition than those who did not and consequently may be less able to invest in the next young (see Clutton-Brock *et al.*, 1982b).

Does an eastern grey kangaroo mother's immediately previous reproductive history affect her probability of rearing the next young to weaning?

Significantly fewer young ( $N=115$ ,  $G=3.114$   $df=1$ ,  $p<0.1$ ) were reared to weaning if their previous sibling had been reared to weaning (26.8%) than if it had disappeared (43.2%), (typically on PEP). This effect of survival of the previous young on the survival of the current young appears to be less influential if the previous young was a daughter rather than a son (table 23). The difference was not significant, but is worth mentioning as it may be related to a differential investment by the mother in rearing sons and daughters. This topic is discussed in section 3.6. Postweaning investment in sons and daughters is discussed in chapter 4.

It is also worth noting that sons lost following PEP were more likely to have had short pouch-lives than those who survived. However, this difference in pouch-life duration between young who survived to weaning and those who did not was not significant for daughters (table 24).

This difference in the probability of a son surviving to weaning according to the duration of his pouch-life might be related to the effect of the previous sibling's survival. This is because a son's pouch-life (as measured from inter-PEP interval) is significantly shorter if he follows a sibling (typically a son) who was reared to weaning (see section 3.6).

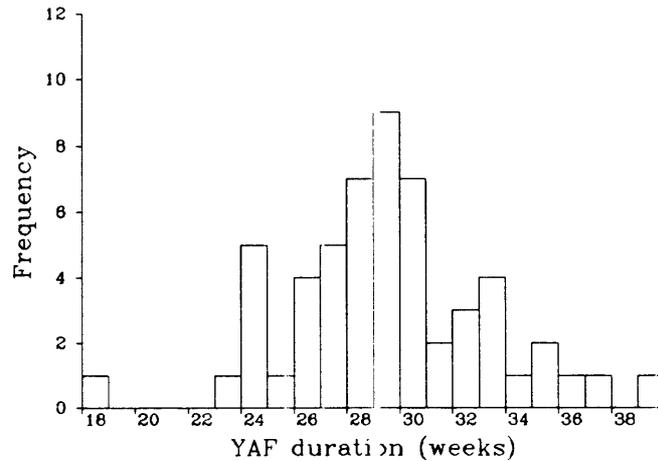


Figure 23: *Frequency distribution of the duration of the YAF phase.*

### 3.6 Variation in the duration of pouch-life, the inter-PEP interval, the YAF phase, and the pouch-infant phase

There is considerable variation in the duration of the stages in the rearing of young by the eastern grey kangaroo female at Wallaby Creek. The inter-PEP interval varied greatly, ranging from 35 to 96 weeks. The maximum duration for pouch-life was estimated as 48 weeks. The pouch-infant phase varied between 13 and 25 weeks, and the duration of the YAF phase ranged between 18 and 39 weeks (figs. 12 and 23).

Previous research has found that mammalian mothers may employ different tactics when rearing different young (see chapter 1); for example, males may be more intensely suckled than females (Trillmich, 1986; Reiter *et al.*, 1978; Clutton-Brock *et al.*, 1982b; Kovacs and Lavigne, 1986; Lee and Moss, 1986). Alternatively, the mothers may be differentiated by the tactics they use to rear young (Altmann, 1980; Clark *et al.*, 1986). This differentiation between mothers need not imply that a mother consistently follows one type of rearing schedule throughout her life (Caro and Bateman, 1986). Maternal rearing tactics can be age-dependant or related to the female's social position or physical condition (Silk *et al.*, 1981; Labov *et al.*, 1986; Charlesworth and Leon, 1976; Coleman *et al.*, 1985; Meikle *et al.*, 1984).

The presence of a variety of rearing schedules in a population does not in itself imply that total maternal-investment may vary between young.

It is not possible to measure parental investment in absolute units (Trivers 1978, 1974; Clutton-Brock and Albon, 1982). However, it is possible to consider whether particular young may have been more costly to the mothers in terms of lowering their ability to invest and rear subsequent young to weaning (Trivers, 1978, 1974). This can be done by investigating the relative delay between a mother's successive reproductive attempts, and a mother's or the subsequent young's probability of survival following the rearing of a previous young (Simpson and Simpson, 1985; Clutton-Brock *et al.*, 1982a and b; Altmann, 1980; Silk *et al.*, 1981; Johnson, 1986a).

There has been much debate in the literature concerning whether mothers should invest more intensely in sons or daughters. (Maynard-Smith, 1980; Trivers and Willard, 1973; see chapter 1). One of the current hypotheses is that if sons have a more variable expected lifetime-reproductive-success than daughters (*ibid.*) then the mothers of a population should invest in total in sons to a greater extent than in daughters. This should be true providing the amount of investment given to a son is positively correlated with his lifetime reproductive success. However, investment in sons and daughters may not be absolutely different; it may just be distributed via different schedules and rates (Dittus, 1979; Clutton-Brock *et al.*, 1982a and b; Johnson, 1985, 1986a; Clark, 1978).

Finally, if mothers differ in their access to the local resources which are necessary for breeding, or in the relative amount they invest in individual young, and sons and daughters are best reared to different schedules, or are differentially affected by the mother's condition and social position, then some mothers may preferentially produce and rear sons, and others daughters (see chapter 1).

With the above ideas in mind, I have examined whether variations in the durations of the stages of rearing young could be interpreted as indicating that there is more than one reproductive strategy which may be followed by mothers. I follow this line of investigation further in section 3.7 to include maternal strategies in the differential production of sons and daughters.

I have already suggested that there may be two maternally-related strategies of rearing young. In this section I discuss whether these mothers differ in other ways, or if they differ because of a fortuitous result of the types of young they rear. Also, as the eastern grey kangaroo male at Wallaby Creek appears to have a more variable lifetime-reproductive-success

than the female (Appendix A), I was particularly interested in determining whether sons and daughters were reared to different schedules and whether either affected the mother's subsequent reproductive attempt to a greater extent than the other.

### 3.6.1 Variations related to the mother's immediate reproductive history

Many mammalian mothers delay their next reproductive attempt after rearing a young to weaning, as compared to their peers who lost that season's young (Paul and Thommen, 1984; Silk *et al.*, 1981; van Schaik and van Noordwijk, 1985; Altmann *et al.*, 1978; Clutton-Brock *et al.*, 1982b). This is typically interpreted as meaning that rearing young to weaning lowers a mother's physical condition, and that delay either allows a mother to regain condition before her next reproductive attempt, or is a physiological consequence of the mother's poor condition.

Just the opposite occurs in the kangaroo mothers at Wallaby Creek! The inter-PEP interval between the permanent emergence of an older sibling who was reared to weaning, and the permanent emergence of the subsequent young is on average shorter, but also less variable, than the inter-PEP interval following the permanent-emergence of a sibling who was lost (table 25).

Remember that sons with short pouch-lives were significantly less likely to survive to weaning than those with longer pouch lives (i.e. those who followed a longer inter-PEP interval).

Perhaps this result, which seems contrary compared to previous studies, is related to some mothers producing peak young only, while others produced young at a rate of more than one per year. The mothers who produced only peak-young were less likely to rear those young to weaning, compared to the other mothers (section 3.5), and consequently their long inter-PEP intervals may have weighted the data.

However, the inter-PEP intervals, when analysed separately for the two types of mothers, were still on average longer following the emergence of a young who was lost, compared to one who was reared to weaning (table 25). The difference was significant for the mothers who produced only peak young but not for the other mothers (table 25).

The question now arises as to whether mothers who produced only peak young were doing so because they tended to lose young, and therefore were more likely to remain with their breeding attempts timed for young to emerge in the peak season.

Basically, there were two exceptions to an average inter-PEP interval of about 46 weeks

Table 25: The mean inter-PEP interval prior to a young's PEP (pouch-life duration) for the two types of mother and according to whether the previous sibling was lost or weaned. *F* tests, *t* tests, and Mann Whitney *U* tests (MWU) on the data are included. Time units are weeks. The percentages of variation in the duration of this interval which is explained by the 'types' of young are included. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an \*.

	inter-PEP interval			test	probability
	sample size	mean	SE		
<b>type of mother:</b>					
'peak only'	42	49.5	1.04	$F=1.40$	$p = 0.252ns$
'offpeak also'	69	45.3	1.30	$t_p = -2.62$	$p = 0.01*$
mean of mothers' averages					
'peak only'	19	50.1	1.14	$F=1.30$	$p = 0.525ns$
'offpeak also'	29	45.0	1.61	$t_p = 2.63$	$p = 0.01*$
<b>previous young:</b>					
lost	74	48.6	1.07	$F=2.72$	$p < 0.001*$
weaned	40	44.8	0.90	$t_{up} = 2.76$	$p = 0.007*$
				MWU, $z = -3.257$	$p = 0.001*$
<b>type of mother X previous young X type of young:</b>					
'offpeak also':					
(peak and offpeak young)					
lost	39	46.7	1.57	$F=2.616$	$p < 0.05*$
weaned	28	44.6	1.15	$t_{up} = 0.095$	$p > 0.1ns$
<b>a(offpeak young)</b>					
lost	21	45.6	0.937	$F=3.405$	$p < 0.05*$
weaned	15	44.6	0.73	$t_{up} = 2.705$	$p < 0.05*$
<b>b(peak young)</b>					
lost	18	47.9	3.31	$F=3.021$	$p < 0.03*$
weaned	13	46.8	2.27	$t_{up} = 0.260$	$p > 0.1ns$
<b>c'peak only':</b>					
lost	32	50.8	1.36	$F=2.805$	$p < 0.05*$
weaned	11	44.8	1.43	$t_{up} = 2.539$	$p < 0.05*$
<b>Variation explained by:</b>					
		% variation	df	<i>F</i> test	probability
the 3 types of young a,b. & c		4.7%	2	2.41	0.95
previous young was lost/weaned		3.8%	1	3.91	0.051
interaction		1.1%	2	0.56	0.571
error		90.4%	93		

(table 25). Offpeak young tended to emerge permanently following a very short average inter-PEP interval of about 43 weeks, if the previous young was reared to weaning. Peak young tended to emerge permanently following a very long inter-PEP interval of 51 weeks, if the previous young was lost, but only if they had mothers who produced peak young solely.

In other words, mothers who produced only peak young were delaying reproduction significantly more after the loss of a young than were mothers who were known to produce at least one offpeak young; and this was regardless of the season of emergence of the latter mothers' young. Consequently, the mothers who produced only peak young were differentiated from the other mothers by more than a fortuitous result of losing more peak season young.

However, it is also worth noting that mothers who were known to produce at least one offpeak young were particularly likely to shorten the pouch-life duration of an offpeak young following a young who was reared to weaning (table 25). Thus these mothers would be more likely to produce fewer consecutive offpeak young if reared to weaning, than consecutive offpeak young whom the mother did not rear to weaning, or consecutive peak young in general.

As the inter-PEP interval does not directly measure pouch-life duration, I decided to look at variation in the infant phase of pouch-life. I felt that this should give a more standard indication of pouch-life duration for all females' young. However, the relationship between the duration of the infant-phase and the inter-PEP intervals of less than 49 weeks (that is those intervals which are assumed to approximate pouch-life duration closely) was not the tight linear function I had expected (fig. 24). Nevertheless, variation in the duration of the pouch-infant phase could still give another relative measure of how much a mother invested in a young. Pouch-infants should be appreciably more metabolically demanding to rear than pouch neonates (Green, 1984; Dove *et al.* 1987; Janssens and Ternouth, 1987). Also, pouch-infants disrupt their mothers' activity schedules to a greater degree than pouch-neonates (chapter 5).

There was little indication, from the means of the durations of the pouch-infant phase that the current young's duration as a pouch-infant was affected by whether or not the previous young was reared to weaning (table 26).

The durations of the YAF stage were slightly but non-significantly shorter for a young following one who was reared to weaning (table 27).

Table 26: The mean durations of the pouch-infant phase for a young following a sibling who was lost or who was weaned. The means for young of the two types of mothers and for those who PEPed in the peak and offpeak seasons are given separately. Units are weeks.

previous young		type of mother		total
		'peak only'	'offpeak also'	
		type of young		
		peak-season	offpeak-season	
		<b>for sons</b>		
<b>lost</b>	(N)	(16)	(4)	(2)
	$\bar{x}$	17.0	14.5	17.0
	SE	0.52	0.75	2.8
<b>weaned</b>	(N)	(3)	(3)	(8)
	$\bar{x}$	15.7	19.7	18.4
	SE	0.82	3.90	1.05
	$\bar{x}$	16.8	16.7	18.1
		<b>for daughters</b>		
<b>lost</b>	(N)	(7)	(6)	(7)
	$\bar{x}$	16.1	16.0	18.0
	SE	0.64	0.75	1.33
<b>weaned</b>	(N)	(3)	(4)	(6)
	$\bar{x}$	16.7	17.3	19.8
	SE	0.41	1.28	0.66
	$\bar{x}$	16.3	16.5	18.8
				17.4

Table 27: Mean durations of the YAF phase for young following a sibling who was lost or who was weaned. Tests comparing means and variances are included. Units are weeks.

YAF phase	previous young		test	probability
	lost	weaned		
sample size	19	7	$F=1.47$	$p = 0.488ns$
mean	30.2	28.1	$t_p=1.00$	$p = 0.326ns$
SE	0.99	1.9		$df=24$

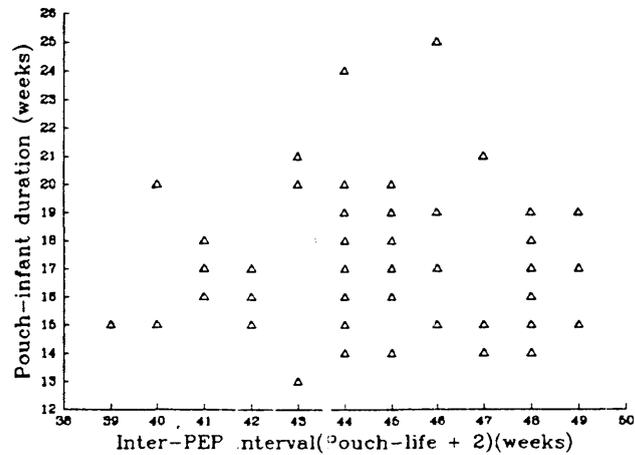


Figure 24: Scattergram depicting the duration of the pouch-infant phase and inter-PEP interval (prior to the young's PEP) for each young. An inter-PEP interval less than 49 weeks approximates pouch-life duration plus 2 weeks. A significant best-fit equation could not be fitted to the data (probability: 0.561); the  $R^2$  was  $0.005 \times 10^{-0.01}$ .

Finally, are male and female young differently affected by whether the previous young was reared to weaning, and does the sex of that previous young affect the timing of the current young's permanent emergence?

Firstly, sons and daughters in total did not permanently emerge from the pouch following significantly different *average durations* of inter-PEP intervals, nor did they *average* significantly different durations in their pouch-infant phases or YAF phases (table 28). However, the inter-PEP intervals preceding the emergence of a son *varied significantly more* than they did preceding the emergence of a daughter (table 28).

The data on the durations of inter-PEP intervals and pouch-infant phases were divided three-ways by type of mother, sex of the young (subsequent young for inter-PEP interval), and whether or not the previous young was reared to weaning; means and statistical tests are presented in table 29. The average durations of the inter-PEP intervals following the permanent emergence of a son versus a daughter who was either reared to or lost before weaning, are presented in table 30, as well as the tests for differences.

The *intervals between permanent-emergences* were significantly affected by whether or not the previous young was reared to weaning for sons, but not for daughters. Neither

Table 28: The mean durations of sons' and daughters' YAF phase, pouch-infant phase, and the inter-PEP interval prior to their PEP. Units are weeks. Tests comparing means and variances are included. Probabilities of between 0.1 and 0.05 are presented with a † and those of less than 0.05 are presented with an \*.

		sons	daughters	test	probability
<b>inter-PEP interval:</b>	sample size	62	45	$F=2.13$	$p = 0.01*$
	mean	47.9	46.8	$t_{up}=0.67$	$p = 0.502ns$
	SE	1.22	0.98		$df=105$
<b>pouch-infant phase:</b>	sample size	36	33	$F=1.29$	$p > 0.1ns$
	mean	17.1	17.4		
	SE	2.71	2.4		
<b>YAF phase:</b>	sample size	30	25	$F=1.22$	$p = 0.63ns$
	mean	23.8	29.4	$t_p=0.61$	$p = 0.542ns$
	SE	0.73	0.72		$df=53$

daughters nor sons were given consistently longer or shorter durations of *pouch-infant phases* according to whether the previous young was lost or reared to weaning.

If mothers were varying the level of investment they gave to sons to a greater extent than they did for daughters, it is possible that the sex of the previous young, as well as whether it was reared to weaning, might affect the next young's inter-PEP interval.

Unfortunately, the data set is now divided into quite small sample sizes (table 30). However, it appears that mothers are more likely to delay their next young's permanent emergence if it is a son who is following a brother who was not reared to weaning; while they are more likely to shorten this son's pouch-life if they had just reared a son to weaning. Daughters appear less influenced by their mothers' previous reproductive history and in turn influence their mothers' future reproductive effort less, as compared to sons.

### 3.6.2 Variation related to the sex of the young, the season of its permanent emergence, and the type of mother

As the mother's condition (section 3.3) and pasture quality (section 2.2) vary seasonally, so too may the mean duration of the inter-PEP interval, pouch-life phase and YAF phase. For example, mothers in good condition may be able to invest in a young at a higher rate, and thereby may decrease the duration of the various stages of the young's life. The mothers may then reproduce comparatively sooner than they would otherwise. Alternatively, a mother in good condition may invest in each young more intensely by extending the various phases

Table 29: The mean inter-PEP interval, pouch infant phase and YAF phase, according to 'type' of mother, sex of young, and whether the previous sibling was weaned or lost. Units are weeks. The percentages of variation explained by each category are included, as well as the results of *F* tests and the respective probabilities. Probabilities of between 0.1 and 0.05 are presented with a † and those of less than 0.05 are presented with an \*.

type of mother: type of young:	sons:			daughters:		
	peak only peak a	offpeak also peak b	offpeak offpeak c	peak only peak a	offpeak also peak b	offpeak offpeak c
<b>inter-PEP interval:</b>						
sample size	28	18	22	15	13	14
mean	50.1	47.1	43.6	48.5	47.9	44.9
SE	1.59	2.99	1.00	1.31	3.04	0.71
<b>pouch-infant phase:</b>						
sample size	19	7	10	10	10	13
mean	16.8	16.7	18.1	16.3	16.5	18.8
SE	0.46	1.76	0.90	0.45	0.63	0.77
<b>YAF phase:</b>						
sample size	6	14	9	10	5	9
mean	31.5	29.3	25.8	29.4	28.4	29.7
SE	2.68	0.99	1.33	1.55	0.67	1.24
<b>variation explained by:</b>				% variation	<i>F</i>	probability
type of young a+b vs c				2	2.17	0.144ns
previous young: lost vs weaned				4	4.14	0.045*
previous young: lost vs weaned				5	4.90	0.029*
type of mother: a vs b+c				2	1.59	0.210ns
type of young: a vs b vs c				5	2.41	0.095†
previous young: lost vs weaned				4	3.91	0.051†
<b>for sons only</b>						
previous young: lost vs weaned				5	2.92	0.093†
type of mother: a vs b+c				2	1.17	0.284ns
<b>for daughters only</b>						
previous young: lost vs weaned				4	1.69	0.201ns
type of mother: a vs b+c				1	0.26	0.616ns

Table 30: The mean durations of sons and daughters inter-PEP intervals (prior to PEP) according to whether the previous sibling was a son or daughter who was lost or weaned. Units are weeks. Tests comparing means, variances, and medians are included. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an \*.

previous young	sons:			daughters:		
	sample size	mean	SE	sample size	mean	SE
<i>lost</i>	40	50.1	1.74	29	47.4	1.17
<i>weaned</i>	22	43.9	0.93	16	45.9	1.81
<i>brother lost</i>	24	52.1	2.71	11	48.5	1.51
<i>sister lost</i>	13	47.3	1.43	15	47.4	1.93
<i>sister weaned</i>	6	46.6	2.48	9	44.2	0.76
<i>brother weaned</i>	16	43.1	0.87	7	48.0	4.00
<b>tests:</b>						
<i>lost vs weaned</i>						
<i>F test</i>	$F=6.35, p < 0.001*$			$F=1.31, p = 0.519ns$		
<i>t test</i>	$t_{up}=3.14, df=56, p = 0.003*$			$t_p=0.73, df=43, p = 0.471ns$		
<i>MWU test</i>	$z=-3.137, p = 0.002*$			$z=-1.442, p = 0.149ns$		
<i>brother lost vs brother weaned</i>						
<i>F test</i>	$F=15.06, p < 0.001*$			$F=4.55, p = 0.035*$		
<i>t test</i>	$t_{up}=3.12, df=27, p = 0.004*$			$t_{up}=0.13, df=8, p = 0.903ns$		
<i>MWU test</i>	$z=-3.039, p = 0.002*$			$z=-1.501, p = 0.133ns$		
<i>brother lost vs sister lost</i>						
<i>F test</i>	$F=6.80, p < 0.001*$			$F=2.23, p = 0.206ns$		
<i>t test</i>	$t_{up}=1.54, df=33, p = 0.13ns$			$t_p=0.44, df=24, p = 0.664ns$		
<i>MWU test</i>	$z=-0.942, p = 0.346ns$			$z=-0.989, p = 0.323ns$		
<i>sister lost vs sister weaned</i>						
<i>F test</i>	$F=1.39, p < 0.594ns$			$F=10.78, p = 0.002*$		
<i>t test</i>	$t_p=0.49, df=17, p = 0.632ns$			$t_{up}=1.53, df=18, p = 0.143ns$		
<i>MWU test</i>	$z=-0.880, p = 0.379ns$			$z=-1.141, p = 0.254ns$		
<i>sister weaned vs brother weaned</i>						
<i>F test</i>	$F=3.07, p < 0.084†$			$F=21.95, p < 0.001*$		
<i>t test</i>	$t_{up}=1.10, df=6, p = 0.313ns$			$t_{up}=0.92, df=6, p = 0.391ns$		
<i>MWU test</i>	$z=-0.448, p = 0.654ns$			$z=-0.324, p = 0.746ns$		

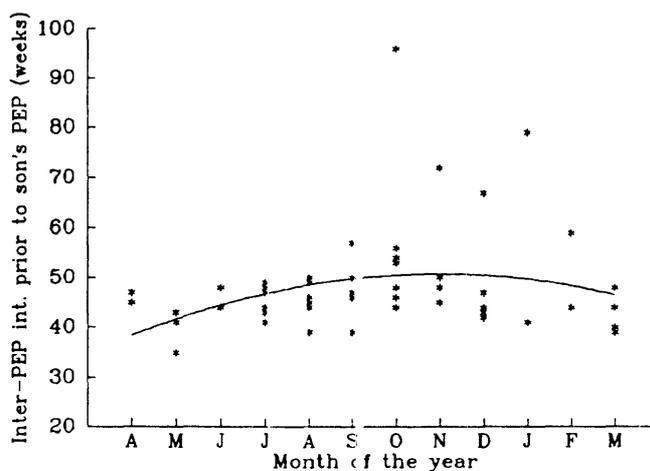


Figure 25: The durations and best-fit curve of the inter-PEP intervals prior to sons' PEP related to the month of the year they PEPed. The  $R^2$  value was 0.101. The equation was:  $(\text{inter-PEP interval}) = 34.6 + 4.07(\text{month}) - 0.26(\text{month})^2$ . The linear and quadratic probabilities were 0.020 and 0.041 respectively. Units are weeks.

of a young's life. In this case, I would expect that the young they produce could expect a greater than average lifetime-reproductive-success (see chapter 1 for theory). Although there is a problem of *post hoc* interpretation, it may be possible to infer the most probable tactics being followed by the mothers by comparing the various relationships between the durations of the reproductive phases and their seasonal timing.

In the previous subsection, I found that sons appeared to be affected by the mother's previous reproductive history to a greater extent than daughters. Hence, the durations of sons' pouch-life, infant phase, and YAF phase also may be more affected by the season of permanent emergence than are the durations of these stages for the daughters.

Both the durations of the inter-PEP interval (preceding the permanent emergence of a young) and the YAF phase varied in a significant relationship with the date of the young's permanent emergence (by month) for sons but not for daughters (figs. 25, 27, 26, and 28). This seasonal difference in the inter-PEP interval was possibly mediated by the type of mother (see previous subsection and table 29). Sons of mothers who produced only peak young followed on average longer inter-PEP intervals than peak sons of mothers who were known to produce an offpeak young. The type of mother might have influenced the

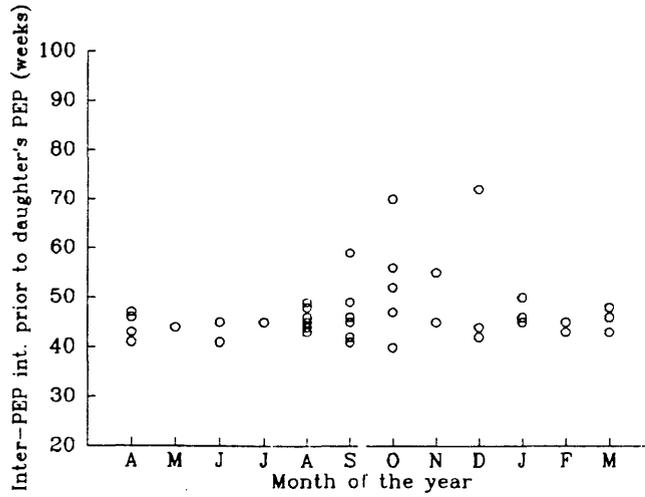


Figure 26: The durations of the inter-PEP intervals prior to daughters' PEP related to the month of the year they PEPed. A significant best-fit equation could not be fitted to the data. Units are weeks.

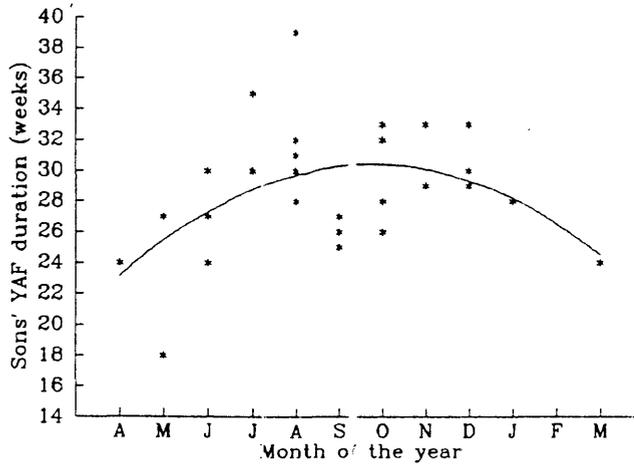


Figure 27: The durations and best-fit curve of the YAF phase, for sons, related to the month of the year they PEPed. The  $R^2$  value was 0.238. The equation was:  
 $(YAF \text{ duration}) = 20.49 + 2.94(\text{month}) - 0.22(\text{month})^2$ .  
 The linear and quadratic probabilities were 0.008 and 0.012 respectively. Units are weeks.

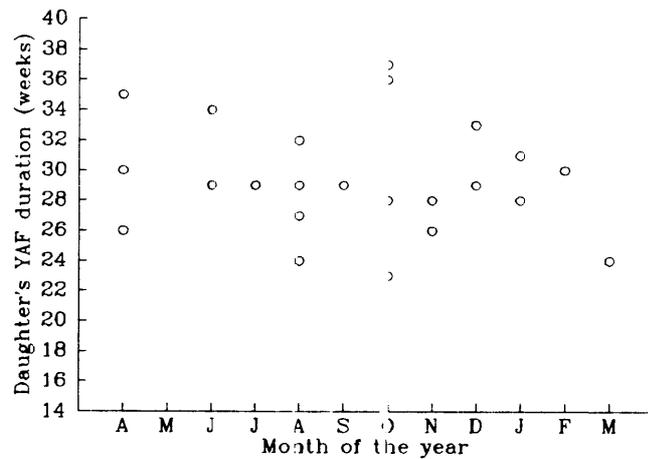


Figure 28: The durations of the YAF phase, for daughters, related to the month of the year they PEPed. A significant best-fit equation could not be fitted to the data. Units are weeks.

duration of a son's YAF phase as peak sons of 'peak only' mothers had slightly longer durations than peak sons of 'offpeak also' mothers. However, there were too few data to make any conclusions either way (table 29).

The variation in the duration of the pouch-infant phase appears better explained by season than by type of mother (table 29). But, unlike the inter-PEP interval and the duration of the YAF phase, the duration of the pouch-infant phase varies seasonally as much for daughters as for sons (table 26). Peak young average short pouch-infant phases of 16 weeks, while offpeak young average longer pouch-infant phases of 18 weeks.

Overall, offpeak sons are most likely to have short YAF phases, and short pouch-life durations, but long pouch-infant phases. Offpeak daughters are likely to have average YAF phases and pouch-life durations, but a pouch-infant phase as long as the offpeak sons. These offpeak young permanently emerge in late summer to mid winter (January to June). Peak sons are likely to have long YAF phases, and an average to long pouch-life. It is rather difficult to deduce whether mothers who produce only peak young are giving their young a longer than average pouch-life, as well as delaying their reproductive attempt to time PEP to the peak season. However, the sons of these mothers are more likely to emerge after longer inter-PEP intervals than are the daughters. Consequently, these sons may have long pouch-lives. Regardless of the duration of their pouch-life and the type of mother, both

sons and daughters who emerged permanently in the peak season have on average short pouch-infant phases. This phase of pouch-life varies for daughters with the season of their emergence, but otherwise daughters are rather consistently reared.

### 3.7 Secondary sex ratios

Maternal investment may vary between the sexes by more than different schedules of investment during rearing. In certain conditions mothers may tend toward producing more of either sex (see chapter 1).

#### 3.7.1 Biased production of the sexes

According to one current theory (Trivers and Willard, 1973), when the males' expected lifetime reproductive success is more variable than that of females in a population, then mothers should preferentially produce sons or invest in each son, preweaning, to a greater extent than in each daughter that they produce (but see chapter 1 for conditions). The total investment in the sexes may be balanced by either a greater postweaning investment in daughters or a difference between mothers, whereby those who may most influence their sons' future reproductive success tend to rear sons, as compared to other mothers who may tend toward rearing daughters (see Clutton-Brock *et al.*, 1982b).

An alternate theory (Altmann, 1980; Dittus, 1979; Silk *et al.*, 1981; Silk, 1983.) proposes that mothers may tend preferentially to rear sons or daughters according to their relative influence on the young's future reproductive success regardless of whether there is significant variance between the sexes' lifetime reproductive success (see chapter 1). In some circumstances high-ranking mothers or those in better condition than their peers may preferentially rear daughters (Verme, 1983; Armitage, 1987; Simpson and Simpson, 1985).

The eastern grey kangaroo male at Wallaby Creek was estimated to have a more variable lifetime reproductive success than females (A<sub>1</sub> appendix A). However, the mother kangaroos did not appear to be investing in each son on average to a greater extent than each daughter, as measured by the durations of the stages in the production of young (section 3.6). Some sons may have cost the mother more than the typical daughter by depressing the probability of the mother rearing her next young to weaning. But other sons, typically those following the 'costly' son, may have been reared relatively 'cheaply'. Daughters are philopatric and as such may represent a post-weaning cost to the mother. About 20 other females share

Table 31: *Offspring sex ratio at conception (estimated) and at PEP, for each of 4 consecutive 12-month periods between April 1982 and March 1986 inclusive. The proportion of females estimated to have conceived while without a current pouch-young (i.e. the subsequent inter-PEP interval was greater than 48 weeks). Tests comparing the observed sex ratios to the expected of 1:1 (male:female) are included. Probabilities of between 0.1 are presented with a † and those less than 0.05 are presented with an \*. Note that if all females conceived via the delayed blastocyst cycle the the sex ratio at conception for each 12-month period should be the same as the sex ratio at PEP for the relevant 12-month period (i.e. 15 month lag).*

conception year: (Jan.-Dec.)	1981	1982	1983	1984
young conceived and sexed to number of females in population	44/53	42/52	40/47	25/37
(%)	(83)	(81)	(85)	(68)
estimated offspring sex ratio at conception				
m/f:	27/17	27/15	23/17	13/12
sex ratio	1.588	1.800	1.353	1.083
$\chi^2$	2.273	3.429	0.900	0.040
probability	ns	< 0.1†	ns	ns
proportion of mothers who conceived without a pouch-young				
number/total:		6/41	10/44	7/26
(%)		(15)	(23)	(27)
PEP year: (April-March)	1982/3	1983/4	1984/5	1985/6
offspring sex ratio at PEP				
m/f:	28/18	30/16	22/18	16/13
sex ratio	1.556	1.875	1.222	1.231
$\chi^2$	2.174	4.261	0.400	0.310
probability	ns	< 0.05*	ns	ns

a mother's home range (chapter 4). According to Johnson (1985) this may mean that a female's relatives may depress her reproductive success at an approximately similar rate, as appears to occur in the red deer matriline on Rhum (Clutton-Brock *et al.*, 1982a and b). In this way daughters may represent a post-weaning cost to a mother.

Do mother kangaroos preferentially produce sons because there is a post-weaning investment in daughters, or because sons have a more variable lifetime reproductive success? Further, are the mothers differentiated in their tendency toward rearing sons and daughters?

A total of 190 young were known to be conceived during the 4 years of my study, and of these 96 were sexed as male and 65 as female. This sex ratio of 1.48 is significantly different from unity ( $\chi^2 = 5.969$ ,  $df=1$ ,  $p=0.015$ ). Thirty-two were not sexed: almost all were lost as pouch-young, and all would have had to be female to change the population's offspring sex

ratio to 1:1. Such an extreme differential mortality of the sexes is improbable, especially as 11 were lost upon their mother's disappearance.

Hence, the offspring sex-ratio bias towards males is either determined at conception, or else some females are preferentially losing female young as blastocysts or as neonates. If mortality of neonates differs between the sexes, I would expect that the male bias would be greatest in the years when more females conceived while without a current pouch-young. The reverse occurs! See table 31.

By whatever means the sex ratio becomes biased, it is distinctly so by the time the young permanently emerge. It remains biased to weaning (section 3.5). Therefore, the mother kangaroos were *rearing significantly more sons than daughters* to weaning. To date this is the greatest bias toward the production of one sex reported for either red or grey kangaroos (see Johnson and Jarman, 1983).

However, some mothers have produced 5 daughters sequentially; others produced sons only. In general there was a significant tendency for mothers to produce a young of the same sex as the young just previously produced ( $\chi^2 = 6.242$  df=1,  $p=0.013$ ).

This difference in preferential production of the sexes between the mothers may be related to inherent differences between the mothers or be a function of an external factor, such as the seasonal timing of their young (Myers *et al.*, 1985; Clark *et al.*, 1986; Stirling, 1971; Coulson and Hickling, 1961; Howe, 1977; Weatherhead, 1983; Fiala, 1981). I will discuss environmental affects on the offspring sex ratios of the kangaroos in the next subsection.

In the former case, there are several predictions from previous research against which my data can be interpreted. Firstly, if a mother can expect to influence her daughter's reproductive success positively, to a greater extent than other mothers, then she should preferentially produce daughters at an early age, rather than a late age, so that she may be present when many of her daughters commence reproduction (Dunbar, 1984). This assumes that mother-daughter pairs may become coalitions which either increase the probability of the individuals obtaining the local resources which are necessary to breed, or reduces the potential competition from non-relatives by, for example feeding in the company of tolerant relatives (Clutton-Brock *et al.*, 1982b). In other circumstances where a daughter inherits her mother's rank or resources (e.g. Harris and Murie, 1984; Michener, 1980; Silk *et al.*, 1981) without the mother necessarily being present while the daughter breeds, then a high ranking mother or mother with access to the best local resources might preferentially produce daughters regardless of her age.

Table 32: Results of tests for relationships between the prortion of daughters among the offspring that a female produced (*FSR*) and some other variables which differentiate the females. The variables were mean inter-PEP interval, size, 'age', rate of weaning young (*RWY*), percentage of young weaned, average relative condition (*ARCond*), home-range site, and breeding 'type'. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an \*.

variable related to FSR	equation	$R^2$	sample size	probability
mean inter-PEP interval		-0.077	50	0.297ns
size		-0.130	45	0.197ns
'age'		-0.295	40	0.032*
<i>RWY</i>		0.183	52	0.097*
	$100RWY = 44.62 - 35.2)(FSR) + 7.42(FSR)^2$	0.127		lin.0.023* quad.0.016*
% weaned	$\%weaned = 3.05 - 2.40(FSR) + 0.52(FSR)^2$	0.080		lin.0.198ns quad.0.148ns
<i>ARcond</i>	$FSR = -3.60 + 7.12(ARcond) - 3.00(ARcond)^2$	0.101		lin.0.478ns quad.0.560ns
	<b>FSR: mean , SE, (sample size)</b>		<b>test</b>	<b>probability</b>
home-range site				
North	1.14, 0.062, (13)		<i>F test</i> , $F=3.09$	0.043*
South	1.51, 0.073, (29)		<i>t test</i> , $t_{up}=3.82$ $df=38$	<0.001*
			<i>MWU test</i> , $z=2.803$	0.005*
type of female				
'peak only'	1.45, 0.079, (23)		<i>F test</i> , $F=1.42$	0.405ns
'offpeak also'	1.36, 0.079, (29)		<i>t test</i> , $t_p=0.81$ $df=50$	0.422ns

If a son's reproductive success is affected by the degree of preweaning investment he receives, then a mother in better-than-average condition, or with greater access to the local resources than her peers, or if old with lowered future reproductive expectations, should produce sons and invest in them intensely (see chapter 1; Clutton-Brock *et al.*, 1986; Charlesworth and Leon, 1976; Meikle *et al.*, 1984; Clutton-Brock 1984; Stearns, 1976).

For each mother, I calculated the relative proportion of her offspring which were daughters. A value of 1.0 meant that the mother produced daughters only, and a value of 0 meant that the mother produced sons only. The average mother produced a proportion of 0.39 daughters (SE 0.05, N=56).

The proportion of daughters among the offspring a female produced was not significantly related to whether she was a 'peak only' or 'offpeak also' female. Nor was the proportion related to her mean inter-PEP interval (her reproductive rate), her size, percent of young she reared to weaning or the mother's average relative condition (see section 3.3) (table 32). This proportion was significantly related to the mother's age and her rate of rearing young to weaning (see appendix A) (table 32). Younger females tended to produce daughters and older females sons; the females who had a higher rate of rearing young to weaning tended to produce more daughters than the females who had a lower rate of rearing young to weaning. Also, females with Northern home-ranges produced significantly more sons than did females with Southern home-ranges (table 32, see chapter 4 for home-ranges). Note that as neither a female's rate of producing young nor the percentage of young she reared to weaning were significantly related to her offspring sex-ratio, whereas her rate of rearing young to weaning was significantly related, both the former two factors are likely to contribute, to the significant relationship of the latter with the offspring sex-ratio.

The relationship between a female's tendency to produce either sons or daughters and her age was in the direction expected by Dunbar (1984) and Clutton-Brock *et al.* (1982).

An interpretation of the relationship between a mother's preferential production of sons or daughters and her rate of weaning young is less obvious. However, as mothers were no more likely to produce sons than daughters according to their relative physical condition, but were more likely to produce sons if they had a North home-range than a South home-range, I suggest that mothers may tend toward producing daughters if they have access to resources of a *consistently* high quality. This suggestion is supported by several findings. According to J. Clarke (pers. comm.) the Southern pasture is consistently higher in quality through the seasons than the Northern pasture. Further, the Southern females averaged

a significantly higher rate of rearing young to weaning than the Northern females (section 3.3). I found the Southern females to be in better condition than the northern females, although M. Jones' index did not support this (table 15). So perhaps the condition of the Northern females fluctuates to a greater extent than does Southern females. In the previous section I suggested that daughters appeared to be reared to a consistent schedule regardless of the season in which they permanently emerged or whether their mother had just reared a previous young to weaning. Finally females with access to a pasture of consistent quality may be able to share the local resources with adult daughters, with less cost to their future reproductive success. All of the above suggestions require substantiation from further research. However, it is worth bearing in mind that the reproductive strategies of females could possibly be affected by the consistency of the availability of their local resources.

Overall, I *propose* that while most females at Wallaby Creek produce a preponderance of sons, if a female is young or has access to consistent high quality pasture, then she may preferentially produce daughters.

### 3.7.2 Facultative adjustment of offspring sex ratios

A number of studies have reported that at least secondary sex ratios may vary from year to year in some species (Paul and Thommen, 1984; Clutton-Brock *et al.*, 1982b; Silk *et al.*, 1981; Reuterwall, 1981; Michener, 1980; Myers *et al.*, 1985; Clarke *et al.*, 1986; Stirling, 1971; Coulson and Hickling, 1961; Howe, 1977; Fiala, 1981; Weatherhead, 1983). Werren and Taylor (1984) and Werren and Charnov (1978) have shown that facultative adjustment of primary sex ratios is theoretically sound and have suggested some types of facultative responses:

1. if cohort size for young varies significantly between years, in years of exceptional recruitment the offspring sex-ratio should favour the sex with the significantly more even distribution of reproductive success over the age classes. In years of very poor recruitment, the other sex, that which reproduces in a few age classes only, should be preferentially produced. Similarly,
2. during a 'good' year the sex ratio should favour the sex with the lower mortality.
3. in the year following a year when particularly low or high adult mortality occurred, the sex ratio may shift.

4. the sex ratio may be related to population recruitment, when recruitment is increasing or decreasing at a constant rate.
5. the sex ratio may be related to population recruitment when recruitment is linearly dependant upon the number of adult females in the population. and
6. if the sexes have different life histories according to the season they were born in, then the one which has the 'better' lifetime reproductive success should be preferentially produced in the respective season.

My interpretation of the above, for eastern grey kangaroos, assuming that on average individual sons cost as much to rear as daughters preweaning, is the following:

- a) If resources are particularly limited and competition between mothers is great, then a mother should produce sons, as many of the other mothers may not reproduce and many of those that do are less likely to rear the young to weaning. So mothers should gamble on sons, who if they survive and reproduce are likely to produce far more young than a daughter could. The sons' expected reproductive success may be negatively correlated with the number of peers they have, to a greater extent than it is for daughters.
- b) If resources are bountiful and most mothers in the population have ready access to them, and may reproduce successfully, then the sex ratio should become more biased toward daughters. Daughters are more likely to survive to reproduce, and are possibly less affected by competition from their peers, than are sons.
- c) However, when the sons' physical condition at the end of the parental investment period is positively correlated with their lifetime reproductive success, then sons should be preferentially produced during periods when young are more likely to be weaned in good condition.

The particular environmental cue to which the mothers respond should be closely correlated to the availability of the resources they require for successful reproduction, and to the level of competition that they and their young will experience.

Was there seasonal variation in the offspring sex ratio at Wallaby Creek? If there was, according to the above prediction sons should be preferentially timed to emerge permanently in the offpeak season, unless their condition at the end of the parental-investment period

Table 33: *Offspring sex ratio at conception (estimated) and at PEP for each of 4 'seasons'. The  $\chi^2$  tests for significant deviations from parity are included. Probabilities of between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an \*.*

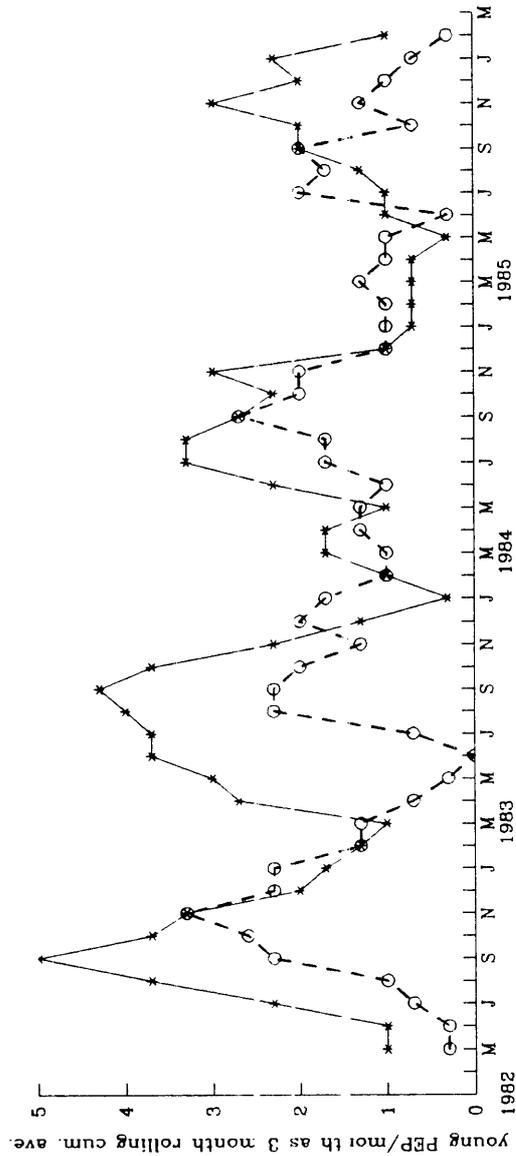
season	PEP date	males	females	sex ratio m/f	$\chi^2$	probability
late offpeak	April, May, June	16	9	1.78	1.96	ns
early peak	July, Aug., Sept.	36	21	1.71	3.95	< 0.05*
late peak	Oct., Nov., Dec.,	32	25	1.28	0.86	ns
early offpeak	Jan., Feb., March	12	10	1.20	0.18	ns
	April to Sep. vs Oct. to March conception date				0.995	ns
	Jan., Feb., March	15	11	1.36	0.31	ns
	April, May, June	33	14	2.36	7.68	< 0.05*
	July, Aug., Sept.	23	20	1.15	0.21	ns
	Oct., Nov., Dec.,	19	17	1.12	0.111	ns

is correlated with their expected lifetime reproductive success. In this latter case, I predict that it is more likely that the sons' YAF phase, rather than pouch-infant phase, would be timed to the season in which they may most readily gain condition. This is because son and daughter eastern grey kangaroos do not show a significant difference in their growth rates until some time post-PEP (Pooie *et al.*, 1982).

I divided the year into 4 seasons each of 3 months duration: early peak, late peak, early offpeak and late offpeak. The offspring sex-ratio, as measured on permanent emergence (see table 33), was significantly male biased in the early peak-season (1.71m/f). It was even more biased towards males in the late offpeak-season (1.78m/f), but not significantly different from parity, as fewer young emerged in this season. The sex ratio for the other two seasons was much lower (1.25m/f). The difference in the frequencies of males to females who permanently emerged was not significant between the two 1.75 versus the two 1.25 seasons. The average number of emergences per month smoothed by 3-month rolling cumulative averages are depicted in figure 29 for sons and daughters separately. There was typically a peak in the emergence of sons around September followed by a smaller peak in the emergence of daughters around October.

In general, there is possibly a stronger tendency for mothers to produce males preferentially if their young will permanently emerge at the beginning of the peak season. Permanent emergence was found to be more seasonally timed to a peak than was conception (section 3.4).

Figure 29: The number of sons and daughters who PEPed each month, as a 3-month rolling cumulative average. Sons are represented by the continuous line and daughters by the broken line.



Young conceived/month as 3 month rolling cum. ave.

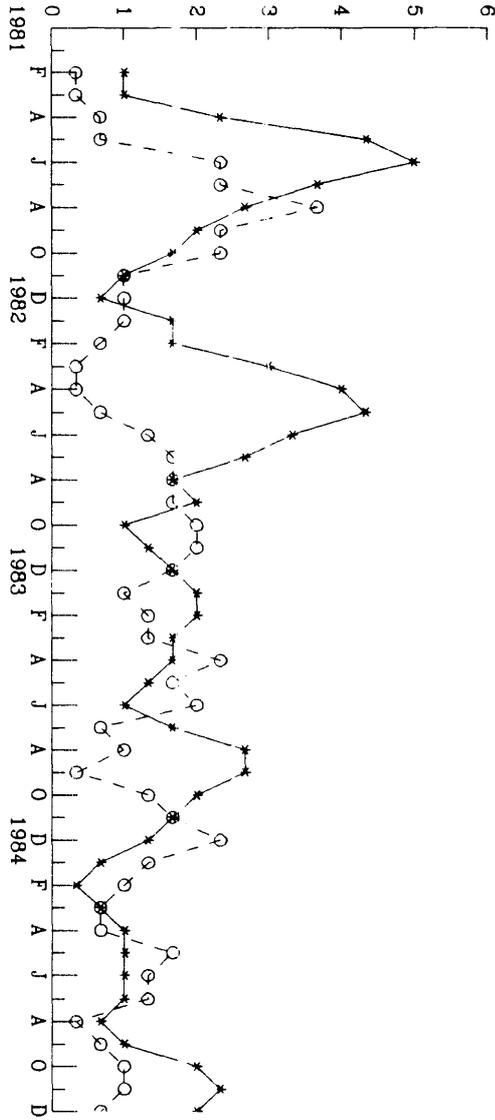


Figure 30: Number of sons and daughters conceived per month as a 3-month rolling cumulative average. The sons are represented by the continuous line and the daughters by the broken line.

However, when preferentially conceiving sons, the females might have been responding to their condition or an environmental cue that did not solely relate to the time of year that their young would emerge. Most females were conceiving about 15 months before their young emerged permanently from the pouch (section 3.2), though a few each year conceived about 11 months prior to their young's emergence. Consequently, if females were 'predicting' the season of their young's emergence when conceiving, rather than using a cue at the time of conception, I would expect that the estimated conception sex-ratios (see section 3.4 for estimating conception dates) would be less biased than the permanent emergence sex-ratios.

The conception sex-ratios for each of the four seasons ranged from 1.12 to 2.36 (table 33). Consequently, I suggest that the females are preferentially conceiving sons in relation to an external cue or their relative condition.

The bias toward conceiving males peaked around the months February to June, according to the combined data from the 4 study years (table 33). However, when I plotted the conception sex ratios as 3-monthly rolling cumulative averages, the date of the peak in the biased conception of males was seen to vary from year to year (fig. 30). Thus, the cue was unlikely to have been related to the length of the daylight hours. Nor could it have been related to the proportion of young being conceived in the population at the same time (but see fig. 31). It was not related to adult mortality or the size of the population (figs. 33 and 32).

Johnson and Jarman (1983) found that the sex ratio of eastern grey kangaroo and red kangaroo pouch-young varied between populations in a significant quadratic function to rainfall. Areas with either an extremely high or low annual rainfall exhibit a male-biased sex ratio, while areas with a moderate annual rainfall (i.e. 700mm for eastern grey kangaroos), have female-biased sex ratios. There was a slightly greater correlation to short-term rainfall than to long-term averages. Consequently, the offspring sex-ratio of the population of eastern grey kangaroos at Wallaby Creek may be directly related to local patterns of rainfall. The male-biased sex ratio of this population was predicted by Johnson and Jarman's curve. Wallaby Creek receives a relatively high annual rainfall (mean 1023mm per year).

There was a significant relationship between the estimated offspring sex-ratio at conception and the average rainfall received in the 2 to 3 months prior to the date of conception (the dates of conception were combined in 3 month blocks) (fig. 34).

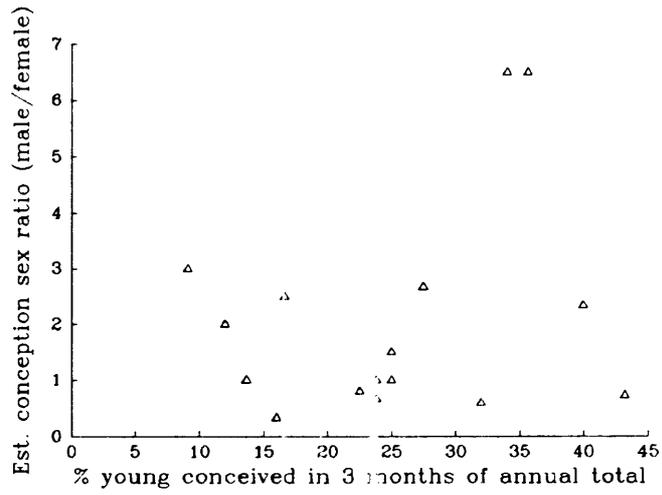


Figure 31: *The offspring sex ratio as estimated for conceptions within 3-month blocks related to the percentage of young disappearing in that 3-month block of the annual total conceived.*

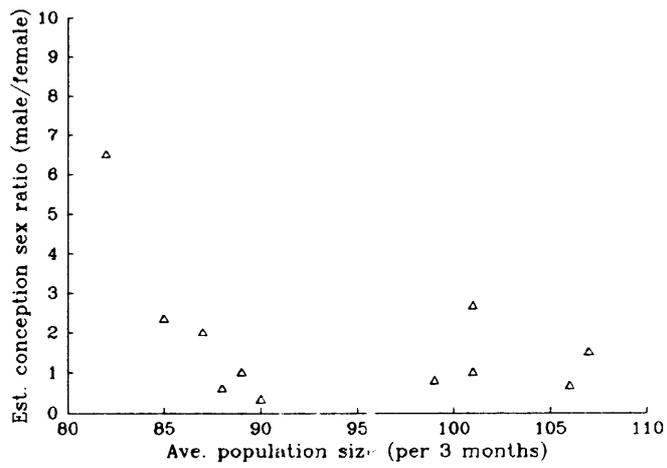


Figure 32: *The offspring sex ratio as estimated for conceptions within 3-month blocks related to the mean population size in that 3-month block.*

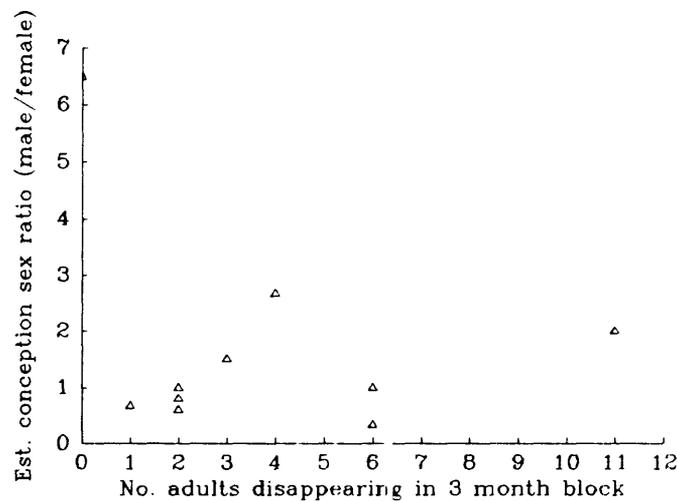


Figure 33: *The offspring sex ratio as estimated for conceptions within 3-month blocks related to the number of adults disappearing in that 3-month block.*

When there is much rain, males tend to be conceived. However, this did not happen in 1984 (fig. 35). I suggest that another variable may mediate the relationship of rainfall and offspring sex-ratios. This variable could be a female's physical condition, or the quality of the pasture.

Most of the females were conceiving when with no or small pouch-young, and were estimated to be in their best condition around February to June (fig. 15). These were the months with the highest average conception sex-ratios. I have suggested in section 3.5 that the females' condition may have been particularly poor in 1984. It was during this year that a distinctly biased peak in the conception of males did not occur (fig. 35), and the estimated annual conception sex-ratio was 1.08m/f as compared to 1.59, 1.80, and 1.35 in 1981 to 1983, respectively.

Further research is required to identify positively the cue to which the mother kangaroos may be facultatively adjusting the offspring sex ratio. I find it a particularly intriguing area of investigation, as most females conceive 15 months prior to their young's permanent emergence. Permanent emergence was more seasonal in distribution than conception (section 3.4). A peak-season permanent emergence might allow YAF to take advantage of spring pasture and increasing daily temperatures. Alternatively, as permanent emergence is the stage with the highest rate of mortality of young, and with mothers typically being in poor

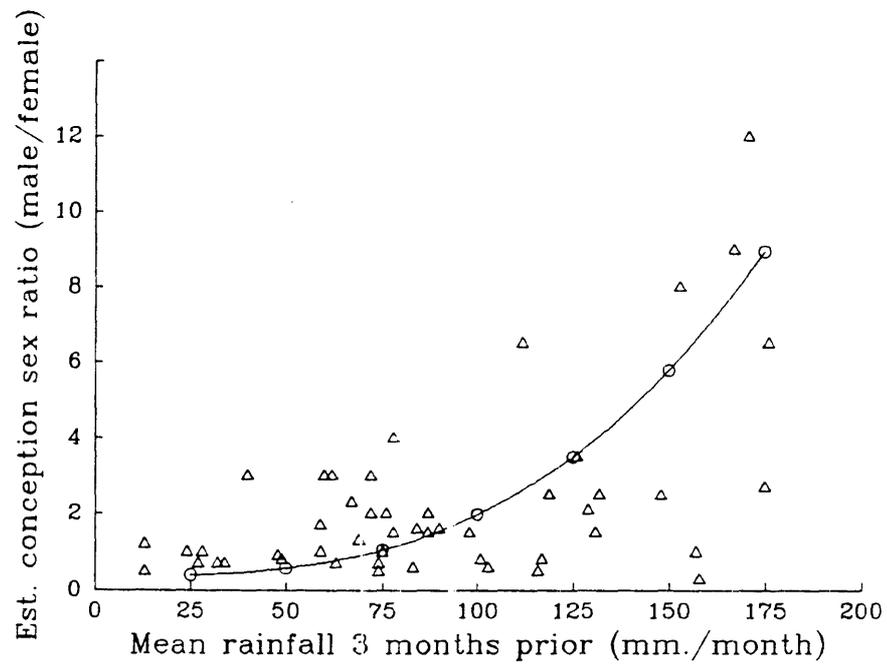


Figure 34: The offspring sex ratio as estimated for conceptions within 3-month blocks related to the mean monthly rainfall in that 3-month block (mm./month). The curve represents the equation which best describes the data. The  $R^2$  value is 0.618. The equation is  $(Sexratio) = 0.386 + 0.0000016(rainfall)^3$ . The probability is 0.0003.

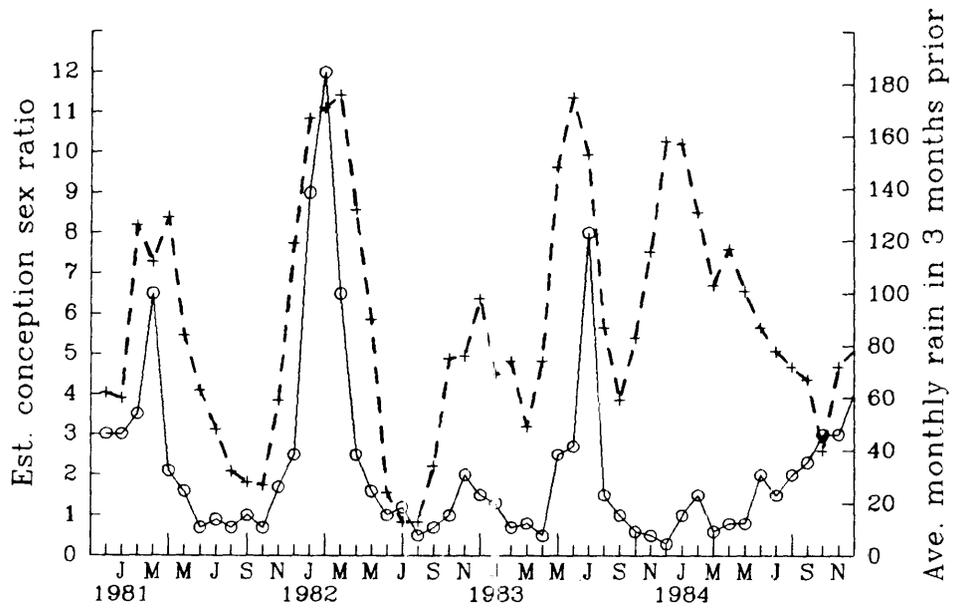


Figure 35: The offspring sex ratio at conception per month as a 3-month rolling cumulative average and the mean monthly rainfall received in the 3 months prior. The sex ratio is represented by the continuous line and the rainfall by the broken line.

condition, the seasonal timing of this stage will strongly influence the young's prospects of survival (section 3.5). However, there are a number of seemingly contradictory aspects of the variation in the offspring sex-ratios at Wallaby Creek.

Firstly, I interpret the following to mean that the sons' physical condition at the end of the parental-investment period is probably positively correlated to their expected reproductive success.

1. sons appear to have been conceived during months when the mothers were in their best physical condition; in 1984 when females on the whole were estimated to be in a relatively poor condition, fewer sons were conceived.
2. sons typically emerged permanently from the pouch at the beginning of the peak season and consequently would have had their YAF phase timed to span the spring-summer pasture flush.
3. older females tended to produce sons.

Hence I would expect that females would invest more intensely in individual sons than daughters (see interpretation for kangaroos c) this section and chapter 1).

However, it would appear from the following that not all sons are likely to have received more intense investment than daughters.

- i) a preponderance of sons were produced in total in the population. Consequently, according to Fisher (1930) each son should on average cost less to rear than each daughter.
- ii) the females who tended toward producing daughters rather than sons were the young females, who are typically in good condition, and females who had a high rate of rearing young to weaning.
- iii) sons, rather than daughters were likely to be given a shorter than average pouch-life either if they followed a sibling who was reared to weaning or if they permanently emerged in the offpeak season. Sons who were lost were more likely to have had a relatively short pouch-life than sons who survived to weaning.
- iv) the peak date for permanent emergence of daughters was in the middle of the peak season rather than early in the peak season as for sons. This could be interpreted as

meaning that the date of a daughter's permanent emergence, rather than her YAF phase, was timed to the increasing daily temperatures or spring pasture, or perhaps to reduce the probability of her loss. Young were more likely to be lost if they permanently emerged in the offpeak season than the peak season (section 3.5).

The key to this seeming contradiction in the females' rearing strategies may be related to the sexes having different optimal parental-investment schedules. A daughter may exact a cost from the mother over a longer period than a son; a son may benefit most by a high rate of maternal investment prior to weaning. In addition, a mother appears to have the option of rearing a son according to one of a variety of levels of investment that is wider than her range of options for rearing a daughter. But a daughter is less likely than is a son to affect the probability of the mother rearing her next young to weaning. Thus, it is possible that mothers may tend toward producing daughters if they have consistent access to high quality pasture (see section 3.7.1), or if their expectation of rearing a young to weaning is relatively high in comparison to their peers' expectations.

## **3.8 Discussion**

### **3.8.1 General patterns of the females' reproductive ecology**

The eastern grey kangaroo mothers at Wallaby Creek appear to be unusually fecund compared to other populations of this species (section 3.2). They typically mated when they had small pouch-young (estimated 77%), and from this I infer that they conceive young which become delayed blastocysts. No other population has been reported as having such a large proportion of the females breeding via the delayed-blastocyst cycle. The young conceived during this period of a mother's reproductive cycle will permanently emerge from the pouch some 15 months later. The average female produced one young every 47 weeks. The average female's breeding life-span was roughly estimated to be 8.5 years.

Females commenced breeding at a later age, about 3.5 years, than other populations (section 3.3). Adult mortality was low and there was a very high probability of young disappearing before weaning (62%). Hence, there is quite likely a very high degree of inter-female competition, if current theories of life-histories and inter-sex competition are correct (Goodman, 1979; Caughley, 1976; Silk and Boyl, 1983; Wasser, 1983; Gadgil and Bossert, 1970; Stearns, 1976). This in turn increases the probability that the females with the

relatively high rates of rearing young to weaning may differ from their peers in their access to resources or physical condition.

However, the frequency distribution of the females' rates of rearing young to weaning was not significantly different from a normal distribution. Nor did I find a significant relationship between the females' physical condition and their rate of rearing young to weaning. Of course, the latter relationship could be complex. Females may be in poor condition because they have reared a young to weaning, or because they have a comparatively reduced access to local resources and thereby are less likely to rear young to weaning.

I did find a significant *positive* relationship between the females' age index values (see section 3.3) and their rate of rearing young to weaning. Such a relationship does not differentiate females in their lifetime reproductive success rates. However, females did appear to differ to some degree in their reproductive tactics; I discuss this further in section 3.8.3.

The most vulnerable period in a young's life appears to be permanent emergence. The rate of loss of young around and just subsequent to this period was outstandingly high. It is comparable to the typically high post natal loss of young found in many ungulate species (Caughley, 1976; Estes and Estes 1979). There are a variety of patterns of the ungulate mother-young relationship immediately subsequent to birth, which are frequently proposed as being adaptations toward reducing the probability of the young's death by predation or separation. I look for this in the following chapters.

Although young were produced at any time of the year, there was a peak period for permanent emergence, which occurred during the months July to December. Mothers could expect that their young who emerged permanently in the offpeak season (January to June) were less likely to be reared to weaning than those whom they produced with a peak-season emergence. Also, the mother's physical condition during an offpeak young's permanent emergence was likely to be poorer than it would be during a peak young's permanent emergence. As the mothers of other reproductive classes were in relatively good condition compared to their condition during other months, I propose that rearing an offpeak young may be more costly to a mother than rearing a peak young.

Offpeak young were typically given longer pouch-infant phases than peak young. This was a rather invariable rearing practice as compared to other seasonally-related rearing patterns. I cannot conclude from the duration of this phase alone that mothers were investing more or less in their offpeak young compared to peak young. However, if offpeak young are more costly, as I have proposed above, then it may be that the longer pouch-infant phase

given to offpeak young is more costly to the mother than a short phase. This interpretation is consistent with my finding in chapter 5 that mothers' activity schedules tend to be disrupted while their infants are outside the pouch.

Offpeak young and those who followed a sibling reared to weaning were more likely than were other young, to have short pouch-lives: or at least the mother was less likely to delay the rearing of this next young. These young also tended to have short YAF phases. It is possible that these young are receiving less intense investment from the mother, especially in view of their greater probability of disappearing prior to weaning. However, it should be noted that this possible lower level of maternal investment received by offpeak young (that is the lower 'benefit' gained by the young), may not be directly related to the 'cost' of the young to the mother. An offpeak young may 'receive' less investment than a peak young but be more 'costly' to a mother by reducing the probability that she will rear her next young to weaning.

Overall, it is intriguing that so many of the mothers were maintaining a high rate of reproduction, rather than delaying their next reproductive attempt until a time when the next young was more likely to survive to weaning.

### 3.8.2 Sons and daughters

The eastern grey kangaroo male at Wallaby Creek was estimated to have a more variable lifetime reproductive success (in terms of young reared to weaning) than a female. Thus, according to Trivers and Willard (1973) and Maynard Smith (1980), at least preweaning maternal-investment in sons should be greater than it is in daughters.

However, the average son did not appear to receive a greater investment than the average daughter, according to the intervals between permanent emergences, and the durations of the YAF and pouch-infant phases. Nor was the mother's average rate of reproduction related to the proportion of daughters she produced (section 3.7).

As there was a slight but non-significant tendency for young following sons to be lost than those following daughters, rearing a son might be (at most) slightly more costly to a mother than rearing a daughter.

Conversely, many more sons were produced in the population than daughters. The sexes were not subject to a differential mortality rate, at least after 3 months of age and prior to weaning. Thus, it appears that prior to weaning the mother kangaroos were investing more in sons than daughters by investing in more sons rather than in each son to a greater

extent than each daughter.

This is an interesting tactic for the mothers to be following, as a *superficial interpretation* of this tactic could be that a son's physical condition at the end of the parental-investment period is not positively correlated to his expected lifetime reproductive success. In section 3.7.2 I concluded the converse: that sons' physical condition at the end of the parental-investment period probably is positively correlated to their expected lifetime-reproductive-success. I suggested this for the following reasons:

1. more sons than daughters are given long YAF phases, and emerge permanently after particularly longer intervals after the previous young's permanent emergence, than daughters (please note that more sons than daughters are given shorter than average pouch-lives and YAF phases, and the means are not different for the sexes);
2. sons tend to affect and be affected by the mother's next reproductive attempt to a greater extent than daughters (probability of survival and pouch-life duration);
3. mothers preferentially conceived sons at times when I estimated the mothers to be in their 'best' physical condition, and
4. more sons than daughters are timed to emerge permanently at the beginning of the peak season, i.e. sons' YAF phases appear to be timed to span the spring-summer growth of the pasture.

I believe that mothers may rear sons to a more variable investment schedule than daughters. A son's condition at the end of the parental-investment period may be positively correlated to his expected lifetime reproductive success. This requires substantiation since my results do not directly show such a relationship, but rather relate to results expected if such a relationship existed. However, assuming it is true, mothers may be preferentially conceiving sons when they can expect to invest intensely in a young, but invest in that son at a low rate if their expectations are not realised. Mothers at Wallaby Creek tend to conceive the next young prior to their current young's permanent emergence. Since most young are lost subsequent to emerging from the pouch permanently, a mother can not 'know' whether she will have invested intensely in rearing a son to weaning until the next young is at least several months old. Mothers are not expected to 'throw good investment after bad'— the Concorde fallacy (see Dawkins and Carlisle, 1976), but they should balance out the value of the present young relative to their future reproductive expectations (Coleman *et al.*, 1985). Consequently, the mothers at Wallaby Creek may be opting to produce young at a high

rate, and variably invest in sons, in relation to whether they reared the previous son to weaning or not and according to the season of the son's permanent emergence.

Overall, there was such a high rate of loss of young that the most adaptive strategy might be to:

- a) produce as many young as possible in the hope that some will survive to reproduce;
- b) invest in sons at a maximum rate preweaning, if possible;
- c) if not, at least attempt to rear the son to weaning;
- d) rear daughters in a consistent manner; and
- e) perhaps produce daughters particularly to emerge permanently when the young is most likely to survive and produce sons to emerge permanently at the beginning of the peak season so that their YAF phase is timed to span the spring-summer pasture (see sections 3.4 and 3.7).

### 3.8.3 Differences between mothers in rearing tactics

My analysis of the variation in the females' rate of rearing young to weaning did not support the conclusion that the females might have been significantly differentiated in their lifetime reproductive success. However, more variation in the females' month-by-month condition indices was explained by inter-female differences rather than month of the year or reproductive class. Further, I later concluded that the females did appear to be separable into those who produced peak young only, and those who did not adhere to one seasonal rearing schedule. These two types of females differed in their rate of rearing young to weaning (section 3.5.3); and the 'peak only' females reared a significantly smaller proportion of young to weaning, as compared to the proportion of peak young which the 'offpeak also' females reared to weaning. Consequently, the two types of females were unlikely to be following different but equally competitive tactics. That is, the 'peak only' females were not necessarily rearing fewer but 'higher quality' young who were more likely to survive and reproduce, than were the 'offpeak also' mothers.

As the 'peak only' females included all primiparae and were significantly more variable in their age (*as measured by a tentative descriptive index*, see section 3.3) than the 'offpeak only' females, I suggest that the two types of tactics may be, in part, age related. Females who are commencing to breed, and old females may be more likely to breed seasonally.

while the middle-aged females may reproduce at a consistently high rate, regardless of the season. It should be noted that young females may commence by producing a peak young, but, as young females also tended to have a higher rate of rearing young to weaning, they are increasingly likely to produce offpeak young in their following reproductive attempts.

These two types of females were not differentiated by a tendency toward producing young of a particular sex.

Young females tended to produce daughters and old females tended to produce sons. This is in accord with current theory (Dunbar, 1984; Clutton-Brock *et al.*, 1982b) that predicts that as a female ages she is more likely to invest relatively intensely in individual young and hence should preferentially produce and invest intensely in sons, rather than daughters. This is providing the lifetime reproductive success of sons' is significantly more variable than it is for daughters (but see section 1.3). Daughters may be more likely to rear young to weaning in the presence of tolerant relatives; hence a mother is more likely to be alive to benefit her daughter if she produces daughters at a young age.

Finally, I proposed in section 3.7 that mothers may have been preferentially producing daughters if they had access to a consistently high quality pasture. Daughters were generally given a consistent rearing schedule, regardless of the season in which they permanently emerged; and daughters affected their mothers' next reproductive attempt to a lesser degree than sons. Southern mothers produced more daughters than the Northern mothers. Mothers who preferentially produced daughters tended to have a higher rate of rearing young to weaning than mothers who preferentially produced sons.