

Chapter 5

Behaviour schedules and structures



Figure 54: ... *"Is there time for a brief spar mum?"*
Mother and large YAF in hug, with subadult daughter close by.

5.1 Introduction

This chapter has two intertwined themes:

1. how the structure of the young's behaviour changes with its age, and
2. how the structure of the mother's behaviour is affected by rearing a young.

It is commonly accepted that a young mammal behaves differently from an adult and most studies within this topic are concerned with either the behavioural mechanisms whereby a young's behaviour slowly differentiates into or incorporates adult patterns (e.g. Bateson, 1982; Plooij, 1984; Rosenblatt, 1976; Bateson, 1976), or the timing and ontogenic sequence of the first appearances of particular activity patterns (e.g. Rosenblatt, 1976; Russell, 1973; Underwood, 1979). I intend to take a slightly different tack and discuss the changing structure of the young's behaviour particularly with respect to its effect on, or rather, interdependence with, the structure of the mother's behaviour. However, in accordance with my previous themes of discussion, I will also discuss differences between sons' and daughters' behaviour and the respective effects on their mothers, as well as investigating whether there are seasonal effects on the structure of the behaviour of both mother and young. The description of the changing structure of the behaviour of both mother and young will also provide an important context for the discussion of the social interactions of mother and young in the next chapter.

I will describe the structure of the behaviour of the mother and young in terms of their activity schedules or budgets, the average duration of their activity states, and the sequential structure of their 'active' behaviour. I use 'activity schedule' to refer to the changing probability that an individual will enter particular activity states throughout the day. An 'activity budget' refers to the percentage of time per day (or part of a day) that an animal or class spends in each of the defined activity states. When I use the phrase 'time budget', I refer to the particular percentage of time per day apportioned to one activity state in particular. Finally, an 'active' behaviour mode refers to a sequence of activity states which did not include the resting activity state.

5.2 Activity schedules

5.2.1 Female daily activity schedules

Various authors (Gadgil and Bossert, 1970; Altmann, 1980, 1983; Dunbar, 1984) have suggested that adult females reproduce within a fairly constrained time budget, or that there is a limit on the time available for the 'active' activities related to reproduction. At certain stages of reproduction the nutritional and energetic demands may be greater than the mother's immediate time budget can accommodate.

Most female eastern grey kangaroos at Wallaby Creek produce one young every 10-11 months. As one young is permanently emerging from the pouch, the next young is developing in the uterus and will be born within a few weeks. If the older sibling is not lost, it will be suckled until the next young begins to poke its head from the pouch for the first time. Thus the mother who continually and successfully rears young to weaning might be expected to be investing a significant proportion of her energy/nutritional budget in immediate aspects of reproduction all year. It is likely that the females' highest rate of immediate investment in their young occurs when they have a large pouch-young, as the young are suckled intensely as well as being carried around (Caughley, 1962; Janssens and Ternouth, 1987; Dove *et al.*, 1987; Green, 1984). However, this has not been quantitatively analysed. In chapter 3 (section 3.3) I have suggested that the females at Wallaby Creek appear in their worst physical condition during the stage when their young permanently emerges. They have just passed through the large-pouch-young stage.

When suckling a young, female baboons (Altmann, 1980), howler monkeys (Smith, 1977) and red deer (Clutton-Brock *et al.* 1982b) increase the time they spend feeding. Others have suggested that it may not always be possible to increase feeding time, and that resting time appears subject to relatively strong constraints (Duncan, 1980; Dunbar, 1978; Jarman and Jarman, 1973). Consequently if activities related to reproduction increase as a percentage of the time budget, then it is at the expense of the proportion of time allotted to feeding. For example, green monkey females (Harrison, 1983) who are suckling a young have shorter daily feeding times than nonlactating mothers.

The demands a young makes on a mother are not necessarily nutritional: they may include disruption to the female's activity budget, such as occurs when female seals haul out to give birth and nurse their young for several weeks without returning to the sea for food (Anderson and Harwood, 1985). Also, females may sacrifice the opportunity to graze

on high-quality food, in order to nurse a newborn young in a relatively safe but low-quality environment (Edwards, 1983; Pratt, and Anderson, 1979). The acts of surveying, nursing, grooming, and interacting with the young also can place added demands on a mother's time budget (Altmann, 1980; Dunbar, 1984).

I have shown that the females at Wallaby Creek tend to isolate themselves in a small home range to a significant although not complete degree during the time when their young is permanently emerging from the pouch (section 4.2). Since Jarman (1987) and Southwell (1981) have found that kangaroos increase the proportion of time they spend surveying when in a small group compared to a large group, might females with small and vulnerable YAF also increase the proportion of time they spend surveying? Clarke and Loudon (1985) found that female red-necked wallabies in the later stages of lactation increased the proportion of time they spent feeding, as well as their bite rate. Do females with large pouch young increase the proportion of time they spend feeding during the day compared to females of other reproductive classes, and do they then change to surveying more intensely as their young permanently emerges from the pouch? Or does feeding remain a high priority? The young might even make other demands on the female such as interacting with her. Overall, how does a female eastern grey kangaroo arrange her activity schedule while rearing a young? And can signs of limitation on female reproduction be detected in the scheduling of activities?

As I did not collect many data from nocturnal observations, I am not able to present 24-hour activity schedules. However, others (Jaremovic, 1984; Priddel, 1986; Southwell, 1981; Jarman, Clarke and Jones, pers. comm.) have reported that kangaroos spend the majority of the nocturnal period feeding. Thus I am assuming that if there are significant differences between the activity schedules for the various reproductive classes I have divided the females into, then the diurnal activity schedules will portray these differences. In summer my observation times spanned 13 hours, while in winter they spanned 11 hours a day. As the kangaroos settle down to rest earlier in the day in summer than winter, I collated my data into summer versus winter activity schedules. Previous work also has found that kangaroo activity schedules vary seasonally (Southwell, 1981; Osazuwa, 1979; Priddel, 1986; Jaremovic, 1984; Croft, 1981a, 1981b). Clarke (pers comm.), in a preliminary analysis of the Wallaby Creek kangaroos' feeding behaviour, has found that individuals spend more time (of a 24-hour time budget) feeding in July, mid winter, compared to the time spent feeding in other seasons. In winter the pasture appears to be at its poorest quality for

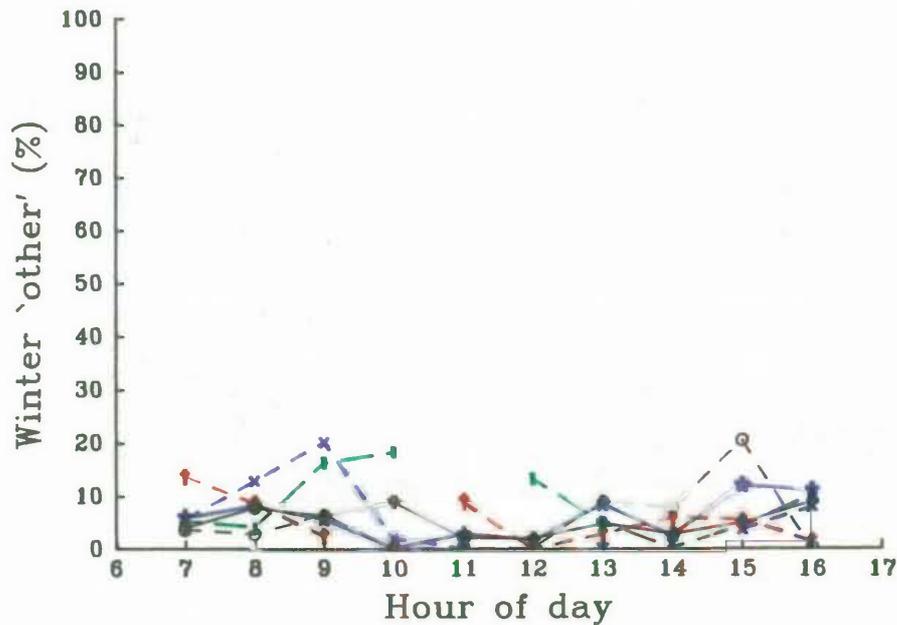


Figure 55: Winter female activity schedules, for the 'other' activity-state. In this figure and all subsequent figures of female activity schedules the female classes are represented by the following. The continuous black line refers to females with N/SPY; the broken blue line refers to females with small PI; the continuous blue line refer to females with MPY; the broken red line refer to those with v. large PI or PEP young; the broken green line refers to those with small YAF; and the broken black line refers to those with large YAF.

grazing by grey kangaroos.

I would like to emphasise that I am not intending to describe a feeding budget, as that is a complex investigation beyond the scope of this thesis. Rather than discussion of time/activity budgets of different classes of females, my aim here is to describe the differences which occur between their activity schedules, and to suggest whether the differences are likely to be affected by seasonal variables. There are some gaps in the diurnal activity schedules because the various classes of females were not represented evenly throughout the year, and I was particularly interested in following individuals. The calculation of activity schedules and budgets involved determining the average percent of time each female was in each of the 4 major activity categories for all (daytime) hours separately. A mean percent of time that the typical female spent in an activity category in a particular hour was determined by finding the average of all females' averages. The method section 2.4 gives a more detailed account of my procedures for collection and analysis of data.

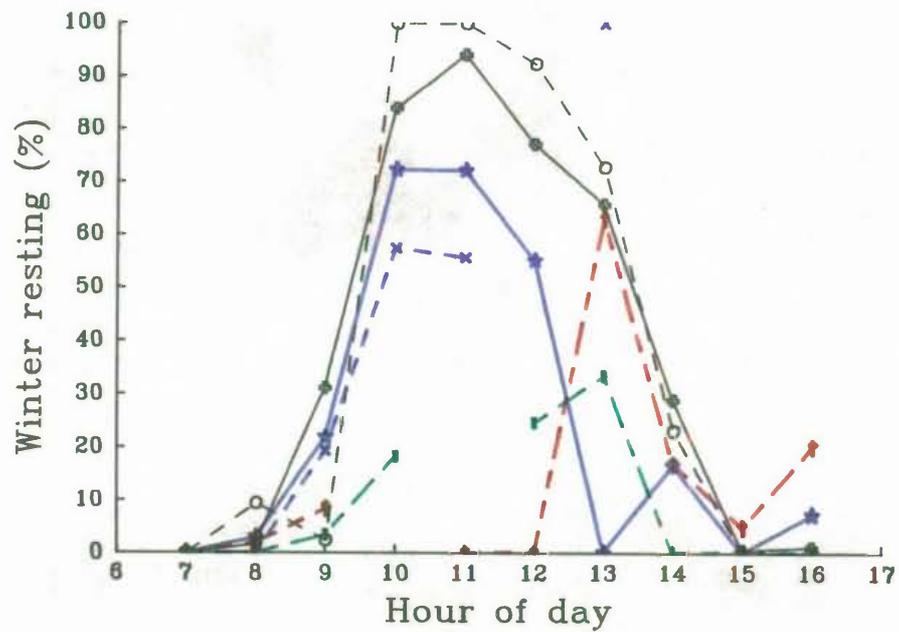


Figure 56: Winter female activity schedules, for the resting activity-state.

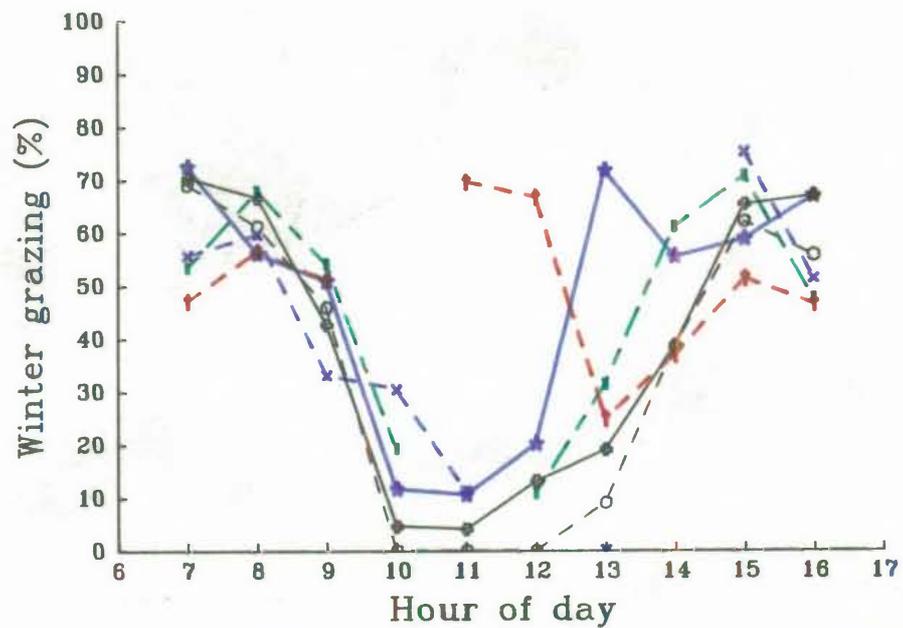


Figure 57: Winter female activity schedules, for the grazing activity-state.

Legend: In the above figures of female activity schedules the female classes are represented by the following. The continuous black line refers to females with N/SPY; the broken blue line refers to females with small PI; the continuous blue line refers to females with MPY; the broken red line refers to those with very large PI or PEP young; the broken green line refers to those with small YAF; and the broken black line refers to those with large YAF.

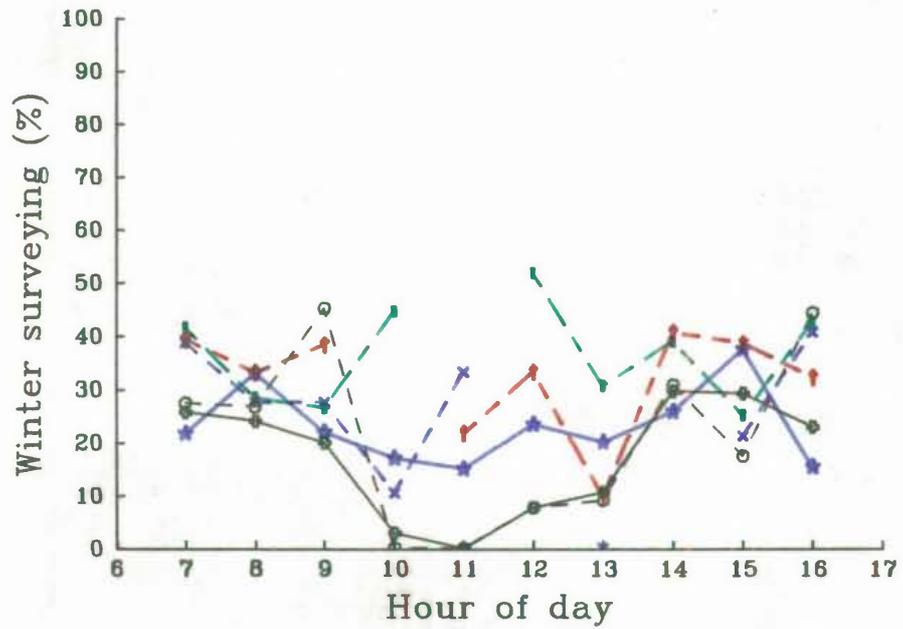


Figure 58: Winter female activity schedules, for the surveying activity-state.

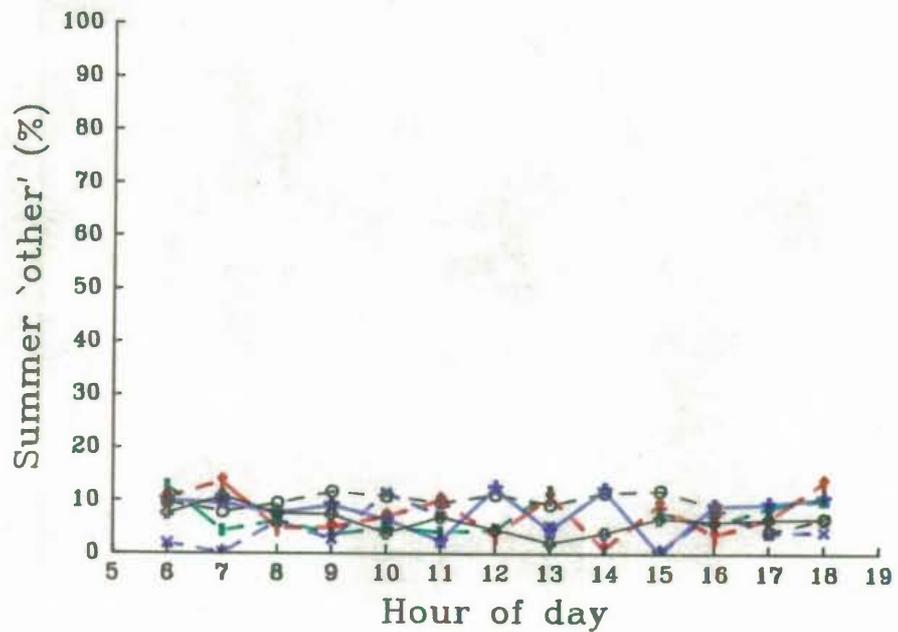


Figure 59: Summer female activity schedules, for the 'other' activity-state.

Legend: In the above figures of female activity schedules the female classes are represented by the following. The continuous black line refers to females with N/SPY; the broken blue line refers to females with small PI; the continuous blue line refers to females with MPY; the broken red line refers to those with very large PI or PEP young; the broken green line refers to those with small YAF; and the broken black line refers to those with large YAF.

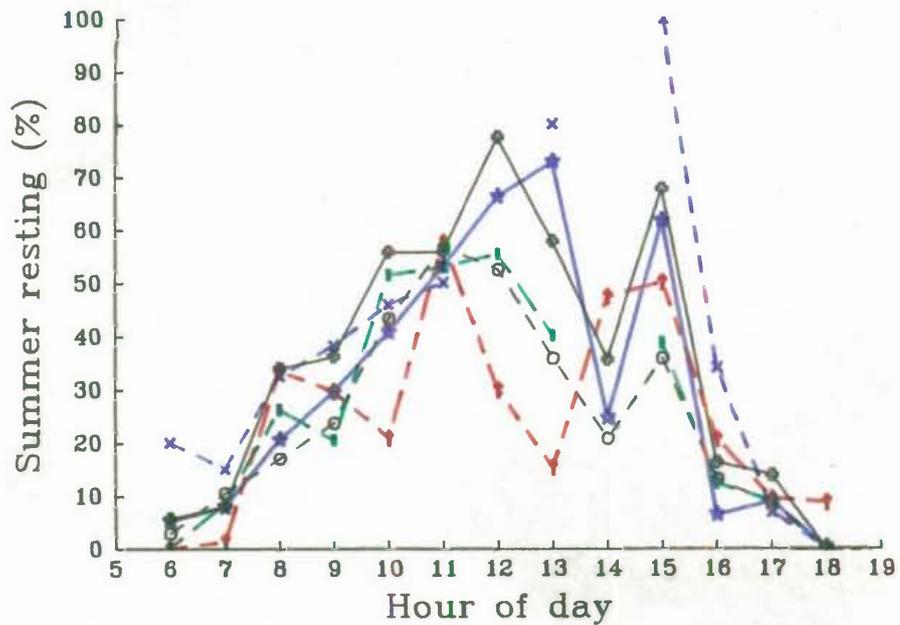


Figure 60: Summer female activity schedules, for the resting activity-state.

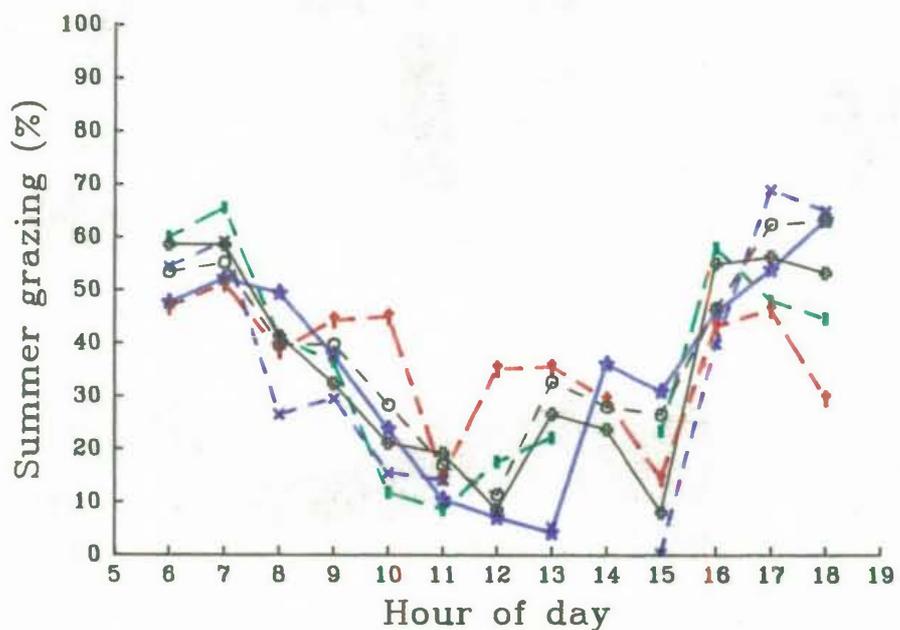


Figure 61: Summer female activity schedules, for the grazing activity-state.

Legend: In the above figures of female activity schedules the female classes are represented by the following. The continuous black line refers to females with N/SPY; the broken blue line refers to females with small PI; the continuous blue line refers to females with MPY; the broken red line refers to those with very large PI or PEP young; the broken green line refers to those with small YAF; and the broken black line refers to those with large YAF.

Table 59: Winter and summer activity budgets for classes of females and YAF.

activity state	Winter				
	female classes				
	(7&8) no/small pouch young	(11→'3) medium to large infants	(14&15) young PEP & v.large infants	(16) small YAF	(17&18) large YAF
surveying	17.3	21.1	29.9	34.0	20.9
grazing	39.1	47.4	46.0	42.9	34.2
resting	38.4	21.7	18.8	15.4	40.0
'other'	5.2	1.8	5.3	7.7	4.9
	small YAF		large YAF		PEP
	male	female	male	female	young
surveying	19.8*	21.0*	14.5	15.7*	25.1*
grazing	27.6*	40.2*	39.8	35.5	22.1*
resting	35.2*	21.5*	31.1	32.5	23.0
sucking	9.7	1.1	7.8	16.3	19.8
'other'	7.6	1.1	7.0	5.9	10.0
'play'	5.6	1.8	—	—	5.4
i.e. 'other' -grooming					

(table continued)

activity state	Summer				
	female classes				
	(7&8) no/small pouch young	(11-13) medium to large infants	(14&15) young PEP & v. large infants	(16) small YAF	(17&18) large YAF
surveying	22.7	21.4	31.3	30.9	27.5
grazing	35.5	33.4	36.3	35.7	38.6
resting	35.7	30.5	24.9	26.6	24.7
'other'	6.1	7.7	7.5	6.8	9.3
	small YAF		large YAF		PEP
	male	female	male	female	young
surveying	17.1*	17.4*	16.0*	15.0*	22.1*
grazing	25.9*	28.1†	35.3	26.4*	16.2*
resting	39.8*	33.6	32.9*	44.4*	22.2
sucking	9.3	11.3	5.9	6.1	25.1
'other'	7.8	5.5	9.7	8.0	14.5
'play'	4.1	5.7	—	—	10.2
i.e. 'other' - grooming					

* Wilcoxon test significant $p < 0.05$ comparing young's time budget average/hour of the day versus the mothers' time budget.

† Same test as above, $p < 0.1$.

— Wilcoxon test significant $p < 0.05$, for the classes at extremes of the line. Hours of the day were matched and differences in the percentages ranked.

— — Same test as above, $p < 0.1$.

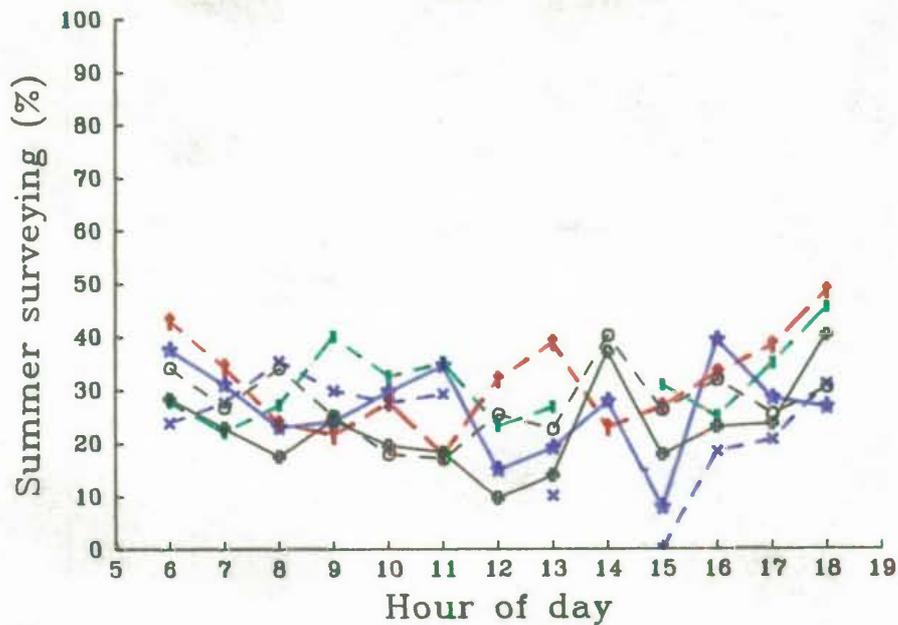


Figure 62: Summer female activity schedules, for the surveying activity-state.[†]

The winter and summer activity schedules for the four activity categories (resting, grazing, surveying, and 'other') are depicted in figs. 55 to 62. In table 59 I summarise my analyses of the differences in the diurnal activity budgets for the average female of the classes: no/small pouch-young, with small pouch-infant, with medium to large pouch-infant, with very large pouch-infant or permanently-emerging young, with small YAF, and with large YAF; as well I present the percentage of the diurnal hours spent in each of the four activity states for the average female of each reproductive class.

The females with no/small pouch-young are the class which I would expect to be least affected by immediate reproductive concerns. The females with large YAF appeared to have activity schedules which resembled those of the females with no/small pouch young. The females of these two classes fed predominantly during the morning and afternoon periods and rested during the midday period. Their daily activity schedule was particularly differentiated into these three periods in winter; in summer the midday resting period was more likely to be interspersed with feeding bouts.

In both summer and winter, females with mid to large pouch-infants spent a little more time surveying, especially in the first half of the day, and a little less time resting than did females with no/small pouch-young. These females also fed on average more in the middle of the day, during winter, but not summer, than females with no/small pouch-young or

[†] Legend: In the above figures of female activity schedules the female classes are represented by the following. The continuous black line refers to females with N/SPY; the broken blue line refers to females with small PI; the continuous blue line refers to females with MPY; the broken red line refers to those with very large PI or PEP young; the broken green line refers to those with small YAF; and the broken black line refers to those with large YAF.

large YAF. Although they averaged a greater percentage of time spent feeding during the day than did the latter females, the difference was not significant.

Females with young permanently emerging from the pouch displayed a considerably disrupted activity schedule: they surveyed, fed, and rested alternately throughout the day. Both these females and females with small YAF surveyed on average significantly more than did females with no/small pouch young. They also tended to survey more than the females with medium to large pouch-infants. This increased time spent surveying appeared to be at the expense of resting time. Females with small YAF rested significantly less than females with no/small pouch-young. Females with young permanently emerging distributed their rest more evenly over the day, and consequently the Wilcoxon matched-pairs test, when matching hours of the day, was unlikely to give a significant result, although overall they rested less than females with no/small pouch-young.

In summer all classes of females fed for about 35% of the daylight hours (this does not include chewing surveying). In winter the females with mid to large pouch-infants or young permanently emerging from the pouch averaged a slightly greater time feeding (47% and 46% respectively) than the other classes of females (40%) but not significantly so. Thus the proportion of time spent feeding varied little between classes. Likewise, the time spent in 'other' activities varied little between each of the female classes (table 59).

The gross effects of rearing young on the females' activity schedules appeared to involve an increase in surveying at the expense of resting, as well as a general disruption of the females' typical schedules. These effects peaked in intensity around the time a mother's young was permanently emerging from the pouch. It should be noted that the differences between the female classes in their activity schedules appeared greater during winter than summer.

5.2.2 Times of pouch-exit of pouch-infants

A pouch young may poke its head from the pouch at about 186 days of age (section 3.2). The head is only lightly furred and the eyes are quite glazed. However, the young develops rapidly and within 2 to 4 weeks it emerges from the pouch for the first time. This very gangly and rather unco-ordinated young does not move much while out of the pouch during its first few emergences. Typically it falls to the ground from the pouch, picks itself up, grabs hold of the pouch for support and pokes its head back into the pouch. It may even briefly survey the outside environment while standing, holding onto the mother's pouch,

Table 60: *Duration of pouch vacation. The means, standard errors (SE) and sample size (N) are given for sons and daughters of the various classes. Units are hours (^o), minutes ([']), and seconds(["]).*

female class	10 <i>small</i>	11	12 <i>to</i>	13	14 <i>very large</i>
<i>pouch-infant</i>					
	<i>both sexes:</i>		<i>sons:</i>		
<i>mean</i>	1'15"	1'42"	14'20"	8'59"	27'26"
<i>SE</i>	9"	17'7"	3'18"	1'56"	7'8"
<i>N</i>	2	2	11	9	11
	<i>daughters:</i>				
<i>mean</i>		4'25"	7'46"	36'36"	29'49"
<i>SE</i>		1'0"	2'10"	12'46"	4'40"
<i>N</i>		18	23	10	16
<i>max. of range</i>		12'20"	34'40"	> 2 ^o 12'	> 1 ^o 30'

but usually it appears to be attempting to re-enter the pouch. The young rarely remains out of the pouch for more than 2 minutes at first, although by the end of 2-3 weeks, the period of vacation may be extended to 10 minutes (table 60). From this time onwards, an excursion from the pouch may vary in duration considerably, and appears to depend on whether a disturbance occurs in the environment. The mother is in immediate control of the times of the young's excursions from the pouch and their duration (see section 6.2).

Overall, small pouch-young were seen out of the pouch from 1 to 10% of the time, as calculated from hourly averages (table 61), and most probably this is a considerable overestimate as pouch-infants are more likely to emerge during the morning or afternoon than the midday periods (figs. 63 and 64), and the gaps in my observations occur principally in the middle of the day. As the young develops, the proportion of time spent out of the pouch increases (table 61). But up until the last few weeks of pouch life the young still remains in the pouch for more than two-thirds of the time. This pouch-infant phase may vary considerably in duration (section 3.2), as do the later stages of a pouch-infant's life. A large pouch-infant may have emerged permanently within the duration of a week or it may still be re-entering the pouch occasionally after three weeks. Between the stages of very large pouch-infant and PEP young the young spends a rapidly increasing amount of its time outside the pouch. The young is out of the pouch not only during the morning (figs. 63 and 64), but at all times of the day.

Table 61: Mean percentage of the day that pouch-infants spent out of the pouch. Estimate calculated from average percentages obtained per each daylight hour. Thus sample size (*N*) refers to the number of hours of the day which were used to obtain the mean percentage.

female classes	10 very small	11	12 to	13	14 very large
pouch-infant					
<i>winter</i>					
mean	9.4	0.6	22.9	14.2	57.7
S.E.	3.9	0.7	5.8	6.2	15.2
hours of day: N	8	10	10	8	7
<i>summer</i>					
mean	1.1	4.6	9.0	32.8	61.5
S.E.	1.2	2.5	2.8	9.4	7.8
hours of day: N	11	11	13	12	13

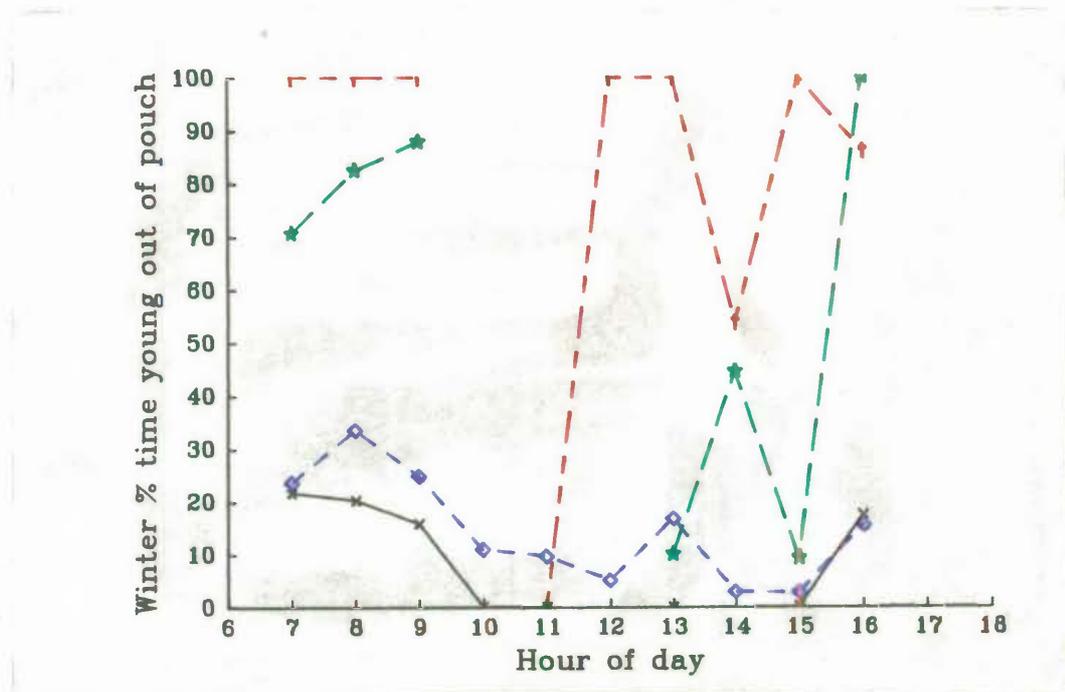


Figure 63: Average percentage of time young spent out of the pouch per hour of the day, for winter. The very small PI are represented by the continuous black line; the medium PY are represented by the broken blue line; the v. large PI are represented by the broken green line; the PEP young are represented by the broken red line.

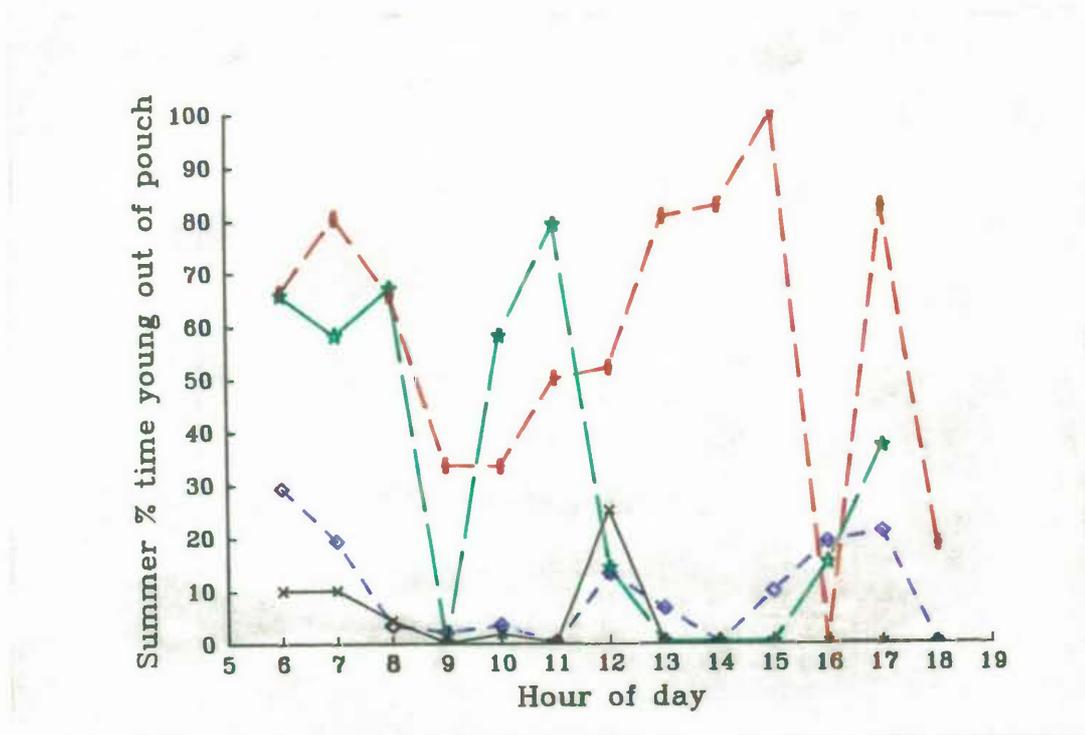


Figure 64: Average percentage of time young are out of the pouch per hour of the day, for summer. The small PI are represented by the continuous black line; the medium PI are represented by the broken blue line; the large PI are represented by the broken green line; and the very large PI are represented by the broken red line. The following Equations significantly described the data of the medium PI and large PI:

$$\% \text{out of pouch} = 90.9 - 5.2(\text{hour}), R^2 = 0.229, p = 0.015$$

$$\text{and } \% \text{out of pouch} = 73.6 - 11.3(\text{hour}) + 0.5(\text{hour})^2, R^2 = 0.091, p = 0.039, \text{ respectively.}$$

5.2.3 The mother's activity while her young is out of the pouch

The disruption and change to a mother's activity schedule which occur as her pouch-infant develops and permanently emerges could be a direct or indirect function of the activities of her young. The mothers' feeding times did not significantly increase, and it is therefore unlikely that metabolic demands dictate the changes. If the young's behaviour is a causal factor, the changes observed in a mother's activity schedule might be emphasised while her pouch-infant is out of the pouch. From my observations in the field, I would expect that a young's out-of-pouch behaviour would affect the mother's behaviour more than its behaviour while in the pouch. Mothers did not appear to attend greatly to their infant while it was inside the pouch; however, the young was constantly initiating interactions with the mother while out of the pouch (sections 6.5 and 6.7). Conversely, if the changes are the result of a mother's general condition, for example reduced ability to outrun a predator, then her behaviour should be either unaffected by whether the infant is in or out of the pouch or affected when the infant is inside of the pouch only. Of course both factors may be involved, in which case there also may be no difference in a mother's behaviour according to whether her infant is in or out of the pouch.

For individual mothers, while their young was out of the pouch only, I calculated the percentage of point-in-time scans for which they were found in each of five activity categories: standing surveying, crouch surveying, surveying, feeding, resting, and 'other'. I then calculated averages for each class of female from these individual percentages (table 62) (note that as crouch surveying takes up relatively little of the activity budget I have combined it with standing surveying in many subsequent analyses). Since there were no obvious trends in the mothers' behaviour as their pouch-infants aged, I combined the classes 11 to 13, that is females with mid to large pouch-infants, for the summer data, and used a G test to analyse for differences in the frequency of the mothers' activity states when their young were out of the pouch versus in the pouch. I used data collected only during the same hours when a mother's infant was observed to leave the pouch. In this way I hoped to standardise for the effects of the time of day when the pouch-infant emerged. The test significantly supported the hypothesis that the females' behaviour was quite different while their infants were out of the pouch from their behaviour when the young were inside the pouch.

Mothers tended to survey more, feed less, rest less, and are observed in 'other' activities more frequently, when their young was out of the pouch than when it was in the pouch (table 63).

In order to discern whether the mother's behaviour is significantly different from 'normal'

Table 62: Mean percentage of time during which mothers were found in each activity state while their young was out of the pouch. Winter and summer presented separately. Results based on individuals' averages. The standard errors are presented in brackets below means.

Winter						
female class	sample size	activity states				
		<i>stand survey</i>	<i>crouch survey</i>	<i>graze</i>	<i>rest</i>	<i>'other'</i>
<i>very small pouch-infant</i>	(5)	43.8 (12.1)	12.1 (7.6)	17.3 (11.4)	1.7 (1.9)	25.1 (7.4)
<i>small pouch-infant</i>	(3)	26.4 (25.0)	0 (-)	15.3 (11.9)	0 (-)	57.7 (23.5)
<i>medium pouch-infant</i>	(11)	35.7 (4.5)	13.7 (3.3)	25.0 (5.6)	7.4 (4.4)	18.1 (4.8)
<i>large pouch-infant</i>	(3)	11.8 (1.0)	4.7 (3.9)	26.9 (16.6)	17.5 (12.1)	38.9 (29.3)
<i>very large pouch-infant</i>	(5)	21.8 (5.7)	12.4 (1.8)	47.5 (6.1)	6.9 (5.3)	10.7 (1.9)

Summer						
female class	sample size	activity states				
		<i>stand survey</i>	<i>crouch survey</i>	<i>graze</i>	<i>rest</i>	<i>'other'</i>
<i>small pouch-infant</i>	(5)	19.4 (10.4)	5.0 (5.6)	27.8 (15.0)	0 (-)	47.8
<i>medium pouch-infant</i>	(9)	44.6 (6.4)	6.1 (3.2)	20.7 (5.1)	13.6 (9.6)	15.0
<i>large pouch-infant</i>	(6)	37.9 (10.2)	8.9 (3.0)	36.7 (14.4)	3.0 (3.3)	13.5
<i>very large pouch-infant</i>	(11)	29.8 (5.5)	9.4 (2.2)	38.1 (6.6)	11.0 (7.4)	11.7

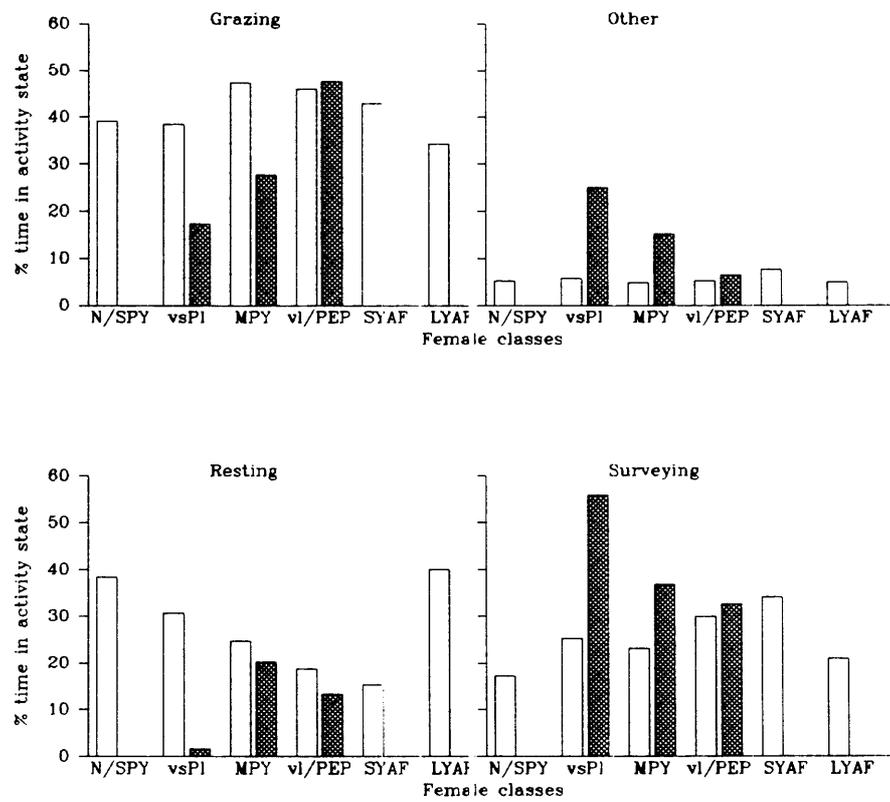


Figure 65: Percentage of various classes of mothers' time budgets for which they were in each of 4 activity-states, comparing when infant was out of the pouch and their overall activity budget. Unhatched columns represent the overall percentage of the time budget, and hatched columns the percentage of the time-budget relating to when the infant was out of the pouch.

Table 63: Mothers' frequency of activity states when infant was inside pouch vs. outside pouch. From summer data. G tests comparing frequencies are included.

	activity states				
	survey	graze	rest	'other'	
inside pouch	98 22%	191 43%	137 31%	19 4%	445
outside pouch	116 51%	57 26%	13 6%	41 41%	229
	214	250	150	60	674
G test:					
all states			$G=132$	$df=3$	$p < 0.005$
surveying vs.	graze, rest, 'other'		$G=55.67$	$df=1$	$p < 0.05$
grazing vs.	survey, rest, 'other'		$G=19.8$	$df=1$	$p < 0.05$
resting vs.	survey, graze, 'other'		$G=65.4$	$df=1$	$p < 0.05$
'other' vs.	survey, graze, rest		$G=32.6$	$df=1$	$p < 0.05$

while her infant is out of the pouch, I first compared the percent of time mothers of different classes spent in each of the 4 activity states, in general, with when their infant was out of the pouch only (fig. 65). Mothers of small pouch-infants tended to spend more time surveying and in 'other' activities, at the expense of feeding and resting, when their infant was out of the pouch as compared to their behaviour in general. However, as small pouch-infants are rarely out of the pouch, the direction of these differences were expected from my previous analysis (table 63). As older pouch-infants spend an increasingly greater percentage of their time out of the pouch, the 'normal' behaviour for a mother of these classes is increasingly likely to be that of her behaviour when the young is out of the pouch. Thus, the effect a pouch-infant has on its mother's behaviour when it is out of the pouch is better understood by comparing the behaviour of the different classes of mothers. Basically, as a pouch-infant passed through the age classes, its mother's behaviour was less likely to emphasise surveying at the expense of resting while the young was out of the pouch. But the de-emphasis did not change at a rate which meant that mothers of all classes had similar time budgets (fig. 65 and also previously found in table 59). As a mother passed through the various reproductive classes from no/small pouch-young to with small YAF, she spent increasingly

more time surveying at the expense of resting. However, the same did not apply for the mother's feeding budget. When pouch-infants begin to exit from the pouch, the mother spends little time feeding while the infant is out of the pouch. During these early stages the mother easily maintains her feeding time budget at a level similar to that of females with no/small pouch-young by feeding during the times when her infant is inside the pouch. Small and medium pouch-infants spend a small proportion only of the day out of the pouch. As the infant ages, it spends increasingly more time out of the pouch. The time a mother spent feeding while her infant was out of the pouch increased as the infant aged, in a manner that maintained her feeding time at a fairly constant level, throughout her young's ontogeny. Overall, feeding time is maintained at a relatively constant level. Surveying time increases absolutely as the infant spends more time out of the pouch, but decreases as a percentage relative to the time the infant spends out of the pouch. Resting time is reduced as a mother's infant approaches permanent emergence.

5.2.4 Pouch-infant activity budget while out of the pouch

Around the period when a mother's young is permanently emerging from the pouch, she is surveying more, and resting less than females with no/small pouch young (section 5.2.1), and her activity schedule is quite disrupted. This might be because the activities of her young are affecting her behaviour states, and as the young is now out of the pouch permanently its affect on her pervades the whole of her daily activity schedule. Alternatively, it might arise because the presence of a small YAF without the protective cover of a pouch available to it requires an alert mother. That is, one who will detect a predator early enough to allow both herself and her young to outrun the predator. Thus, what are the activity schedules of pouch young and YAF, how do they vary over time, and in what way might they be directly affecting the mothers' activity schedules? I explore these areas in this and the next sections.

In spite of a few studies having investigated the activity budgets of the young of various mammalian species (e.g. Jackson *et al.*, 1972; Arnold and Trillmich, 1985; Boy and Duncan, 1979; Harrison, 1983; Duncan *et al.*, 1984; and see references in Clutton-Brock, 1977) only a few of these have attempted to put their findings in a developmental perspective which compares the adaptiveness of the young's changing schedules to those of the mother and other adults in the population (Vogt *et al.*, 1978; Altmann, 1980). Most work on the

nonsocial behaviour of young has been concerned with the first occurrence of particular behaviour patterns, and with various aspects of play behaviour (e.g. Plooij, 1984; Rosenblatt, 1976; Simpson, 1976; Young, *et al.*, 1982). However, current theory suggests that young may be under no fewer time constraints to their activity budgets than are adults (Fagen, 1981, 1977; Baldwin and Baldwin, 1974; Lee, 1984b).

For example, the amount of energy and time devoted to play can vary greatly within a species across habitats or between sexes (Berger, 1979b; Duncan *et al.*, 1984). If the amount of time young spend resting is related to their developmental state (Jackson *et al.*, 1972), and the proportion of the day spent feeding is related to the amount of nutrition a young receives from sucking, as well as its developmental physiology, then the time available above these requirements might well be apportioned to play. I am assuming that the mothers and other adults of the group might be depended upon to survey for predators (see Russell, 1983). It has been suggested (Baldwin and Baldwin, 1978) that young will play significantly less if they are on a low nutritional plane, or the type of food they ingest is relatively time-consuming.

However, play itself may have important long-term effects on a young's development or its future reproductive success (Fagen, 1981; Simpson, 1976). The consequences are likely to be relative to the individual's social environment and the amount of play its peers/future competitors indulge in (Baldwin and Baldwin, 1973). Many studies have found that male young of polygynous mammalian species play more frequently and often more roughly than the female young (Arnold and Trillmich, 1985; Duncan *et al.*, 1984; Byers, 1980; Sachs and Harris, 1978; Caine and Mitchell, 1979). Presumably, the immediate risks involved are outweighed by the development of the male's fighting skills, which will be used later to gain access to oestrous females (Fagen, 1981). If a male's reproductive success is at least in part a function of his skill as a fighter, while for a female it is not, then male young might even be expected to forego investing energy in growth in order to spend time as a juvenile playing (*ibid.*).

As play may involve risks of injury, or even death, and involves using metabolic resources which might otherwise be channelled into physiological development, the activity budgets of young probably balance the proportion of time a young spends on behaviours with immediate positive effects, such as feeding, resting, grooming, and perhaps following the mother (Lent, 1974), with the long term advantages of play (Fagen, 1981). The mother may facilitate a differentiation in the behaviour between young, for example by investing

more in a son preweaning via suckling it proportionally more than she would a daughter (see chapter 1 for a discussion on differential parental investment schedules between the sexes), and in this way enable a son to grow at a similar rate to a daughter, while playing more (Duncan *et al.*, 1984). Finally, as the young develops the optimal activity-schedule will change. For example, according to Fagen (1981) young should play less in periods of their ontogeny which are associated with a high risk of mortality.

Overall, a young's activity budget and the rate at which it changes is likely to be as finely adapted to the environment and its life-history strategies as an adult's activity budget.

What are the implications of the above for the young of eastern grey kangaroos? Male young should play more than female young, or more roughly. If they do, the mother kangaroos might be suckling them more intensely than they suckle daughters, or the sons might be grazing more intensely than daughters, but resting less. Poole *et al.* (1982) did not find a significant difference between the growth of male and female eastern grey kangaroo young in captivity until some time after they vacated the pouch. Since there is a high rate of mortality of small YAF, if Fagen (1981) is right, young should not play much while they are permanently emerging from the pouch and for the following few months. As the young probably do not greatly rely on grazing for their nutritional requirements until they permanently emerge from the pouch (Janssens and Ternouth, 1987; Dove *et al.*, 1987), I suggest that the pouch-infant phase should provide the young with the greatest opportunity to play. Mid-sized pouch-infants are out of the pouch for 10% to 30% of the day; they would rest inside the pouch. Though Croft (1983) has described, in detail, play fights in kangaroos, macropods are still commonly believed to be one of the least playful of the mammalian species (Fagen, 1981). This might be because few published studies have quantified the activity of pouch-infants (only Russell, 1973), and YAF may not play much as they are subject to a high risk of mortality and graze for part of their nutritional requirements.

The percentages of the activity budgets of pouch-infants (table 64) are not averages of the activity budgets of individual pouch-infants, as were those determined for the mothers. This was because individual pouch-infants usually returned to the pouch within a half-hour observation bout; and thus I was not consistently able to collect large data sets for each individual infant. Further, the data have been divided according to the season in which they were collected, by the class of the pouch-infant and the sex of the infant; and the behaviour of the infant has been differentiated into a greater number of states than it was for the mothers. I was interested in the proportion of time infants spent in various states

Table 64: Estimate of percentage of time spent in each activity state for pouch-infants when they were out of the pouch.

survey	graze	rest	activity states				'suck'
			'other'				
			travell	groom	interact	miscell.	
			small pouch-infants				
17.6	2.9	0	14.7	2.9	12.7	2.0	47.2
			medium pouch-infants				
16.5	2.9	0.8	16.8	8.6	12.0	2.6	39.7
			large pouch-infants				
20.1	4.3	0.4	20.5	10.3	10.3	2.6	31.5
			very large pouch-infants				
22.6	11.0	0.6	8.6	4.9	4.4	1.1	46.8
'other'-groom = 'play'			'suckmg'				
male	female		male	female	season		
			small pouch-infants				
18.2	34.8		57.6	52.0	winter		
			-	19.0	summer		
			medium pouch-infants				
23.8	36.5		51.2	31.6	winter		
			47.4	27.8	summer		
			large pouch-infants				
32.1	36.5		39.0	-	winter		
			-	24.4	summer		
			very large pouch-infants				
16.2	18.0		59.5	31.4	winter		
			42.3	37.4	summer		
			49.5	31.9			

Table 65: *G* tests for ‘sucking’ frequency by season and sex, for medium pouch-infants. Activity-state categories are ‘sucking’ vs not ‘sucking’.

test	<i>G</i>	<i>df</i>	<i>p</i>
<i>G</i> 3-way test of independence	17.62	4	<0.05
season × activity state	0.2	1	ns.
season × sex	1.322	1	ns.
activity state × sex	15.5	1	<0.05
activity state × sex × season	0.582	1	ns.

such as grooming, interacting, and hopping, all of which for mothers, I had combined within the category ‘other’.

If the pouch-infant was a male, when it was out of the pouch it spent about 50% of the time with its head in the pouch (sucking?); if it was a female, it spent about 32% of the time with its head in the pouch. There were no obvious trends in the data relating the duration of time ‘sucking’ to the age of the pouch-infant (table 64). In order to test whether the difference between the male and female young might be significant, and whether there might be a seasonal difference, I conducted a *G* test on the data from medium pouch-infants (class 12). The seasonal difference was not significant, but the difference between the sexes was (table 65).

When the activity states were tested together without ‘sucking’ incorporated in the total frequency count, the difference between the sexes did not extend to the proportion of time spent by the young in each of the activity states (table 66): feeding, surveying, hopping, interacting, and ‘other’. However, when I combined the activity states travelling, interacting, and ‘other’ (i.e. play) versus surveying, feeding, grooming, and ‘sucking’, medium pouch-infant daughters spent significantly more time ‘playing’ than did the medium pouch-infant sons (table 66)!

Whether there is an absolute difference depends on the proportion of the day for which male and female young are out of the pouch. Unfortunately, I did not have enough data to estimate separately the percentage of a day spent out of the pouch by pouch-infant sons and daughters. However, there was no obvious difference in the durations of the bouts of

Table 66: *G* tests for activity-state frequency, excluding 'sucking', for medium pouch-infants, differences by sex of young and season. The activity state categories were: surveying, grazing, travelling, interacting, and 'other'. Also presented is the result from a test comparing frequencies of 'play' vs 'survey, graze, rest, and groom' between the sexes.

test	G	df	probability
<i>G</i> 3-way test of independence	14.6	13	ns.
season \times activity state	3.0	4	ns.
season \times sex	1.2	1	ns.
activity state \times sex	2.6	1	ns.
interaction			
activity state \times sex \times season	7.8	4	ns.
<i>G</i> test 2-way			
'play' vs 'survey, graze, rest vs groom'	14.2	1	$p < 0.001$

pouch exit between the sexes (table 60). The male infants would have to be out of the pouch for about twice as much time in total as the female infants if they were to spend as much time playing. I did not gain any such impression when I was in the field.

In general, the activities of pouch-infants appear quite different from their mothers' activities. They spent much less time surveying (16–23%) than their mothers did (approximately 30%) while the infants were out of the pouch, although the proportion of time for which pouch-infants surveyed (table 64) was not different from the estimated percentage of time spent surveying (17% and 23%, winter and summer respectively) by females with no/small pouch young (table 59). Pouch-infants also spent very little time feeding or resting outside the pouch. Rather, most of their time when not 'sucking' was spent in 'play' (38% to 51%). Pouch-infants were out of the pouch between 10% and 30% of the time (section 5.3). Consequently, they were probably 'playing' about 8% of the day, which according to Fagen (1981) is very comparable to many eutherian species.

I did not find a significant difference in the frequency of the pouch-infants' activity-states between classes of the young, except for comparing very large pouch-infants (class 14) with the other infants (11 to 13)(table 67). I did not compare the behaviour of very small pouch-infants (class 10) with the others, as these young were obviously very different

Table 67: *G* tests comparing the frequency of activity states between classes of pouch-infants, medium to very large. The activity-states were: surveying, grazing, resting, 'other', and 'sucking'.

test	G	df	probability
<i>all classes by all states</i>	101.2	12	<0.001
<i>small P.I. vs. medium P.I.</i>	3.3	4	<i>ns.</i>
<i>medium P.I. vs. large P.I.</i>	6.8	4	<i>ns.</i>
<i>large P.I. vs. v. large P.I.</i>	58.0	4	<0.001
<i>medium P.I. vs. v. large P.I.</i>	64.7	4	<0.001

Table 68: *Estimated percent of the day a pouch-infant, PEP-young, and small YAF spend in 'play'.*

pouch-infants				class of young					
				PEP young		smallYAF			
small	medium	large	very large	winter	summer	winter male	winter female	summer male	summer female
0.8	4.8	7.8	8.4	5.4	10.2	5.6	3.8	4.1	4.7

from the others. Their behaviour repertoire was quite narrow (see sections 5.2.2 and 6.2.2). As pouch-infants get closer to emerging permanently they increased the proportion of time in which they grazed (from 3% to 11%), and reduced the proportion of time in which they were involved in 'other' activities (from more than 35% to around 19%). Very large pouch-infants were out of the pouch for about 60% of the day: thus while their grazing behaviour would have increased absolutely even more than the 8% difference mentioned above, they were estimated to be still 'playing' absolutely about as much as the medium pouch-infants (table 68). Also, when out of the pouch very large pouch-infants continued to poke their head in the pouch a considerable proportion of the time (30% to 60%).

As permanently-emerging young were out of the pouch for most of the day I was able to analyse their activity budgets much as I had done for the adult females, i.e. by the hour of the day. This gave me an activity schedule from which to estimate a daily activity budget (table 59). The young were changing so rapidly at this age that the estimated activity budget was not *typical* of the activity budgets of the young of this stage: it merely shows the mean activity budget of young in this phase of transition between the stages of very large pouch-infants and small YAF (table 64). The young at permanent emergence

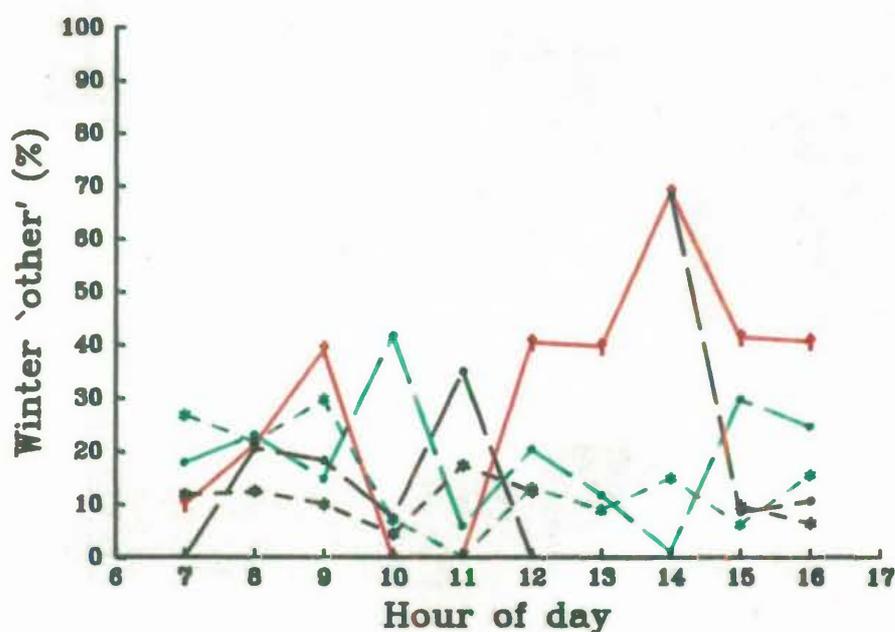


Figure 66: Winter YAF activity schedules, for the 'other' activity-state. For this figure and all figures of the activity schedules and of the % time sucking of PEP young and YAF, the continuous red line refers to PEP young; the short-dash green line refers to male small YAF; the long-dash green line refers to female small YAF; the short-dash black line refers to male large YAF; and the long-dash black line refers to female large YAF.

start resting outside the pouch, and spent almost as much time feeding as females with no/small pouch-young (table 59). These young 'sucked' and 'played' less frequently than pouch-infants, not only relative to the time they were out of the pouch, but also in total. (table 68)

5.2.5 Activity schedules of YAF

The activity schedules of YAF are presented in figs 66 to 73 and the estimated activity budgets of YAF, derived from the schedules, are presented in table 59. The summer and winter schedules and budgets were calculated separately for male and female young of the classes: PEP young, small YAF, and large YAF.

In order to test for differences between the sexes, over the seasons, and between the ages, I first analysed the proportion of scans in which the different categories of YAF had their head in the pouch (sucking). I felt I could combine the data from different hours of the day because I did not obtain a significant relationship between sucking and the time

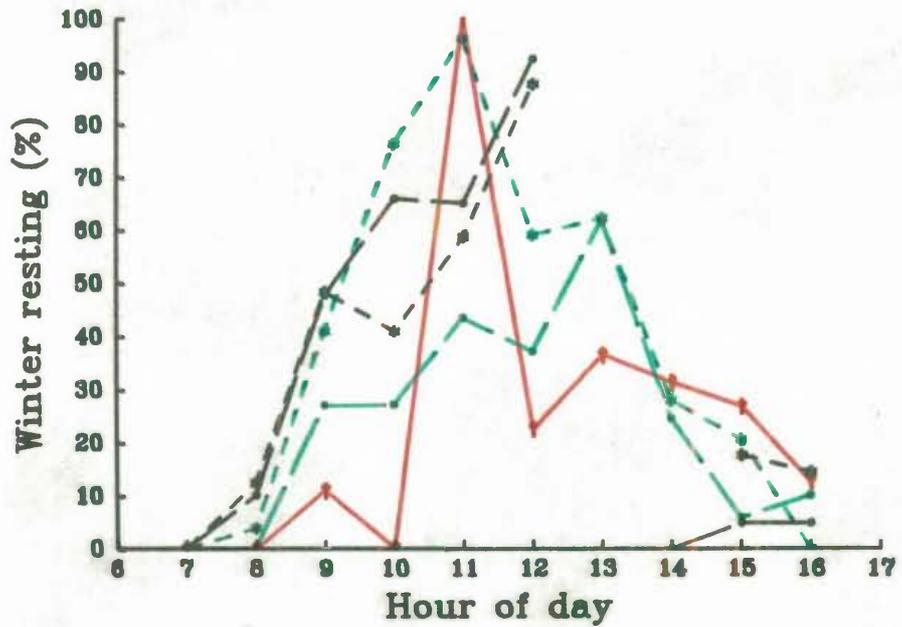


Figure 67: Winter YAF activity schedules, for the resting activity-state.

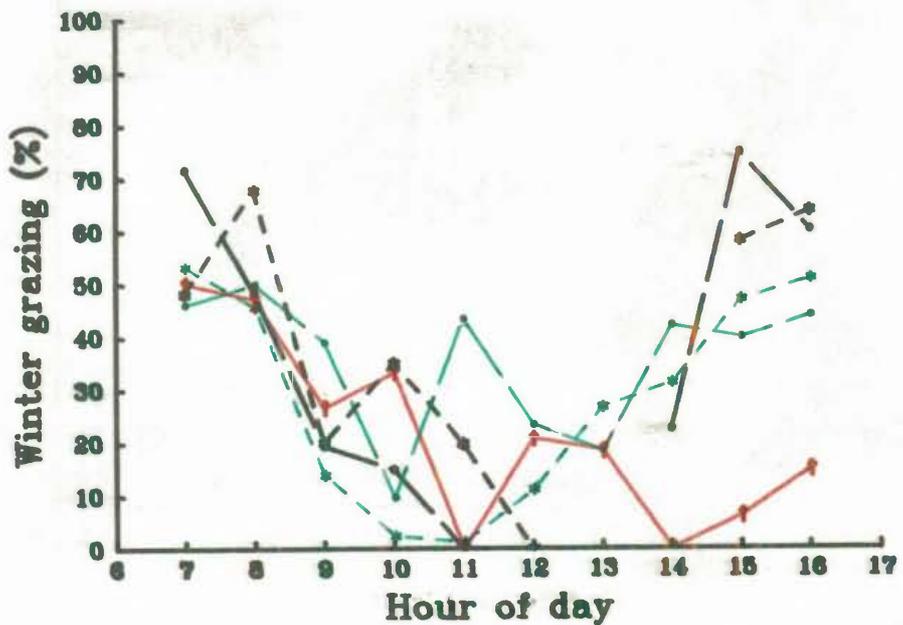


Figure 68: Winter YAF activity schedules, for the grazing activity-state.

Legend: In the above figures the continuous red line refers to PEP young; the short-dash green line refers to male small YAF; the long-dash green line refers to female small YAF; the short-dash black line refers to male large YAF; and the long-dash black line refers to female large YAF.

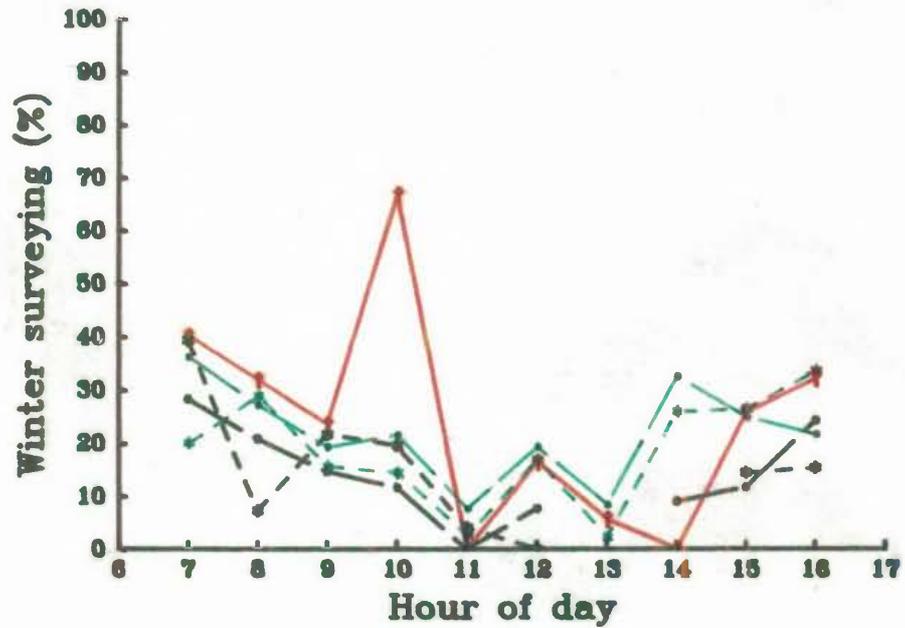


Figure 69: Winter YAF activity schedules, for the surveying activity-state.

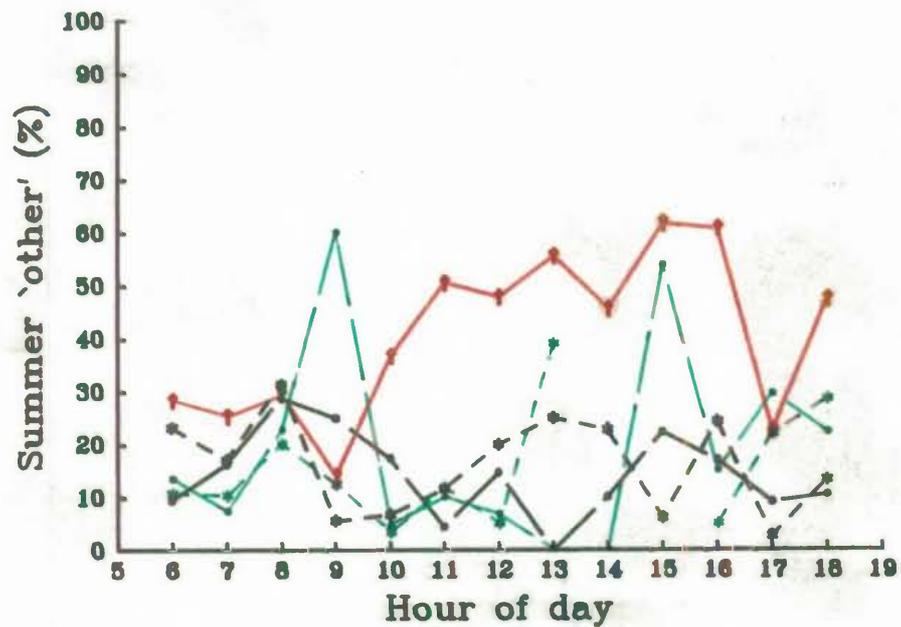


Figure 70: Summer YAF activity schedules, for the 'other' activity-state.

Legend: In the above figures the continuous red line refers to PEP young; the short-dash green line refers to male small YAF; the long-dash green line refers to female small YAF; the short-dash black line refers to male large YAF; and the long-dash black line refers to female large YAF.

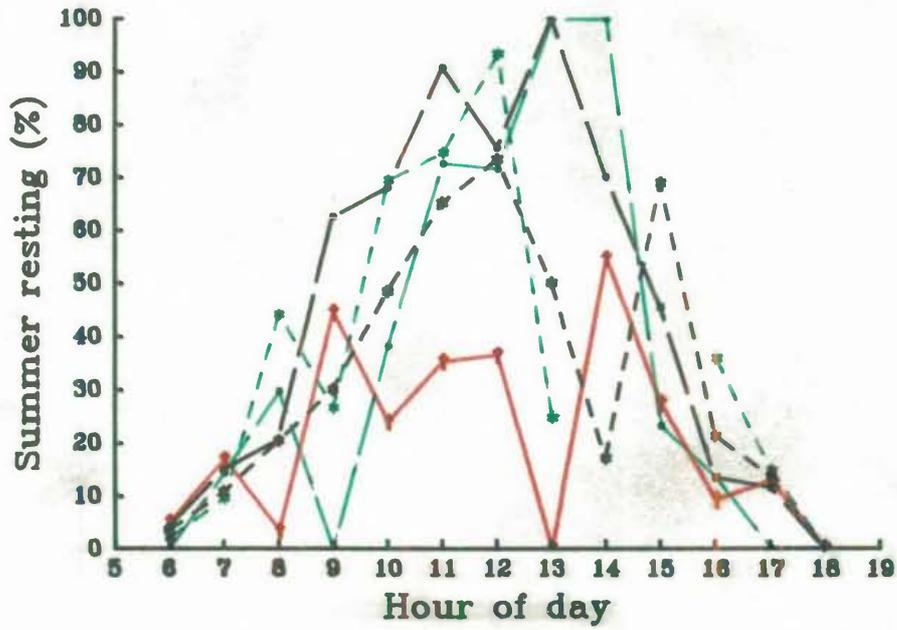


Figure 71: Summer YAF activity schedules, for the resting activity-state.

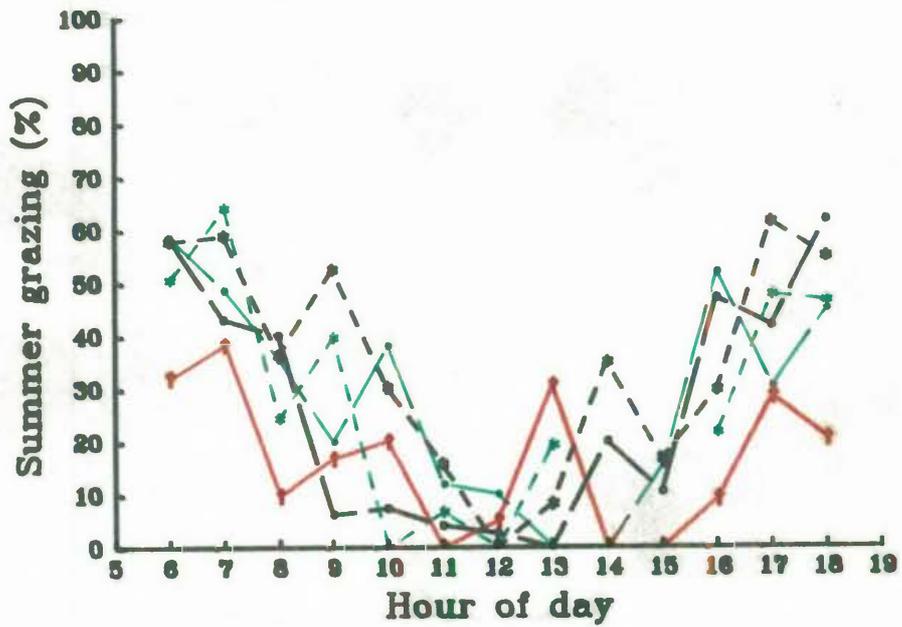


Figure 72: Summer YAF activity schedules, for the grazing activity-state.

Legend: In the above figures the continuous red line refers to PEP young; the short-dash green line refers to male small YAF; the long-dash green line refers to female small YAF; the short-dash black line refers to male large YAF; and the long-dash black line refers to female large YAF.

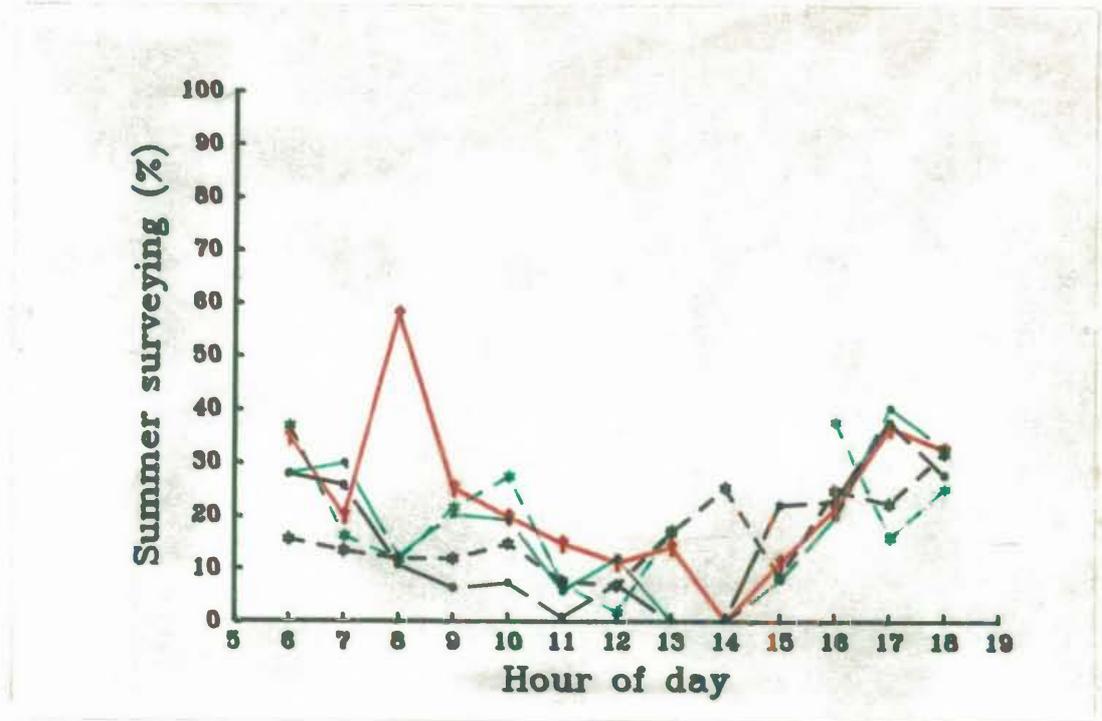


Figure 73: Summer YAF activity schedules, for the surveying activity-state.

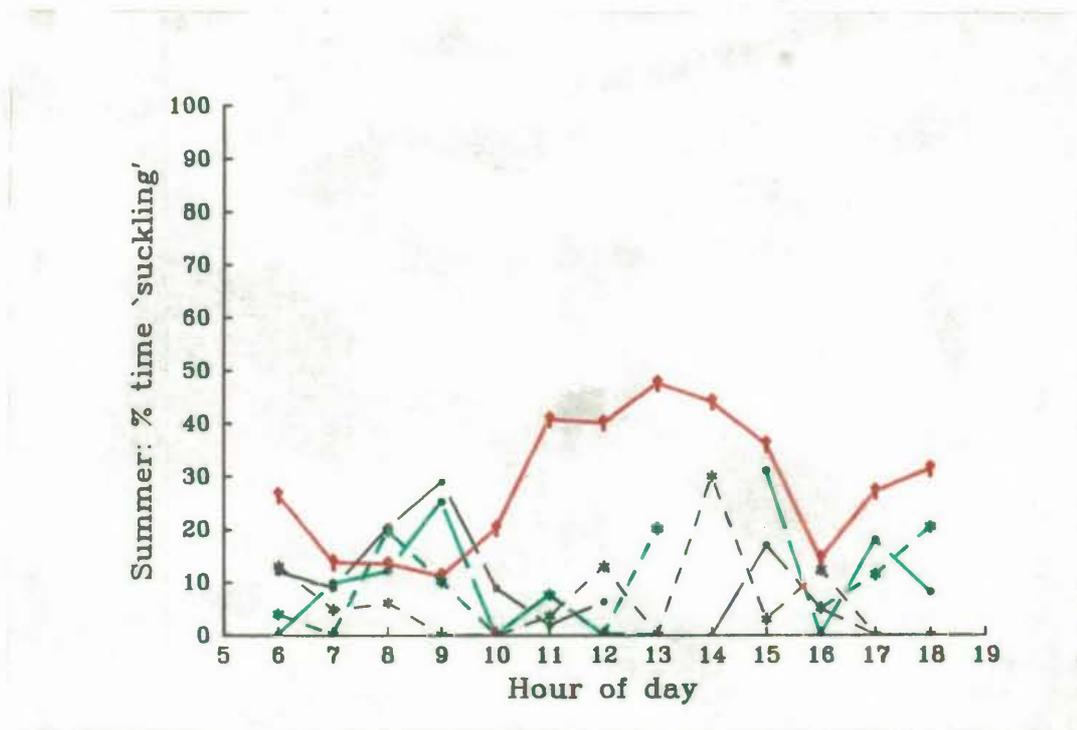


Figure 74: Average percent of each hour of the day that YAF were observed suckling.

Legend: In the above figures the continuous red line refers to PEP young; the short-dash green line refers to male small YAF; the long-dash green line refers to female small YAF; the short-dash black line refers to male large YAF; and the long-dash black line refers to female large YAF.

Table 69: Mann-Whitney U tests for differences between male and female sucking bout durations. YAF were tested separately by months post-PEP. N^1 and N^2 are sample sizes for males and females respectively.

Mann Whitney U tests months post-PEP	U	N_1	N_2	p 1-tail
1	122	23	14	ns.
2	78	13	15	ns.
3	47.5	13	11	ns.
4	24	7	11	ns.
≥ 5	31	14	8	ns.

Table 70: The mean durations of YAF sons' and daughters' sucking bouts according to the time elapsed since PEP. The units are minutes (') and seconds (").

	PEP	months from PEP					mean
		1	2	3	4	≥ 5	
<i>males:</i>							
sample size	4	12	13	11	7	5	6
mean	11'53"	11'52"	10'51"	13'46"	13'41"	16'25"	13'5"
<i>females:</i>							
sample size	-	20	10	11	9	14	5
mean	-	11'26"	12'4"	13'13"	12'15"	15'43"	12'56"
SE	-	46"	1'13"	53"	1'8"	48"	1'41"

of the day for small or large YAF (fig. 74) on the summer data. Neither small nor large YAF males sucked a significantly different proportion of the time than did the female small YAF ($G=0.252$ summer, $G=1.003$ winter $df=1$) and female large YAF ($G=0.910$ summer, $G=1.709$ winter $df=1$). Thus I could combine the sexes and test for a difference between the seasons. The result was not significant for small ($G=1.578$, $df=1$) or large ($G=0.339$, $df=1$) YAF. I then combined seasons and sexes to test for a difference between the sucking frequencies of small and large YAF. Large YAF sucked for a significantly smaller proportion of scans than did small YAF ($G=73.939$, $df=1$ $p < 0.001$).

The duration of sucking bouts was not significantly different between the sexes for YAF at any age following permanent emergence (MWU tests table 69 and means table 70).

The durations of sucking bouts increased with the age of the YAF (table 70). If small YAF were sucking 9.9% of the day (this is an average calculated from the averages

presented in table 59) and each bout was about 11 minutes in duration, then they were probably sucking in about 6 bouts during a 12 hour day. If large YAF were sucking about 7.5% (average of averages from table 59) of the day with each bout lasting 15 minutes, I estimated that they were probably sucking about 4 times during a 12 hour day.

I compared the proportion of time estimated to be spent in the activities surveying, feeding, and lying, between the sexes, over the YAF age categories and for summer and winter separately, by using Wilcoxon matched-pairs tests on the hourly percentages determined by averaging data from individuals. Table 59 shows the significant comparisons. In general male and female YAF did not behave significantly differently. The exceptions were that small female YAF rested significantly less than small male YAF in winter and a similar trend existed in the summer data, and that large YAF males fed more, significantly in summer but nonsignificantly in winter.

As YAF aged, their activity budgets and schedules changed. However, the greatest change occurred during the permanent emergence phase. Permanently-emerging young have activity schedules which appear almost as indistinctly divided into the three daily activity periods, morning feeding, noon resting, and afternoon feeding as are the activity schedules of the mothers of these young. YAF exhibited activity schedules which were differentiated into the three periods. Permanent emergence is a transition stage between pouch-infant activity patterns and YAF activity patterns (section 5.2.4): these young are on average feeding less, resting less, and sucking more than are the small YAF. The differences were not significant in some comparisons possibly because of the permanently-emerging young's relatively undifferentiated activity schedules. I did not investigate whether there were differences between the sexes, because I lacked enough data to do so. This stage lasts about 10 days only.

One interesting point is that the surveying activity-state, unlike the grazing and resting states, does not change in a unidirectional manner with the age of the young. Medium pouch-infants averaged about 17% of their time surveying when out of the pouch. This figure increased to 22% and 25% (winter and summer respectively table 59) during permanent emergence when both mother and young tend to be separated from conspecifics. It decreases to about 15% for large YAF. The 'other' activity-states became less frequent as the young emerged permanently, but thereafter remained at a level of about 7% (this includes about 4% 'play' and 3% grooming) for YAF.

I also compared the surveying, feeding, and resting time budgets of the young of each

stage with the appropriate mothers' time budgets (table 59). In general, the activity budgets and schedules of YAF (see fig. 66 to 73) appeared to be progressing toward the pattern found in females with no/small pouch young.

5.2.6 Discussion

I have posed several topics for discussion in the previous sections on activity schedules and budgets. These were:

1. does the behaviour of the young directly or indirectly affect the observed changes in the mother's activities as the young develops? Thus,
2. how does the activity schedule of the young change as it develops? In particular,
3. is the pouch-infant phase the period when young are most likely to play?
4. is there a difference between sons' and daughters' activity schedules: for example, do sons play and suck more than daughters? And
5. might there be seasonal effects on the activity schedules?

As I intend to relate the structure of the behaviour of mother and young in general to these topics at the end of the chapter, in this section I will only discuss my interpretations of the activity schedule results in order to give a brief integrated summary.

It was rather difficult to test for seasonal differences because I did not investigate the activity schedules on a 24-hour basis, and the seasonal data involved different observational time spans. However, the activity schedules of the mothers are less distinctly divided into three activity periods, typified by feeding, resting, and feeding, in summer than in winter. Thus the difference between the very disrupted activity schedules of mothers with small YAF and permanently-emerging young, and of the respective young themselves, versus the activity schedules of the other classes of females and YAF also becomes less distinct in summer. While I did not test for differences in the time budgets of various activity states between the seasons, there was a consistently greater proportion of time spent in grazing for all classes of mothers and YAF in winter than in summer. This is in accord with Clarke's (pers. commun.) 24-hour data from the same population.

The activity schedules of sons and daughters differed in a few aspects only. These differences all appeared consistent with sons' behaviour being adapted towards investing

more of their metabolic energies in growth than the daughters' behaviour. That is, sons fed more during the day when they were large YAF than daughters did at the same age. Also, small YAF sons rested more than the daughters. Finally, pouch-infant sons spent more time with their head in the pouch (sucking?) when they were out of the pouch and less time in 'play' activities than did daughters. However, I was not able to assess whether sons were out of the pouch for the same proportion of the day as daughters. The durations of their out-of-pouch bouts were similar. Since they principally leave the pouch during the morning, I suspect that the sexes probably do spend a similar amount of time out of the pouch. Chapter 6 discusses further differences in the play of sons and daughters.

Pouch-infants exhibit activity schedules which are very different from those of the adults. Until they become very large pouch-infants (class 14) they spend more than 70% of their time inside the pouch. When out of the pouch and not poking their head into the pouch, they are very playful and do not rest outside the pouch. Nor do they begin to graze seriously until they permanently emerge from the pouch. Indeed permanent emergence is a time of rapid change in the young's activity schedules. Once the young has become a YAF its activity schedules are not much different from the activity schedules of females with no/small pouch-young. Play behaviours are less frequently observed in YAF than pouch-infants, and sucking occurs in about 4 to 6 discrete bouts of 11 to 15 minutes duration per bout during the daylight hours.

The activity schedules of mothers with mid to large pouch-infants vary from those of females with no/small pouch-infants by involving a greater proportion of time spent surveying, less time resting, and feeding becoming dispersed through all times of the day rather than restricted to morning and afternoon periods. These differences are especially apparent while the young is out of the pouch. Thus I suggested in section 5.2.3 that either the young may directly affect the mother's behavior or the mother may spend more time surveying for predators or their pouch-infant's position in the environment. Young are very playful at this age and frequently interact with their mother. As a young spends an increasing percentage of the day out of the pouch, the mother's behaviour simultaneously becomes less differentiated into modes in which either feeding or resting predominate; also the mother spends an increasing percentage of her time surveying. These effects peak at the time of the young's permanent emergence from the pouch. Thereafter, the mother's activity schedule slowly resumes a pattern typical of females with no/small pouch-young.

5.3 Rate of change and duration of behaviour state

Behaviour can change structurally not just according to the frequency of occurrence of each activity state but also according to how often an individual changes its activity state. Moreover, fast and slow rates of change may arise because the duration of one or many of the states is reduced or increased. As the activity schedules of pouch-young were very different from those of the adult females, I was interested in whether young maintain a standard duration for each behaviour state as they age. That is, whether only the frequencies of the states change and perhaps their interdependency (which I discuss in section 5.4), or whether the durations of the activity states vary as well as the frequencies, possibly in a manner adapted to the social and physical environment of the young. However, there is a third possibility. The durations and frequencies of activity states might be functionally interdependent and determined by the probability of an individual being in any one activity state (Fagen and Young, 1978). In the following sections I intend to present a rough sketch of the types of changes in the activity state durations which appear to be occurring in the young's development, rather than discussing the adaptiveness of the changes.

The structure of the mothers' behaviour also may not be rigorously defined. As the mothers with pouch-infants have disturbed activity schedules, while their infants are out of the pouch, they might also exhibit different durations of their activity states. If the infants are directly responsible for the mothers' changed activity frequencies by interrupting a mother's behaviour state, then the durations of the mother's activity states might all be reduced. However, if the change occurs predominantly because the mother is maintaining a surveillance for predators or her young's position in the environment, she may increase the durations of her surveying states, while reducing the durations of her other activity states.

5.3.1 Rates of change of activity state

I will first present analyses of the general rates of change of activity state in mothers and young, and then discuss trends in the durations of the individual activity states in the next subsection.

To test the hypotheses that compared to mothers, pouch-infants change their activity state more frequently while YAF do not, and that mothers with pouch-infants also change their activity state while their infant is out of the pouch, at a rate which is different to that of mothers with the less active YAF. I considered the mid-sized pouch-infants (class 12),

Table 71: The average duration of all activity states in a 'nonresting period'. Duration in seconds. MWU tests comparing pairs of classes are included. Probabilities between 0.1 and 0.05 are presented with a † and those less than 0.05 are presented with an *.

class	sample size	mean	S.E.
mothers of pouch-infants	24	20.5	4.6
...of sons	10	17.5	1.6
...of daughters	14	22.7	7.1
pouch-infants	24	13.1	2.1
sons	10	15.9	3.4
daughters	14	11.1	2.4
mothers of large YAF			
...of sons	7	14.3	0.9
...of daughters	7	13.8	1.5
large YAF			
sons	7	14.0	1.6
daughters	7	13.0	0.9

Mann Whitney U tests	U	N ₁	N ₂	p 1-tail
mothers of PI sons vs sons	41	10	10	ns
mothers of PI daughters vs daughters	28	14	14	<0.001*
mothers of PI:				
with sons vs with daughters	54	10	14	ns
mothers of YAF vs PI daughters	0.5	14	14	<0.001*
mothers of YAF sons vs sons	29	7	7	ns
mothers of YAF daughters vs daughters	22	7	7	ns
Z				
mothers of PI vs mothers of YAF	1.558	14	24	0.06†

the large YAF class, and their respective mothers. As mothers and YAF do not change their activity state greatly while resting, and pouch-infants rest inside the pouch, I confined my analyses to their more active feeding periods.

The average length of an activity state in a nonresting period for the above mentioned classes, with the young also categorised according to their sex, and tests comparing classes, are presented in table 71. While out of the pouch, female pouch-infants did change their activity state significantly more frequently than their mothers did and also more frequently than the mothers of large YAF. Male pouch-infants did not change their activity state significantly more often than their mothers. They even averaged a longer activity-state duration than did mothers with YAF. Female and male YAF also did not have an average activity-state duration which significantly differed from those of their mothers. Also, mothers with pouch-infants who were out of the pouch changed their activity state less frequently than did the mothers with large YAF.

It is possible that male pouch-infants changed their activity state less frequently frequently than female pouch-infants solely because they spent more of their time 'sucking' (i.e. bouts of other states were of similar duration for males and females). 'Sucking' was usually longer in duration than other activity states (section 5.4). I was not able to test for differences in the duration of activity states of the sexes (next subsection); it is worth bearing in mind that apart from 'sucking' there may not be a significant difference.

The reduced rate of change of activity state of mothers while their pouch-infant is out of the pouch might be related to them surveying for a greater percentage of their time than other mothers. I look at this in the next subsection.

Finally, this section has also shown that not only do large YAF have activity schedules which are similar to adult females' activity schedules, but also they are changing their activity state at a similar rate. It is probable that the young's activity state begins to change less frequently while its activity schedule is altering dramatically during the stage of permanent emergence. If this is so, then the average duration of each type of activity state should increase on the young's permanent emergence and thereafter change only slightly.

5.3.2 The duration of activity states

The duration of an activity state can vary considerably. The frequency distributions of duration of behaviour states as analysed by other researchers "are often described by simple or compound negative exponential probability distribution" (Fagen and Young, 197

p.98) which implies that behaviour states are commonly terminated by interruptions. Consequently, unless the data set of the durations of activity states is large, statistical tests attempting to discern significant differences between classes are likely to be unsuccessful. I do not have such a data set. Hence, I will present only averages and their standard errors of the average durations from individuals of the activity states standing surveying, crouched surveying, walking, grooming, sucking, and 'other'. I did this separately for the classes: mother with large YAF, mother with small YAF, mother with PEP young, mother with pouch-infant, large YAF, small YAF, PEP young, and pouch-infant.

The sequence observations (see methods: section 2.4) which I used in this section to average activity state duration did not include YAF sucking bouts or mother and young resting bouts. I omitted these observations in order to reduce the variance in the durations of the activity states I was measuring, by not mixing the activity-state durations of the predominantly resting mode with those of the predominantly grazing mode. I decided to describe the structure of the latter mode only, as it was more likely to portray differences between the classes with a minimum of variance. The period when a YAF sucks also could be defined as a different behaviour mode for both mother and young; the mother surveys predominantly for the 8 or more minutes during which a YAF sucks from her.

I did not include hopping with walking because it is frequently observed in pouch-infants as a 'play' behaviour. Further, as the frequency of hopping in adult females was rather small, I preferred to combine hopping in the 'other' category along with interacting, manipulating objects, etc..

Table 72 presents the average duration of activity states of the various classes. I must emphasise that without the support of statistical analyses the differences are not confirmed with a high probability of being biologically significant. Nevertheless, the following patterns were obtained:

1. mothers with pouch-infants or with permanently emerging young survey on average for longer durations when their young is out of the pouch, than do mothers with small or large YAF;
2. mothers with pouch-infants feed for shorter durations, and groom for longer durations, when their infant is out, than do other mothers;
3. pouch-infants have much shorter surveying and feeding bouts than do any other class;

Table 72: Average duration of activity states. Standard error in brackets. Units are seconds.

sample size	stand survey	crouch survey	activity states				
			graze	walk	groom	'other'	'suckle'
mothers of large YAF							
(7)	13.1 (1.63)	6.2 (0.98)	23.9 (3.27)	1.9 (0.29)	6.5 (1.06)	7.6 (2.33)	
mothers of small YAF							
(5)	9.3 (2.60)	4.8 (0.90)	20.4 (4.37)	1.3 (0.10)	6.2 (1.85)	6.5 (1.90)	
mothers of PEP young							
(6)	18.9 (5.90)	6.4 (2.10)	21.6 (5.28)	1.8 (0.22)	6.7 (2.50)	8.0 (2.33)	
mothers of pouch-infants							
(6)	18.5 (3.76)	10.1 (3.49)	12.7 (3.58)	1.3 (0.31)	10.0 (2.06)	6.7 (1.30)	
large YAF							
(7)	11.7 (1.47)	4.0 (0.82)	21.7 (3.27)	1.5 (0.12)	6.7 (0.90)	6.2 (0.78)	
small YAF							
(5)	14.6 (4.65)	7.6 (3.10)	16.9 (3.87)	1.5 (0.20)	6.8 (1.30)	3.5 (1.25)	
PEP young							
(6)	11.1 (5.90)	4.9 (0.54)	11.8 (2.07)	1.9 (0.22)	6.0 (2.68)	8.8 (2.19)	62.5 (44.36)
pouch-infants							
(6)	7.6 (1.79)	4.6 (0.54)	5.7 (0.97)	1.9 (0.13)	6.2 (1.25)	4.6 (0.94)	43.9 (19.32)

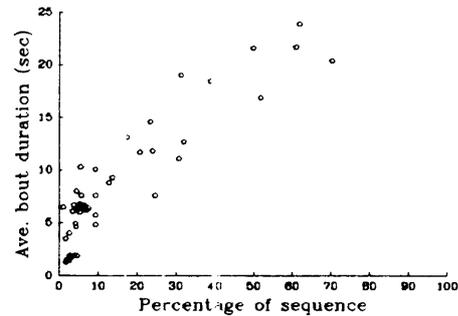


Figure 75: Average durations of activity states against the average percentage of time spent in each activity state. Averages have been calculated for each class.

4. the durations of the activity bouts of YAF, especially large YAF, resembled those of their mothers;
5. pouch-infants 'sucking' bouts averaged a much longer duration than any of their other activity states; and
6. in general grooming, walking, and 'other' activity states varied little between the classes: all were typically states with short durations.

Fig. 75 presents the average durations of each of the activity states of each class against the average percentage of a half-hour sequence-observation which the average individual of the respective class spent in each activity state. The durations of activity bouts do appear related to the probability of the individual being in that state, although 'sucking' would appear to be an exception (table 72).

The duration of eastern grey kangaroo mothers' and young's activity states is probably related to the probability of an individual being in a particular activity state. The reduced rate of change of activity state of a mother with a pouch-infant out of the pouch possibly occurs because she spends much of her time surveying for bouts which are on average longer than those of mothers with YAF. The pouch-infants who have high rates of change of activity state do not feed intensely, and no activity state predominates, unless it is 'sucking' as occurs for male pouch-infants (section 5.2). Overall, the durations of the activity states of young most probably change in concert with the changes I have described as occurring in the frequencies of their activity states (section 5.2).

5.4 The sequential structure of behaviour

Some researchers (Meissner and Ganslosser, 1985; Wilhelm and Ganslosser, unpubl.) have suggested that young have less structured activity patterns; the probability of one activity state following another appears related to random factors. The development of the young's behaviour sequences, at least in part, are supposed to follow an ontogenic course of differentiation (Plooij, 1984). Others (see Fagen, 1981) have suggested that the sequential structure of young's activities is just as likely to be adaptively determined as are the adult patterns. Otherwise, the argument continues, the young should be born with the adult activity sequences. Hence, the partial flexibility of the sequences of the young's behaviour might provide a framework within which learning occurs (see Bateson, 1976, for more detailed discussion).

As the activity schedules of pouch-infants are very different from those of adult females, while the activity schedules of YAF are very similar, I would expect that the same might apply for the sequential patterns of behaviour of pouch-infants and YAF. But are the sequences of pouch-infants's activity states random or defined by a different set of principles? Further, are the sequential structures of male and female young's behaviour similar or different? Their adult life histories are very different.

The activity schedules of mothers with pouch-infants who are out of the pouch differ strongly from those of mothers with no/small pouch-young or large YAF. They survey more frequently and for longer durations, and graze less frequently and for shorter durations. How do these changes relate to the sequential structure of their behaviour? Surveying might follow the other activity states in a more random manner or perhaps an activity state, which previously did not lead to it, now does. Thus either the the mother's behavior becomes less structured or restructured.

5.4.1 The results

I selected the class 12 pouch-infants (as they were in the middle of the pouch infant phase) and their mothers, to compare the sequential structure of their behaviour with each other and with the large YAF and their mothers. I used data gathered from sequence observations (see methods section 2.4) which did not include much resting behaviour, for the same reasons given in section 5.3. Furthermore by narrowing the range of behaviour I was analysing, I hoped that first-order Markov chains would suffice for describing differences between the

behaviour of the various classes. Two types of tests were conducted on the data. As there typically is a problem of skewed frequency tables when analysing the full matrix tables of Markov chains (Colgan and Smith, 1978), I tested for whether activity states followed each other in a random manner, by looking for 1st-order relationships between activity states separately for each activity state. That is, I compared for each activity state separately the obtained and expected frequencies of activity states which followed that activity state. In order to find out whether there might be significant between-class differences, I used the standardised deviates of full-order multiple-contingency-table tests on the complete matrices, to determine which behaviour transitions were outstandingly different in their frequency between pairs of classes.

The transition matrices for first order Markov chains are presented in table 73. As would be expected the mothers of large YAF do not enter activity states at random (table 74 for χ^2 tests). The kinematic diagrams in fig. 76 displays the most probable of their activity-state transitions. The major function of these diagrams is to show that there appear to be two groups of particularly intra-related activity states: a) standing-surveying, grooming and 'other' and b) grazing, walking, and crouch-surveying. These two groups are most distinct for mothers of YAF. While their infants were out of the pouch, the mothers of the pouch-infants tended to be more likely to survey from all of the activity states, thus reducing the structured form of their activity-state sequences, especially for the mothers of male pouch-infants. However, their behaviour did not become random. The pouch-infants also appeared to have a less structured but not random sequence of activities. The male pouch-infants particularly had a less structured behaviour sequence. For example, almost any of their activity states had a high probability of leading to an 'other' activity-state (note that 'sucking' is included in 'other'), while for female pouch-infants walking, surveying and grooming were more likely to lead to an 'other' state than were grazing and crouch-surveying. YAF had activity sequences as structured as those of their mothers: that is, all of their activity states lead to other states in a nonrandom manner.

Table 73: Transition matrices for first order Markov chains describing activity-state sequences. Matrices are presented for the classes: mothers of medium PI sons, mothers of medium PI daughters, medium PI sons, medium PI daughters, mothers of large YAF, large YAF sons, and large YAF daughters. The following activity states were abbreviated accordingly stand survey to *std*, crouch survey to *crch*, graze to *grz*, walk to *wlk*, groom to *grm*, and 'other' to *oth*. For mothers with pouch-infants, only activity-state transitions which occurred while their infant was out of the pouch have been used. The indices are averages of individuals' transition indices.

1st state	mothers of pouch-infants:													
	sons							daughters						
	2nd state													
	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>
<i>std</i>	0	1.8	5.2	3.3	9.5	13.0	32.8	0	2.2	10.0	5.3	4.6	12.0	34.2
<i>crch</i>	3.8	0	2.3	0.8	0.7	2.6	10.2	4.3	0	4.1	1.0	0.4	2.0	11.7
<i>grz</i>	7.0	3.6	0	1.1	0.2	3.4	15.5	8.1	6.1	0	2.9	0.6	3.4	21.2
<i>wlk</i>	1.2	0.3	2.1	0	0.0	2.6	6.2	3.4	0.8	4.8	0	0	1.0	9.9
<i>grm</i>	5.5	1.5	2.6	0.7	2.0	2.2	14.5	2.1	0.3	1.9	0.4	0.3	2.6	6.7
<i>oth</i>	12.2	1.8	2.4	0.3	0.2	3.1	20.6	10.7	0.9	1.1	0.4	0.9	2.1	16.2
	calc. from 948 transitions							calc. from 1,561 transitions						
1st state	pouch-infants:													
	sons							daughters						
	2nd state													
	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>
<i>std</i>	0	0.6	0.7	4.2	2.6	10.9	19.0	0	0.5	1.8	3.0	3.5	11.9	20.8
<i>crch</i>	1.0	0	0.3	1.3	1.7	2.2	6.5	0.8	0	0.6	1.6	1.0	2.3	6.3
<i>grz</i>	1.0	0.2	0	0.8	0.5	2.1	4.6	2.2	0.4	0	1.9	0.6	2.3	7.4
<i>wlk</i>	1.4	0.8	1.5	0	0.2	7.5	11.4	3.4	1.0	2.4	0	0.6	6.1	13.5
<i>grm</i>	1.0	0.6	0.4	1.1	1.2	5.7	10.0	1.0	0.5	0.4	1.3	1.3	4.5	9.1
<i>oth</i>	13.0	3.3	1.6	5.0	2.5	23.1	48.4	13.0	4.6	2.3	5.3	2.3	15.6	42.9
	calc. from 1,629 transitions							calc. from 2,893 transitions						
1st state	large YAF:													
	sons							daughters						
	2nd state													
	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>
<i>std</i>	0	0.7	9.7	3.0	3.5	4.1	21.0	0	0.5	9.9	2.9	4.7	2.2	20.4
<i>crch</i>	1.5	0	9.2	1.5	0.3	0.6	13.1	2.4	0	9.3	1.6	0.6	0.5	14.4
<i>grz</i>	11.2	10.5	0	10.3	0.9	0.3	33.2	11.3	11.1	0	9.5	1.8	0.7	34.9
<i>wlk</i>	1.5	1.4	11.8	0	0.1	0.5	16.1	1.5	1.4	11.9	0	0.1	0.1	15.5
<i>grm</i>	1.9	0.4	2.1	0.8	0.3	0.4	6.0	2.4	1.0	3.2	0.9	0.5	1.6	9.9
<i>oth</i>	4.3	0.3	2.0	0.9	0.2	3.0	10.6	1.5	0.2	1.9	0.5	0.2	0.5	4.9
	calc. from 3,444 transitions							calc. from 4,494 transitions						

(table continued)
mothers of large YAF:

1st state	2nd state						
	<i>std</i>	<i>crch</i>	<i>grz</i>	<i>wlk</i>	<i>grm</i>	<i>oth</i>	<i>tot</i>
<i>std</i>	0	0.6	3.1	3.5	3.4	2.1	17.6
<i>crch</i>	2.9	0	0.3	2.5	1.3	0.4	17.4
<i>grz</i>	8.3	14.5	0	9.7	1.4	0.9	34.8
<i>wlk</i>	1.4	1.3	2.7	0	0.2	0.6	16.2
<i>grm</i>	2.4	0.5	2.6	0.8	0.8	0.8	7.9
<i>oth</i>	2.0	0.3	1.7	0.4	0.4	1.3	6.1

calc. from 7,632 transitions

Table 74: The results of χ^2 -tests conducted to determine whether transitions were made randomly or non-randomly from the given initial state. A high χ^2 value indicates that transition from that state to others was significantly non-random, i.e. organised or structured.

class	initial state	df	χ^2	p
<i>mothers of large YAF</i>	<i>stand-survey</i>	4	27.765	<0.01
	<i>grace</i>	4	19.315	<0.01
	<i>crouch-survey</i>	4	13.517	<0.01
	<i>walk</i>	4	56.783	<0.01
	<i>groom</i>	5	20.787	<0.01
	<i>'other'</i>	5	71.518	<0.01
<i>large YAF sons</i>	<i>stand-survey</i>	4	26.293	<0.01
	<i>grace</i>	4	28.017	<0.01
	<i>crouch-survey</i>	4	42.079	<0.01
	<i>walk</i>	4	54.005	<0.01
	<i>groom</i>	5	11.519	<0.05
	<i>'other'</i>	5	68.254	<0.01
<i>large YAF daughters</i>	<i>stand-survey</i>	4	122.236	<0.01
	<i>grace</i>	4	15.489	<0.01
	<i>crouch-survey</i>	4	21.973	<0.01
	<i>walk</i>	4	77.139	<0.01
	<i>groom</i>	5	33.259	<0.01
	<i>'other'</i>	5	21.719	<0.01

(tbl. continued)

class	initial state	df	χ^2	p
<i>mothers of pouch-infant sons</i>	<i>stand-survey</i>	4	13.734	<0.01
	<i>graze</i>	4	28.373	<0.01
	<i>crouch-survey</i>	4	6.602	<i>ns.</i>
	<i>walk</i>	4	93.780	<0.01
	<i>groom</i>	5	3.400	<i>ns.</i>
	<i>'other'</i>	5	32.605	<0.01
<i>mothers of pouch-infant daughters</i>	<i>stand-survey</i>	4	12.936	<0.02
	<i>graze</i>	4	18.830	<0.01
	<i>crouch-survey</i>	4	8.516	<0.1
	<i>walk</i>	4	39.365	<0.01
	<i>groom</i>	5	38.894	<0.01
	<i>'other'</i>	5	48.225	<0.01
<i>pouch-infant sons</i>	<i>stand-survey</i>	4	8.272	<0.1
	<i>graze</i>	4	3.348	<i>ns.</i>
	<i>crouch-survey</i>	4	33.897	<0.01
	<i>walk</i>	4	18.192	<0.01
	<i>groom</i>	5	6.697	<i>ns.</i>
	<i>'other'</i>	5	6.132	<i>ns.</i>
<i>pouch-infant daughters</i>	<i>stand-survey</i>	4	7.338	<i>ns.</i>
	<i>graze</i>	4	17.139	<0.01
	<i>crouch-survey</i>	4	18.493	<0.01
	<i>walk</i>	4	13.936	<0.01
	<i>groom</i>	5	10.086	<0.1
	<i>'other'</i>	5	10.500	<0.1

The activity-state transitions which occur with a greatly different frequency between classes have been presented in table 75. As would be expected from the above analyses, mothers of YAF sons or daughters did not have activity-state transitions which varied greatly in their relative frequency from their respective sons' and daughters' activity-state transitions. Nor were YAF sons different from the YAF daughters, nor the mothers of YAF sons different from the mothers of YAF daughters. In spite of the apparently greater random component in pouch-infant sons' activity sequences, they too did not have activity-state transitions which varied greatly in their relative frequency from those of the pouch-infant daughters. In contrast, there were quite a few transitions which were considerably more or less frequent in the activity-state sequences of pouch-infants than those of YAF. In general, the types of activity-state transitions which pouch-infants exhibited more frequently than the YAF, were those in which an activity state from the mothers' group 'a' followed or preceded a group 'b' activity state, while YAF had some within-group transitions which occurred at a greater frequency than existed in the pouch-infant's behaviour. I was not able to detect any consistent patterns in the male and female pouch-infants' activity-state sequences. Their activity-state sequences might arise from random transitions and combining individual's transitions to test for deviations from random (table 74) might have resulted in significant differences which are not valid. Further research is required to check whether pouch-infants do make random transitions or whether they have more subtle relationships between their activity states.

The overall activity-state sequences of the mothers and YAF while in an 'active mode' are very similar. There are no striking between-sex differences for YAF, though male pouch-infants tend to have an even less adult-like pattern of activity-state sequences than do pouch-infant daughters. The differences between YAF and pouch-infants emphasised the less structured nature of the pouch-infant's activity-state sequences, rather than a pattern which was different but as structured. When their infants were out of the pouch, the mothers of pouch-infant males were more likely to exhibit transitions in which an activity state from group 'a' would precede or follow one from group 'b' (table 75), than mothers of male YAF. However, the same was not true for mothers of female young; there were no obvious differences in the frequencies of their activity-state transitions. It would appear that male pouch-infants disrupt their mother's behaviour more than do female pouch-infants.

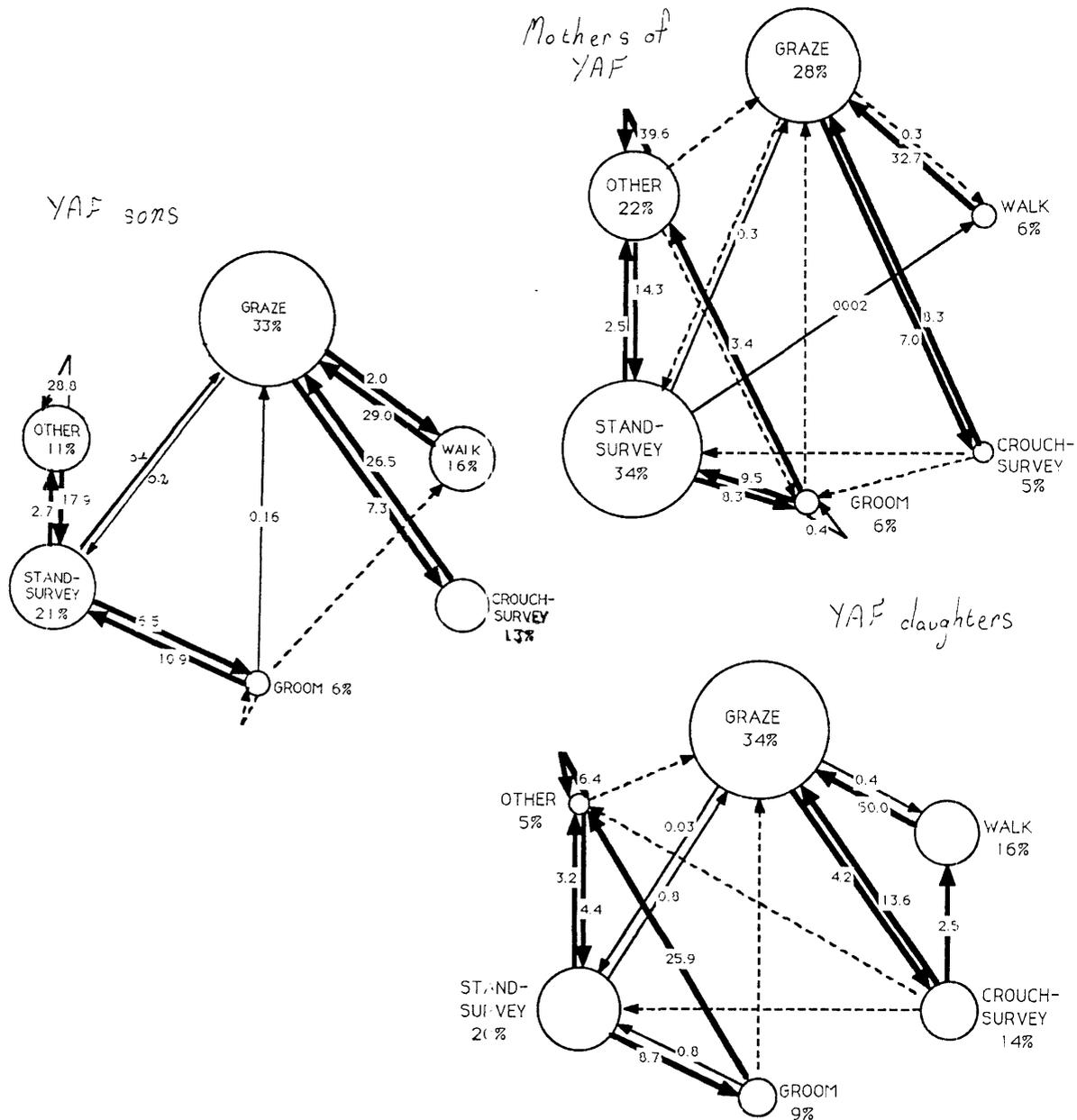
Table 75: The standardised deviates determined from comparing the frequencies of full-order Markov matrices between classes. Only standardised deviates greater than 2.0 are presented. The type of transition, whether it was a between or within transition for the state-categories 'a' and 'b', are included.

class compared	activity-state transition	and type betw vs within	standardised deviates for class with	
			more freq. transition	less freq. transition
mothers vs. YAF sons			none > 2.0	
mothers vs. YAF daughters			none > 2.0	
mothers vs. PI sons	stand → graze	betw	PI 6.1	(M -1.7)
	graze → groom	betw	PI 3.0	M -2.6
	walk → stand	betw	M 2.1	(PI -1.2)
	groom → graze	betw	PI 3.7	(M -1.4)
	'other' → graze	betw	M 2.1	PI -3.6
	'other' → walk	betw	(PI 0.8)	M -2.2
mothers vs. PI daughters	graze → crouch	within	M 2.3	PI -3.8
	graze → 'other'	betw	(PI 1.8)	M -2.7
	groom → 'other'	within	M 2.2	(PI -0.9)
	'other' → graze	betw	PI 2.1	M -3.0
	'other' → groom	within	M 3.4	(PI -1.1)
	'other' → 'other'	within	M 3.1	(PI -0.7)
mothers of sons YAF vs. PI	stand → graze	betw	(MYF 1.7)	MPI -2.9
	graze → stand	betw	MPI 2.1	(MYF -0.9)
	graze → groom	betw	(MYF 1.0)	MPI -2.2
	crouch → graze	within	(MYF 0.9)	MPI -2.6
	crouch → 'other'	betw	MPI 2.5	(MYF -2.0)
	walk → stand	betw	MPI 2.7	(MYF -1.1)
	'other' → stand	within	MYF 3.8	(MPI 2.0)
	'other' → graze	betw	MPI 4.3	MYF 6.0
	'other' → 'other'	within	MYF 9.0	MPI 2.9
mothers of daughters YAF vs. PI			none > 2.0	

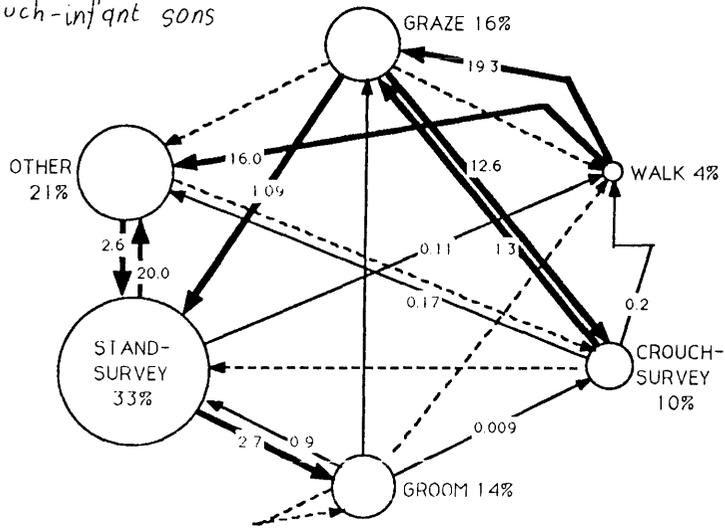
(table continued)

class compared	activity-state transition	and type <i>betw vs within</i>	standardised deviates <i>for class with</i>	
			<i>more freq. transition</i>	<i>less freq. transition</i>
<i>YAF sons vs. YAF daughters</i>			<i>none > 2.0</i>	
<i>PI sons vs. PI daughters</i>			<i>none > 2.0</i>	
<i>PI sons vs. YAF sons</i>	<i>stand→groom</i>	<i>within</i>	<i>(YF 1.6)</i>	<i>PI -2.0</i>
	<i>graze→crouch</i>	<i>within</i>	<i>(YF 0.8)</i>	<i>PI -2.9</i>
	<i>graze→groom</i>	<i>betw</i>	<i>PI 2.4</i>	<i>(YF -1.1)</i>
	<i>graze→'other'</i>	<i>betw</i>	<i>PI 4.5</i>	<i>YF -3.0</i>
	<i>crouch→graze</i>	<i>within</i>	<i>(YF 0.6)</i>	<i>PI -2.6</i>
	<i>'other'→graze</i>	<i>betw</i>	<i>PI 2.9</i>	<i>(YF -1.8)</i>
	<i>'other'→crouch</i>	<i>betw</i>	<i>PI 2.5</i>	<i>YF -3.3</i>
	<i>'other'→'other'</i>	<i>within</i>	<i>YF 7.4</i>	<i>PI -2.1</i>
<i>PI daughters vs. YAF daughters</i>	<i>stand→graze</i>	<i>betw</i>	<i>PI 2.8</i>	<i>(YF -1.0)</i>
	<i>graze→crouch</i>	<i>within</i>	<i>(YF 1.1)</i>	<i>PI -3.7</i>
	<i>graze→'other'</i>	<i>betw</i>	<i>PI 2.9</i>	<i>YF -2.4</i>
	<i>walk→stand</i>	<i>betw</i>	<i>PI 2.1</i>	<i>YF -2.1</i>
	<i>walk→graze</i>	<i>within</i>	<i>(YF 0.8)</i>	<i>PI -2.1</i>
	<i>groom→stand</i>	<i>within</i>	<i>(YF 2.0)</i>	<i>PI -2.6</i>
	<i>'other'→crouch</i>	<i>betw</i>	<i>(PI 1.9)</i>	<i>YF -3.4</i>
	<i>'other'→'other'</i>	<i>within</i>	<i>YF 5.9</i>	<i>(PI -1.2)</i>

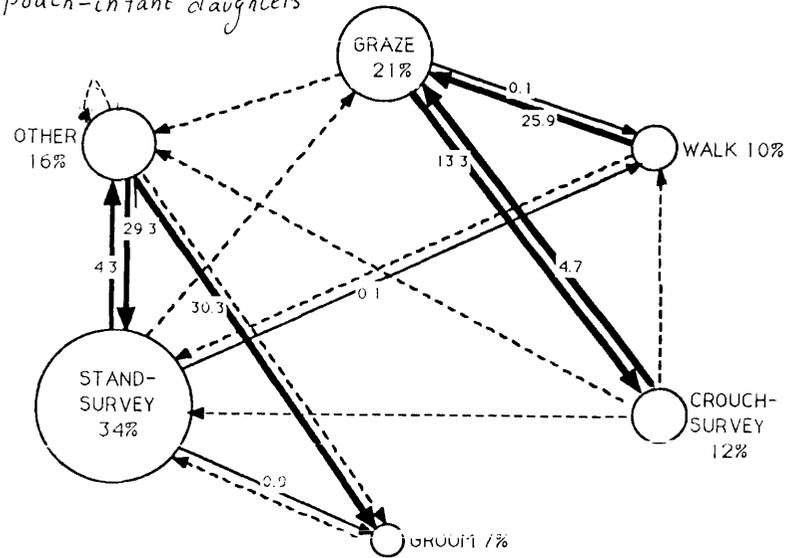
Figure 76: Kinematic diagrams of the 1st order Markov transitions for activity-state sequences. The circles represent activity states and their size is in proportion to the percentage of time spent in that activity state (also see percent value next to the name of the state). No arrow between states (circles) implies the transition occurs less than expected from random transitions and the χ^2 cell value is 1.0 or greater. A broken arrow between states implies the transition occurs slightly less than expected from random, but definitely not significantly. The χ^2 value for that cell was not greater than 1.0. A continuous fine arrow between states implies the transition occurs slightly more often than expected from random, but not significantly so. The χ^2 cell value was not greater than 1.0. A continuous thick line between states implies the transition occurs more frequently than expected and the χ^2 cell value was greater than 1.0. The important point to note is that for mothers of YAF and YAF, but not the other classes, the states groom, stand survey, and 'other' are more likely to lead to each other than to the other states, and the states graze, walk, and crouch survey are also more likely to lead to each other than to any of the other 3 states.



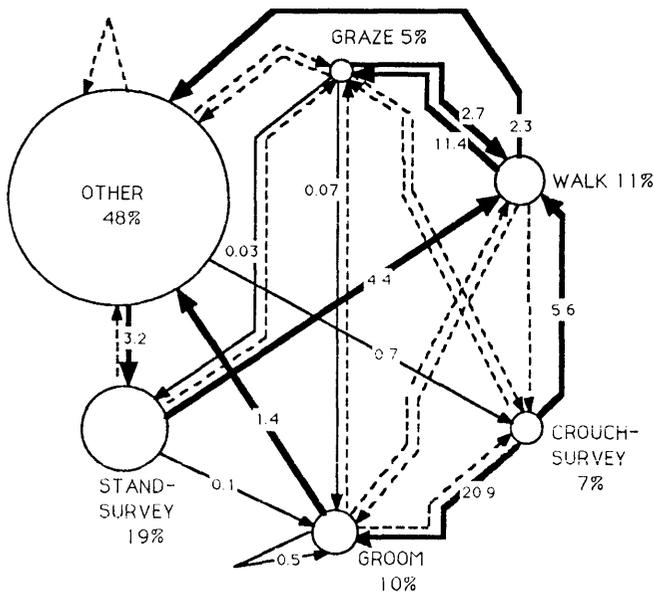
Mothers of pouch-infant sons



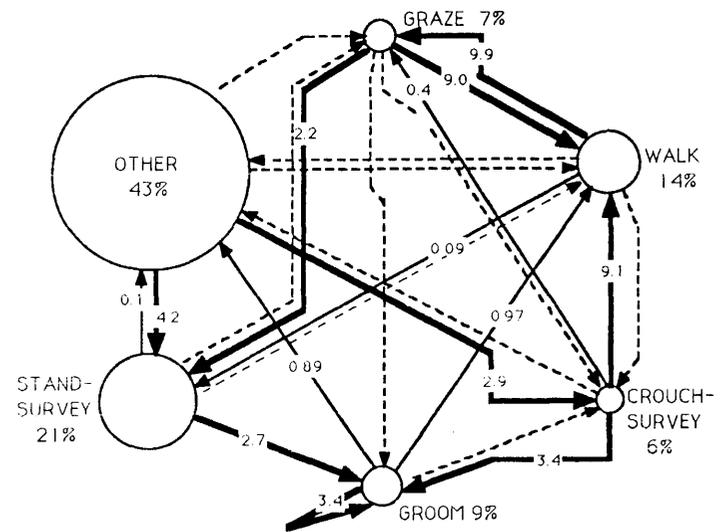
Mothers of pouch-infant daughters



pouch-infant sons



pouch-infant daughters



5.5 Discussion

5.5.1 The pouch-infant phase

Pouch-infants behave very differently from their mothers or other females or YAF. Adult females and YAF typically have quite structured activity sequences and spend a considerable proportion of their time in any one of 3 activity states: grazing, resting, or surveying. Pouch-infants graze infrequently, and divide most of their time when out of the pouch between poking their head into their mother's pouch, which could involve sucking, or in 'play' behaviours. It is at this stage in a young's life that 'play' activities predominate above grazing or surveying. There have been many functions suggested for play (Bekoff, 1972; Fagen, 1981 and 1976, Baldwin and Baldwin, 1973 and 1974). Emphasis is usually placed on the importance of play for exercise and learning to respond to environmental cues in a locally or culturally adaptive manner. Assuming that these are important functions of play, it is appropriate that the major 'play' age for kangaroos should be the pouch-infant phase. It is a phase with a comparatively low risk of mortality for young, which is consistent with Fagen's (1981) suggestions for play-ages. Further, the young are learning to co-ordinate their limbs and respond to changes in the environment. Whenever a situation becomes threatening the young can and do retreat to the pouch.

It is virtually impossible to identify whether an infant is sucking or just poking its head into the pouch. But, regardless of this uncertainty, pouch-infants are very strongly oriented toward the pouch. There are considerable advantages of this aspect of their behaviour, such as increasing the probability of a young being ready to dive into the pouch when danger threatens. I discuss this further in chapter 6.

When out of the pouch, male infants spend proportionally more of their time in this 'sucking' posture. For a variety of reasons, including the fact that the rate at which milk is suckled is not necessarily constant (Green, 1984, Loudon and Kay, 1984), males may not be receiving more milk than female infants. However, if they are out of the pouch for the same proportion of the day as females, then they are exchanging time, which female infants would spend in play, for 'sucking'. Possibly as a consequence, they change their activity-state in total less frequently than female pouch-infants do. Also, more of the male's activity states lead with a high probability to an 'other' activity state, which includes 'sucking' and 'play', than do those of pouch-infant females. The female infant's activity-state sequences appear slightly more structured and similar to the structure of an adult female's activity-state

sequences than does a male pouch-infant's behaviour.

While their offspring are out of the pouch, the mothers of sons are very likely to show activity-state transitions which are not typical for mothers or young with structured activity-state sequences, including the mothers of pouch-infant daughters. It could arise because infant sons have slightly more random activity-state sequences and perhaps interrupt the mothers' behaviour more than do infant daughters; or because mothers tend to survey while their infants suckle and infant sons tend to suck more than infant daughters. The latter is less likely to apply since mothers of pouch-infant sons changed their activity state at a higher rate (though not significantly so) than mothers of pouch-infant daughters. Surveying, of all activity states, appeared to be the one in which the duration of bouts increased while the mother's infant was outside the pouch and therefore would be expected to be related to a reduced rate of activity-state change. In chapter 6 I look at whether sons interact more with their mothers than do daughters.

5.5.2 The permanent emergence stage

As the young permanently emerges, its behaviour changes dramatically. Until less than a fortnight prior to this stage the young typically spends more than 70% of the day in the pouch. During the permanent emergence stage the young spends most of its time out of the pouch, only returning when danger threatens. The young now spends much less time 'playing', relative to the time it spends out of the pouch, and in winter absolutely less time. The young also begins to graze intensely, to rest out of the pouch, and to suck in about 6 discrete bouts of 8 minutes duration per day. By the time the young becomes a small YAF, its activity budget has become very similar to the activity budget of a female with no/small pouch-young. Thus the transition to the YAF stage for a young is not a smooth process, and this fact might be one more reason for the mother and young to seek relative isolation from conspecifics during this stage (see chapter 4).

The mother's behaviour schedule also changes considerably while her young is permanently emerging. The activity-state sequences and budgets of mothers with pouch-infants changed principally while the young was out of the pouch. During the permanent-emergence stage, the disruption to the mother's behaviour is not just confined to a mere 30% or less of the day but pervades the whole of the day. Mothers of permanently emerging young survey at a fairly constant and elevated frequency throughout the day, even with the consequence of a disrupted activity schedule and a reduction in their resting time. Although

these females probably have been through their most metabolically demanding stage i.e. carrying and suckling a large pouch young (Dove *et al.*, 1987; Green, 1984), their daily grazing time does not appear to increase. They graze at a reduced intensity throughout the day. Consequently, it is quite tenable that females with permanently emerging young should average the poorest condition of all female reproductive classes (section 3.3).

I am not able to determine whether mothers of permanently emerging young have disrupted behaviour patterns because they tend to be found in small subgroups (section 4.3), which necessarily entails an increase in their surveying behaviour (Southwell, 1981; Jarman, 1987) or whether their behaviour would be disrupted regardless of the size of the group they are in and whether it consequently becomes adaptive for mothers with a conspicuous activity schedule to avoid large groups (Jarman, 1974). Either way the permanently emerging young are small and vulnerable and also have very conspicuous behaviour patterns until near the end of the stage and should avoid large subgroups. However, as the disruption to the mother's behaviour is considerable, I suggest that it might be adaptive to both individuals to minimise the duration of this stage. Thus the behaviour of the young reaches a significant turning point at permanent emergence, when an adult-like pattern rapidly develops. A young with an adult behaviour schedule and structure is more likely to be co-ordinated with its mother, be a less conspicuous group member, and even take some responsibility in the detection of predators.

Pouch-infants, with their very different behaviour pattern, also disrupt their mothers' behaviour, but principally for less than 30% of the day. Pouch-infants may not be let out of the pouch for any greater percentage of the day because the metabolic constraints on a mother's activity-budget might not allow for the increased disruption to her behaviour that would follow. When young must vacate the pouch permanently, their behaviour changes rapidly, possibly in relation to reducing the intensity of the disruptive influence on their mothers, as well as reducing their conspicuousness to predators during this critical period.

5.5.3 The YAF stage

Mothers and their YAF begin to associate with their conspecifics on a more typical level anywhere from two weeks to three months following permanent emergence (section 4.3). Around this time the mothers' activity schedules begin to return to the schedules typical of the other females, who feed intensively during the morning and afternoon and rest during the middle of the day. Mothers of large YAF and the large YAF themselves have

activity schedules and activity-state durations which resemble those of the females with no/small pouch-young. If I assume that these latter females have few immediate reproductive demands on their activities, then a large YAF appears to affect the mother's behaviour minimally. Further, the sequential structure of the 'active behaviour mode' of large YAF is as structured as the behaviour of their mothers. Thus apart from still 'sucking', the behaviour of large YAF appears quite adult-like.

There are few behavioural differences between sons and daughters or the mothers of sons and the mothers of daughters during the YAF stage. Both sexes suck for similar durations and frequencies. The sequential structure of their 'active behaviour mode' is very similar. The principal differences in the activity schedules of YAF sons versus daughters are that small YAF daughters show a trend toward resting less than small YAF sons, and large YAF sons tend to graze for a greater percentage of the daytime than large YAF daughters. These differences are rather similar to those found during the pouch-infant phase, during which males appeared to suck more and play less than the females. Captive studies have found a trend for males to grow at a faster rate following permanent emergence than females (Poole *et al.*, 1982). Further, the growth of kangaroos can respond to different nutritional regimes (Green, 1984). Hence, the male young may well have been concentrating their metabolic functions and behavioural activities toward growth. Alternatively, the males might be expending energy more intensely for short bursts than the female YAF, and therefore require longer periods of rest or to graze for longer durations. I discuss this further in chapter 6.

5.5.4 Seasonal differences

Since there is a peak season for permanent emergence, it is possible that the activity schedules of the females and their young are affected, perhaps particularly stressed, during the offpeak season. The offpeak and peak seasons both straddle the winter and summer seasons. But young who permanently emerged in the peak season have a summer YAF-phase and a winter subadult-phase, while young who permanently emerged in the offpeak season have a winter YAF-phase and a summer subadult-phase. Large YAF sons grazed significantly more than the other YAF in summer, but not winter. The proportion of the day for which they grazed was rather similar to that found for both sexes of large YAF in winter. If this percentage represents a ceiling for the grazing time of YAF, then it may be that winter YAF sons cannot manipulate their activity budget to gain extra nutrition for growth or are less active than they are in summer. I have not analysed data which would enable me

to construct an activity budget for subadults, but it is probable that they too would be affected by any seasonal difference in the quality of the pasture. I believe that the growth strategies of young and subadults and the environmental effects on their growth deserve further study. It may be more important for a son to have his early life-stages timed to a particular seasonal schedule than it is for daughters. I discuss this further in chapter 7.

In winter the females also appeared to increase the proportion of time they spent feeding. As my data represent only the daytime activity-budgets, my interpretations of the females' time budgets are rather limited. However, these findings are consistent with Clarke's preliminary results on 24-hour feeding budgets of the kangaroos at Wallaby Creek. Thus, compared to a spring or early summer permanent-emergence, a winter permanent-emergence might be particularly stressful for females (see also section 3.3).

Finally, while mothers who have a permanently emerging young or small YAF in summer have activity schedules which are as disrupted as they would be in winter, the females of the other classes also have activity schedules which are less distinctly differentiated into feeding versus resting periods in the day. In chapter 4, I mentioned that females with peak-season young did not isolate themselves as strongly during permanent emergence as did females with offpeak-season young. This difference may arise not just because there are more young around in the peak season, therefore making a female with a permanently emerging young less conspicuous, but also because the mother and young's behaviour is in general less distinct from that of the other females.