THE DEVELOPMENTAL BEHAVIOURAL ECOLOGY OF INFANT BABOONS (*Papio cynocephalus ursinus*)

by

JOHN EDWARD LYCETT

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DECLARATION

The data described in this thesis were collected in the Cathedral Peak Reserve, Drakensberg Mountains from April 1991 to February 1993, under the supervision of Professor S. Peter Henzi.

I declare that the design and execution of the studies on which this thesis is based are my sole and unaided work unless otherwise indicated and acknowledged in the text, and that no part has been submitted for any other degree at any university.

J.E. Lycett

Department of Psychology
University of Natal
DURBAN
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ABSTRACT

Presented in this thesis are the results of a 23-month field study (April 1991 - February 1993) which focused on infant development in a free-ranging baboon troop (*Papio cynocephalus ursinus*) inhabiting the Cathedral Peak Reserve in the Drakensberg Mountains, Natal Province (South Africa). The troop selected for study was, in demographic composition, representative of the greater Drakensberg baboon population. During the course of the study, five infants were born into the troop. At the end of the data collection period, the infants ranged in age from 11-months to 17-months old. The data presented are extracted primarily from 2678 half-hourly scan samples, representing approximately 1340 hours of observation.

Data presented in this study indicate that baboon births in the Drakensberg are seasonally timed such that mothers are afforded some measure of relief from the energetic costs associated with intense infant dependency, particularly during the first few months postpartum. However, the timing of births is not optimal in terms of the development of infant nutritional independence. This has implications for the interbirth interval (38.4 months) which, for the Drakensberg females, is substantially longer than that for comparative studies, while the rate of infant survivorship through to 12-months (95%) is considerably higher than for other baboon populations.

The development of independent feeding for the Drakensberg infants is, when compared with infants from other studies, considerably slower. The delayed transition to independent feeding which was observed is explained with reference to seasonally variable ecological conditions in the Drakensberg which necessarily resulted in infants remaining nutritionally dependent on mothers for a longer time than would normally be expected. The relationship between dependent and independent feeding, as alternate infant strategies, is considered within the context of weaning and its role in the promotion of independence. A model which purports to delineate the weaning period with reference to the rate of decline in various measures of maternal investment is applied to the data for this study, as well as for comparative studies. No clear consistency is evident in the rate of decline across the various measures for the present study.

The trajectories of infant behavioural development toward the adult model of independent activity are described and considered. With the exception of nutritional independence, all other trajectories of infant behaviour followed similar developmental patterns to infants in comparative studies. Thus the appearance of particular behaviours, and the age at which transitions to independence were made, confirmed a general baboon pattern. The implications and consequences of delayed feeding independence for changes in behavioural development are considered within the context of general activity budgets.

Data are also presented which examine the contexts within which adult males interact with infants. These data are considered in relation to the possible functional purposes served by male interaction with infants, as well as in terms of the effect male interaction with infants has on inter-male interaction. The data indicate individual male variability in both the extent and contexts of interaction with infants.

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- **Pg. 47**: c^2 should read χ^2
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- **Pg. 173**: Lines 4,5: c^2 should read χ^2
- **Pg. 175**: Line 4: x should read $\bar{x}$
- **Pg. 208**: Line 6: c^2 should read χ^2
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- **Pg. 218**: Lines 3,4,8,11: c^2 should read χ^2

CHAPTER 1
COMPETENCE IN DEVELOPMENTAL PERSPECTIVE

> "Ontogenies reflect adaptations. Developmental rates are biological dependent variables keyed to environmental demands in a way that results in the greatest possible number of surviving offspring. Developmental rates evolve. The patterns of response of developing organisms to environmental variation are themselves adaptations molded by natural selection" (Fagen 1981, p.252).

The point made by Fagen that ontogenies reflect adaptations is one that may not *intuitively* appear to provide any new insight on developmental processes. It makes sense that the rate and age at which a behaviourally flexible animal completes life transitions will be determined, at least partly, by the conditions -both social and ecological- within which the developing individual finds itself. Thus, for example, and with particular emphasis on individual ontogeny, previous infant baboon studies have pointed out that the rate and age at which infants make the transition to independent feeding will, to some degree, be dependent on the availability of appropriate weaning foods in the habitat at that time (cf: Altmann 1980; Nicolson 1982). That is to say, and obviously so, an animal will be able to make the transition from a dependent (suckling) diet to feeding for itself *only* if there is, in fact, food in the habitat on which it can feed[1]. Having said that this seems obvious and hence not necessarily worthy of being pointed out, there have been, however, few primate studies using free-ranging animals which have clearly demonstrated the relationships between emergent independence, maternal care and investment, and the ecological context within which these relationships are played out. This absence of a demonstrated relationship is particularly true for a non-seasonally breeding species such as baboons, where births have been observed to occur during all months of the year (see references in Chapter 3), and hence the relationship *for individual animals* between timing of birth and prevailing ecological conditions is masked in data presentation which emphasizes 'the mean', with little examination of individual variation.

In the study which follows, the relationships referred to above will become clearer. This becomes possible for this study on account of what will be shown to be a seasonal effect on the timing of reproductive events for the Drakensberg Mountain baboons where all, or most, infants experience similar ecological conditions at each stage of development which, it will be shown, impact in a considerable way on the emergence of independence and the attainment of competence. Before the data for this study are presented in the chapters which follow, I will use the remainder of this introductory chapter to consider and elaborate on what is meant, or what is inherent in the usage of the terms *infancy*, *competence*, and *development*. I will

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[1] This statement presupposes that any other skills, knowledge, or abilities that the animal might require for independent feeding are available.

also introduce previous baboon studies which have taken infants and their development as a prime focus. The specific findings of these studies will not be considered in detail in this chapter as they are presented in subsequent chapters as comparative data for the present study.

1.1 INFANCY, COMPETENCE AND DEVELOPMENT

1.1.1 INFANCY

Primate infancy is usually defined as the period during which an immature animal is physically dependent on its mother (Walters 1987), where physical dependency is functionally interpreted as referring to the infant's inability, in the absence of being adopted by another care-giver, to survive the death of its mother. In terms of this perspective, primate infancy is then *primarily* defined in terms of an infant nutritional and, to a lesser extent, locomotor reliance on mothers.

Probably the most characteristic feature of primate infancy is the overwhelming dependence of infants on their mothers for just about all their care requirements. This is especially true during the first few months after parturition, following which the extent of dependency decreases with increasing age as infants gradually begin to become self-sufficient. Cross-species primate studies have highlighted this invariant pattern of declining dependence with increasing independence, although differences are manifest in the rates, or ages, at which transitions to independent behaviour are made (Case 1978). Thus, for example, among smaller-bodied species, infancy may last for less than a year (Charles-Dominique 1977) and yet may extend for at least four years in the great apes (Horr 1977; Fossey 1979).

The extended duration of the primate prereproductive period, which combines the infancy and juvenile periods, has been explained in a number of ways. A life-historical perspective (eg. Stearns 1977) emphasizes the dependency of primates on learning where the " .... beneficial effects of learning during the prereproductive period on adult reproductive success may justify delaying reproduction" (Walters 1987 p.359). This suggests that the skills, both physical and social, that young animals will require to function in their world as competent adults are acquired during the period of immaturity. This point is emphasized by Pereira and Altmann (1985) who have suggested that primate behavioural development can be viewed properly only as "... a life-long process that results in a continual shaping and reshaping of the ways in which an individual responds to the myriad ecological and social features of its environment" (p.217). Delayed maturation has also been considered to be a physiological consequence of neonatal brain size and fetal growth patterns (Walters 1987), where physiological and energetic constraints on postnatal growth are imposed by a large brain size at birth. In terms of this perspective, learning during the prereproductive phase is not so much a cause of extended immaturity as it is an effect (Walters 1987). Infancy has also been associated with further physiological changes, notably insofar as the gut is concerned where, with age, the organisms ability to tolerate the digestion and assimilation of solid food items is enhanced (Pereira and Altmann 1985; Lee 1987).

1.1.2 COMPETENCE

As a starting point, and in the absence of a formal definition of the concept, nonhuman primate competence can most readily be seen and understood in terms of *what adult animals do.* In other words, adults who function and cope within the socio-ecological arena are, necessarily, competent[2] in the specific behaviours which constitute the general activity repertoire for their group or species. For behaviourally flexible animals such as primates, adult animals, by virtue of their adulthood, must have acquired the requisite skills and knowledge which comprise the integrated acts and sequences of behaviour which are utilized during the course of normal everyday activity. Given this, and from the perspective of an infant, the question then revolves around identifying which components of the adult (competent) model of behaviour are absent from the immature repertoire and, probably more importantly, the nature of the developmental process(es) by which these components are acquired during ontogeny.

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[2] The point is noted that immature animals may be competent *as immature animals* to the extent that immaturity, in itself, requires some measure of competence for the range of activities that immature animals engage in. The point, however, is that competence as is being referred to here is conceived of as being the end-point of development.

Attempts to identify specific nonhuman primate competencies, abilities, and cognitive processes have been conducted largely under laboratory conditions (reviewed by Dasser 1985), although there has recently been an extension of these attempts to include animals in natural settings. Many of the attempts to elucidate competence and competencies have been guided by the Piagetian approach to cognitive development. From these studies, particularly using the great apes as subjects, it has been shown that human and nonhuman primates follow the same developmental sequence during the sensorimotor period, displaying similar abilities within each phase or stage (eg. Bard 1987; Bragio *et al* 1979; Chevalier-Skolnikoff 1977, 1981, 1982, 1983; Gillan 1981; Gillan *et al* 1981; Hall *et al* 1980; Hughes and Redshaw 1974; Mathieu and Bergeron 1981; Mathieu *et al* 1976, 1980; Natale *et al* 1986; Parker 1977; Parker and Gibson 1977; Pasnak 1979; Redshaw 1978; Thomas and Walden 1985; Vauclair 1982; Vauclair and Bard 1983; Vaughter *et al* 1972; Wise *et al* 1974; Wood *et al* 1980; See Bard 1987 for a general review of findings), although differences between human and nonhuman subjects are apparent in both the rate and the endpoint of development (Bard 1987). With rare exception, however, what most of these studies have demonstrated is the presence or absence of particular competencies at either an inter-specific level, or at different ages. There has been little systematic effort to chart the processes and mechanisms that underlie *change* from one age (or stage) to another. It is the notion of *change*, and the factors that motivate and facilitate change that need to become the focus of true developmental studies, rather than a focus on specific abilities or competencies that individuals are, or are not, capable of at specific ages. While informative in themselves, the majority of the studies that have been conducted suffer -in a truly developmental sense- from being more *descriptive* than *explanatory* in understanding the development of adult-typical competence (cf. Brainerd 1978). At one level, it seems surprising that the processes that lead to the development of competence have remained largely unexplored in primate studies given that the emergence of competence links together both social and ecological processes and thereby makes it possible to understand the origins of cultural processes.

1.1.3 DEVELOPMENT

Competence, or adult species-typical behaviour, represents the end-product of a developmental process which, particularly for the primates, is largely reliant on the role played by learning, where learning is premised on information gained at one point in time being available for use at a later time (Essock-Vitale and Seyfarth 1987). While the means by which learning might proceed may take on different forms, the acquisition of information is most efficiently achieved through social means rather than through individual trial and error experimentation with features of the environment and members of the social group (Bonner 1980; Galef 1976; Henzi 1989, 1990; Jolly 1966/1988; Kummer 1971; Nishida 1987).

The direct benefits and mechanisms of socially mediated learning will be most apparent in the domain of diet selectivity where, for example, in the case of howler monkeys (*Alouatta palliata*), infants are confronted with the task of learning an appropriate diet in an habitat which includes an array of items of which some are toxic and hence potentially fatal to an infant (Whitehead 1986). The essence of this problem is contained in what Rozin (1977) has termed the *omnivores paradox* which states that the omnivore must "... try and explore the full nutritional potential of its environment, while at the same time minimizing ingestion of poisonous substances" (Rozin 1977, p.559). In other words, socially mediated learning would allow the 'uninformed' individual to benefit from the accumulated knowledge of other, presumably older, more informed conspecific animals, rather than having to negotiate the alternate and risky prospect of interrogating the environment individually (cf: Henzi 1990). Not only does the need for learning apply in the specific domain of diet selectivity;- infants will have to learn not only the different foods items which will constitute their independent diet and which may vary both temporally and spatially in their availability in the habitat (cf. Whitehead 1986), but they will also need to develop and practise the skills which will be required to harvest the food items (see S. Altmann 1991). Thus the necessity for extended immaturity and hence opportunity for skill practising is made by Hauser (in press) when he points out that because primate infants are initially fed a diet of milk, they thus obtain only an indirect introduction to the foraging environment. Given this, the processes whereby, and the ability of nonhuman primates to learn from members of the social group has continued to serve as a consistent theme in research (Hall 1963; Kawamura 1963; Stephenson 1967; Rowell 1976; Jouventin, Pasteur, and Cambefort 1976; Kaufman 1976; McGrew 1977; Rozin 1977; Mainardi 1980; Cambefort 1981; Whitehead 1986; Nishida 1987; Cheney and Seyfarth 1988; Hauser 1988; Henzi 1989; Lycett and Henzi 1992; Whiten and Ham 1992).

Infant development, aspects thereof, as well as mother-infant interactions as they facilitate and contribute to emergent infant independence have been widely documented from primate studies at both inter and intra-specific levels (Baboons: Nash 1978; Young and Hankins 1979; Altmann 1980; Bolwig 1980; Nicolson 1982; Rhine *et al* 1984, 1985; Marsh 1992: Vervets: Struhsaker 1971; Lancaster 1972; Harrison 1983; Lee 1984a, 1986, 1987; Henzi 1989; Lycett 1990; Lycett and Henzi 1992; Hauser 1993, in press; Hauser and Fairbanks 1988: Capuchins: Fragaszy 1986; Fragaszy and Visalberghi 1990: Chimpanzees: Silk 1978, 1979; Boesch1991: Howler monkeys: Whitehead 1986; Clarke 1990: Macaques (*Macaca spp.*): Hinde and Spencer Booth 1971; Murray and Murdoch 1977; Berman 1978; Bolwig 1980; Negayama 1981; Stevenson-Hinde and Simpson 1981; Johnson and Southwick 1984; Rosenblum and Paully 1984; Johnson 1986; Collinge 1987; Gomendio 1989; Karssemeijer, Vos, and van Hooff 1990; Simpson and Tartabini 1992; Vos, Karssemeijer, and van Hooff 1992; Deng 1993; Titi monkeys: Fragaszy, Schwarz, and Shimosaka 1982: Patas monkeys: Chism 1986: Tamarins: Pryce 1988: Marmosets: Ingram 1977: General reviews: Suomi 1976; Nash and Wheeler

1982; Nicolson 1987). The invariant cross-species pattern of declining infant dependence with increasing independence, which these studies have demonstrated, has been noted above. What has further become apparent from intra-specific studies is further variability between and within study populations in development. For baboons, Rowell *et al* (1968), Altmann *et al* (1978), and Nicolson (1982) have all reported that the greater protectiveness and restrictiveness of infants by lower-ranking females resulted in slower rates of infant acquisition of independence. There is also compelling evidence to show that habitat quality and variable ecological conditions have significant effects on mother-infant interactions and the timing of independence (Lee 1986; Hauser and Fairbanks 1988; Hauser, in press; Vos *et al* 1992; But see Johnson and Southwick 1984). These latter studies have demonstrated intra-specific variability in maternal strategies between groups inhabiting different ecological niches within the same habitat. Such variability, it has been suggested, probably reflects a facultative adaptation to local environmental and social conditions which affect female reproductive success (Nicolson 1982). It is this latter point which brings us back to the initial statement by Fagen, and which links together the concepts of infancy, competence, and development.

Regardless of the reason(s) why infancy and extended immaturity has been selected for among nonhuman primates, the point remains that infants are incompetent to the degree that the range of skills, abilities, or competencies that are required for adult functioning are not present at birth. They are acquired during ontogeny. At the same time, however, the development of particular behaviours is not simply an unfolding, with increasing age, of sequences of action. The expression of behaviour, it has been claimed above, will be influenced by both the social and ecological context. This was illustrated with the example of the development of independent feeding where the availability of easily obtained, easily digested, and easily harvested infant weaning foods will, necessarily, dictate when feeding starts. Similarly, maternal styles (eg. laissez faire, restrictive cf: Altmann 1980) which reflect female responses to social and environmental circumstances (eg. predation threat, low social rank), may inhibit the expression of infant independence. Ultimately, the rate and length of development will probably be a function of the 'amount' or complexity of skills, abilities, or competencies that an individual animal requires to participate as a competent adult in the socioecological arena. Ensuring that each successive infant acquires, or has the *opportunity* to acquire these skills, will thus represent a major investment for mothers, hence intraspecific variability in maternal styles and individual ontogeny.

1.2 BABOONS: DISTRIBUTION AND PREVIOUS RESEARCH

1.2.1 DISTRIBUTION OF BABOONS

Baboons (*Papio* spp.) are distributed throughout most parts of sub-Saharan Africa, occupying areas which range in vegetation type from semi-desert, savannah, woodlands, rain forest, riverine forest, to montane and coastal areas (Wolfheim 1983; Melnick and Pearl 1987). In terms of feeding ecology, throughout their range baboons have been reported to feed on grass, tubers, bulbs, corms, rhizomes, flowers, fruits, leaves, seeds, tree gum, insects, and eggs (Melnick and Pearl 1987), while particularly adult animals occasionally eat meat of small animals that they catch (Stoltz and Saayman 1970; Hausfater 1975; Strum 1975). DeVore and Hall (1965) have suggested that it is probably easier to list the food items which baboons do not eat than it is to provide a complete account of what they do. Thus Hamilton, Buskirk and Buskirk (1978) have described (savanna) baboons as 'generalized feeders', while Whiten *et al* (1990) characterize the feeding style of baboons as being eclectic yet, at the same time, highly selective. By virtue of their ability to exploit widely differing habitats, this broad and general diet of baboons has been argued to be at least partially responsible for their wide geographical distribution (Harding 1976; Ransom 1981; Post 1982).

1.2.2 PREVIOUS RESEARCH ON BABOONS

The behaviour, as well as the socioecology of baboons, have been the focus of extensive research, both long and short term, throughout most African habitat types in which they occur (J. Altmann 1978, 1980, 1983, 1984, 1986; S. Altmann 1991; Altmann and Altmann 1970; Altmann and Samuels 1992; Altmann *et al* 1977, 1978, 1988, 1994; Anderson 1982, 1990; Barton 1990, 1993, Barton and Whiten 1993; Bercovitch 1983, 1986, 1987a,b, 1988, 1989, 1990, Bercovitch and

Harding 1994; Busse 1984, Busse and Hamilton 1981; Byrne *et al* 1987, 1990a,b, 1993; Cheney 1978, Cheney and Seyfarth 1977; Collins 1981, Collins *et al* 1984; Davidge 1978; DeVore 1963, 1965, DeVore and Hall 1965; Dunbar 1980, 1984, 1989, 1992, Dunbar and Dunbar 1988; Hall 1962; Hamilton *et al* 1978; Harding 1976; Hausfater 1975, 1976; Henzi and Lycett 1995; Henzi *et al* 1990, 1992, under review *a,b*; Kummer 1968; Manzolillo 1982; Marsh 1992; Nash 1978; Nicolson 1982; Noë 1986a,b, 1990; Norton *et al* 1987; Packer 1979a,b, 1980; Pereira 1984; Post 1982, Post *et al* 1980; Ransom 1981, Ransom and Rowell 1972; Rasmussen 1980; Rhine 1992, Rhine *et al* 1984, 1985, 1988, 1989; Rowell 1966, Rowell *et al* 1968; Saayman 1970, 1971; Seyfarth 1976; Sigg *et al* 1982; Silk 1986, 1987; Smuts 1985; Stein 1981, 1984, Stein and Stacey 1981; Stoltz and Saayman 1970; Strum 1975, 1984, 1987; Washburn and DeVore 1961; Wasser 1983, Wasser and Starling 1988; Whiten *et al* 1987, 1990; Young and Bramblett 1977, Young and Hankins 1979). From these studies has emerged a picture of wide variability in the social structure and behaviour of the populations inhabiting different study locations, with a body of evidence suggesting that the observed variability is related to ecology and the adaptive pressures each population is subjected to (eg. Eisenberg *et al* 1972; Jolly 1972; S. Altmann 1974; Popp 1983; Dunbar 1988; van Schaik 1989; Lee 1991; Henzi *et al* under review *a*).

Data from particularly the early studies of baboons led to attempts to extrapolate from "the baboon model" to explain the evolution of human behaviour (reviewed by Smuts and Mitchell

1987). Underlying certain of these attempts was the supposition that "... because baboons and early hominids shared the same ecology with a similar primate biology, they reasoned that the baboon data could help identify the problems facing ancient humans and offer suggestions about the solutions available to hominids" (Smuts and Mitchell 1987 p.88). At the same time, but referring to primates in general rather than to baboons in particular, Pereira and Altmann (1985) have argued that primates serve as an appropriate mammalian order for investigations concerned with the origins of cultural processes. They suggest that among extant organisms, nonhuman primates are phylogenetically the closest relatives humans have where, compared to other non-primate mammals of similar body mass, nonhuman primates exhibit large brains, long prereproductive developmental phases, complexity in parental care, long periods of adolescent sterility, long interbirth intervals, and generally long lifespans. In identifying the factor(s) which make nonhuman primates an appropriate model for the study of human behavioural development, Pereira and Altmann (1985) emphasize the long prereproductive period of development in that both human and nonhuman primates rely on extensive learning abilities during ontogeny to acquire the skills necessary to function as a competent and flexible adult.

1.2.3 INFANCY AND DEVELOPMENT: BABOON STUDIES

Previous baboon studies that have focused *primarily* on infants and their development (Olive baboons *Papio anubis*: Nash

1978; Nicolson 1982; Marsh 1992; Yellow baboons *Papio cynocephalus*: Altmann 1980; S. Altmann 1991; Rhine *et al* 1984, 1985) are relatively few given the extent to which baboons, their behaviour and socioecology, have been researched (see above). However, infants have, additionally, been studied in relation to, or as part of, research investigating wider issues which concern baboons (Bolwig 1980; Busse 1984, Busse and Hamilton 1981; Cheney 1978; Oliver and Lee 1978; Owens 1975; Packer 1980; Post *et al* 1980; Ransom and Rowell 1972; Rowell *et al* 1968; Stein 1981, 1984; Stein and Stacey 1981; Strum 1984; Young and Bramblett 1977; Young and Hankins 1979). While each of the latter set of studies have documented, in some way, particular aspects of infant life or behaviour, there have been limited systematic attempts to integrate individual domains of behaviour, and thus to provide a comprehensive profile on infant developmental trajectories toward competence. The study which is reported in the pages which follow attempts to do this and, in doing so, will contrast the findings of the present study with those of previous studies which have been referred to in this section.

1.3 STRUCTURE OF THIS THESIS

In this thesis I consider the developmental trajectories toward independence of baboon infants (*Papio cynocephalus ursinus*) inhabiting the Drakensberg Mountains of Natal Province, South Africa. Descriptions of the study area, the study animals, and the methodology used in the study are provided in CHAPTER 2.

In CHAPTER 3 I consider the period of infancy from the perspective of a baboon mother. I will argue that the reproductive events of females in this population are constrained by ecological conditions in terms of the timing of conceptions and hence births, and that this has consequences for the provision of care for infants. The ultimate expression of these consequences is found in the length of the interval between successive births which, it will be shown for the Drakensberg, compares unfavourably with other baboon study sites throughout Africa. However, extended care of infants also reduces the probability of infant mortality. Interbirth intervals and infant mortality are considered in terms of strategies of parental care.

CHAPTER 4 describes the development of independent feeding for the Drakensberg infants. Data will be presented detailing the relationship between dependent feeding (suckling) and independent feeding as alternate strategies. I will argue that the timing of the infant transition from a dependent diet to an independent one is contingent on the availability in the habitat of appropriate infant foods which, in the Drakensberg, are seasonally available. Attention will also be given to the concept of weaning. An attempt is made to delineate the weaning period as measured by rates in decline on various measures of maternal investment. The lack of any consistency across the measures for the mother-infant pairs in this study lends support for a reinterpretation of the way in which weaning has traditionally been thought to promote infant independence.

CHAPTER 5 continues with the description of the development of infant independence. Where the previous chapter focused primarily on the development of independent feeding, this chapter describes changes in infant activity with increasing age. Thus, emphasis is placed on the expanding social world of infants which results from increased mobility with the transition from being dependent on mothers for transport to independent locomotion. Changes in infant activity budgets are presented in terms of behavioural development.

In CHAPTER 6 I consider the nature of the relationships adult males had with infants. While these relationships are not, in this thesis, claimed to be directly related to any specific aspect of infant development, they are presented here to assess hypotheses in the literature that suggest that male associations with infants serve to enhance male mating opportunities. They are also presented here to demonstrate that infants, as an age class, are able to influence in some way the nature of interactions males have with one another. While limited by conceptual and methodological short-comings during the course of data collection, and hence working from an incomplete data set, the nature and extent of male interactions with infants observed during the course of this study do not appear to support the hypothetical predictions, although no firm conclusions are supported by the data.

In CHAPTER 7 I briefly recap on the major findings of the study. These are contextualized within the aims of the study as it was originally conceived. I propose that the study, as it was intended, would not have been possible without the findings of the present study becoming known. Directions for future research are proposed.

CHAPTER 2

STUDY SITE, STUDY ANIMALS, METHODS

2.1. STUDY SITE

This study was conducted in the Cathedral Peak Reserve [CPR], a protected area of approximately 33000 Ha in the Drakensberg Mountains of Natal Province, South Africa (latitude 29°00' S; 29°15' E). Additional data, where specified, are taken from a previous study of Drakensberg baboons conducted in the Giants Castle Game Reserve [GCGR] (see 2.2.1 below). A detailed description of GCGR has been provided elsewhere (Whiten *et al* 1987).

2.1.1. GENERAL DESCRIPTION OF THE STUDY SITE

The Drakensberg Mountains form part of the Great Escarpment at the eastern edge of the interior plateau of Southern Africa which extends for approximately 960km from the eastern Cape Province to the northern Transvaal Province (Killick 1963). The Natal section of the Drakensberg Mountain range extends for about 180 km, forming the western boundary of Natal with Lesotho (Pearse 1978). The location of the Natal Drakensberg, including the position of the CPR and GCGR within the Drakensberg Conservation region, is presented in Figure 1.

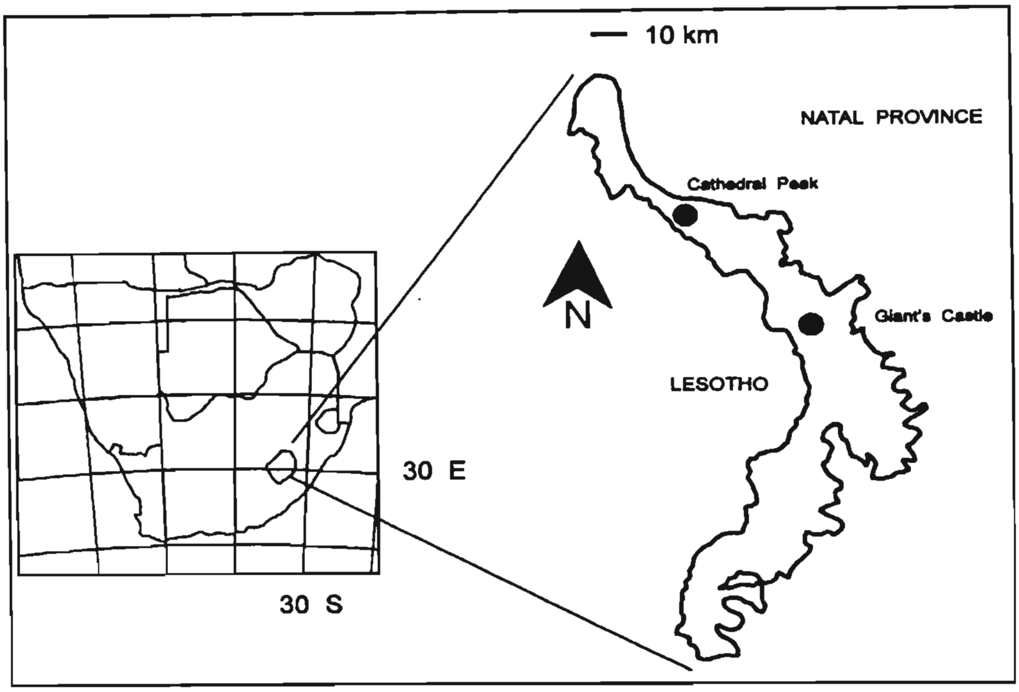


Figure 1: Location of the Natal section of the Drakensberg Mountain range. The position within the mountain range of Cathedral Peak Reserve and Giants Castle Game Reserve is also shown.

Geologically, the Natal Drakensberg is characterized by the distinction made between what are termed the 'little berg' and the 'main (or high) berg'. The little berg, described by Killick as ".... a terrace consisting of finger-like spurs ...." lies between 1300m (a.s.l) and 2000m (a.s.l), and is comprised primarily of sandstone formations. Superimposed on the little berg is the main berg: - a basalt wall rising steeply from 2000m (a.s.l) to c. 3400m (a.s.l).

The vegetation of the Drakensberg Mountains comprises three distinct belts (Killick 1963) :-

The montane belt (1280m - 1829m) extends from the valley floors to the summit of the little berg;

The subalpine belt (1829m - 2865m) extends from the summit of the little berg to just below the summit of the main berg;
The alpine belt (2866m - c. 3353m) occupies a narrow strip at the edge of the Drakensberg escarpment.

Given that the study animals ranged predominantly in the montane belt, making only occasional excursions into the low altitudes of the subalpine belt during the summer months, only the vegetation of the montane belt will be considered here. (For details on the other two vegetation belts, see Killick 1963)

2.1.2 THE FAUNA AND FLORA OF THE MONTANE BELT

2.1.2.1. FLORA OF THE MONTANE BELT

Killick (1963) noted that, at Cathedral Peak, the greater part of this vegetation belt is occupied by tussock grassland, primarily *Themeda triandra*, although *Hyparrhenia* grassland and *Miscanthidium-Cymbopogon* grassland are also present. Species of *Protea* are scattered throughout the grassland forming *Protea* savannah. Further, the woody communities that do occur are Boulder-Bed scrub, Streambank scrub, *Leucosidia-Buddleia* scrub, *Greyia-Cussonia* associes, Cliff scrub, *Widdringtonia dracomontana* Consocies and the climax community of the Montane belt, *Podocarpus latifolius* forest which is generally confined to sheltered gorges.

2.1.2.2 FAUNA OF THE MONTANE BELT

Baboons share the CPR with a number of species of ungulates. Killick (1963) reported the occurrence of the grey rhebuck (*Pelaea capreolus*), the common reedbuck (*Redunca fulvorufula*), the duiker (*Sylvicapra grimmia burchellii*), Cape klipspringer (*Oreotragus oreotragus oreotragus*), and the Cape bushbuck (*Tragelaphus scriptus sylvaticus*). Other small mammals present in the CPR listed by Killick (1963) include the porcupine (*Hystrix africae-australis*), the dassie (*Procavia capensis*), and the hare (*Lepus* spp. and *Pronolagus* spp.). As reported by Whiten *et al* (1987), no serious predators pose problems for the Drakensberg baboons. Leopards (*Panthera pardus*) have neither been sighted nor been recorded as being in the reserve for a number of years. Small predators which may pose a *potential*, albeit minimal, threat to immature animals include black eagle (*Aquila verrauxi*), black-backed jackal (*Canis mesomalis*), caracal (*Felis caracal*), and serval (*Felis serval*).

2.1.3 THE CLIMATE OF CATHEDRAL PEAK

The Drakensberg Mountains, including Cathedral Peak, experience extreme climatic seasonal variation. Rainfall (Figure 3) is largely confined to the summer months when temperatures are at their highest (Figure 2). Winter temperatures, which regularly drop below 0°C during the nighttime, thus coincide with the dry season. The mean temperature for the summer months (16.83°C) is significantly higher than the mean temperature for the winter months (11.11°C) ($t = 8.92$, $p < 0.05$: average monthly summer (Nov. -

March) range:- 15.58^{o}C - 18.95^{o}C; average monthly winter (May - August) range:- 9.10^{o}C - 13.41^{o}C), while rain falls significantly more during the summer months than during the winter months (t = 7.81, $p < 0.05$: average monthly winter range:- 1.4mm - 7.6mm; average monthly summer range:- 109.5mm - 212mm).

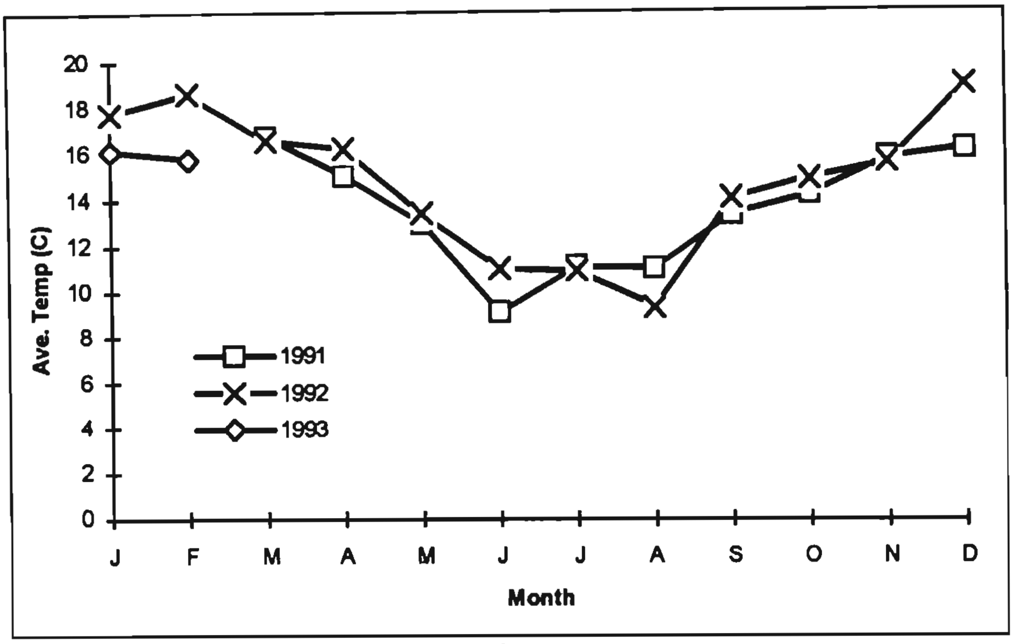
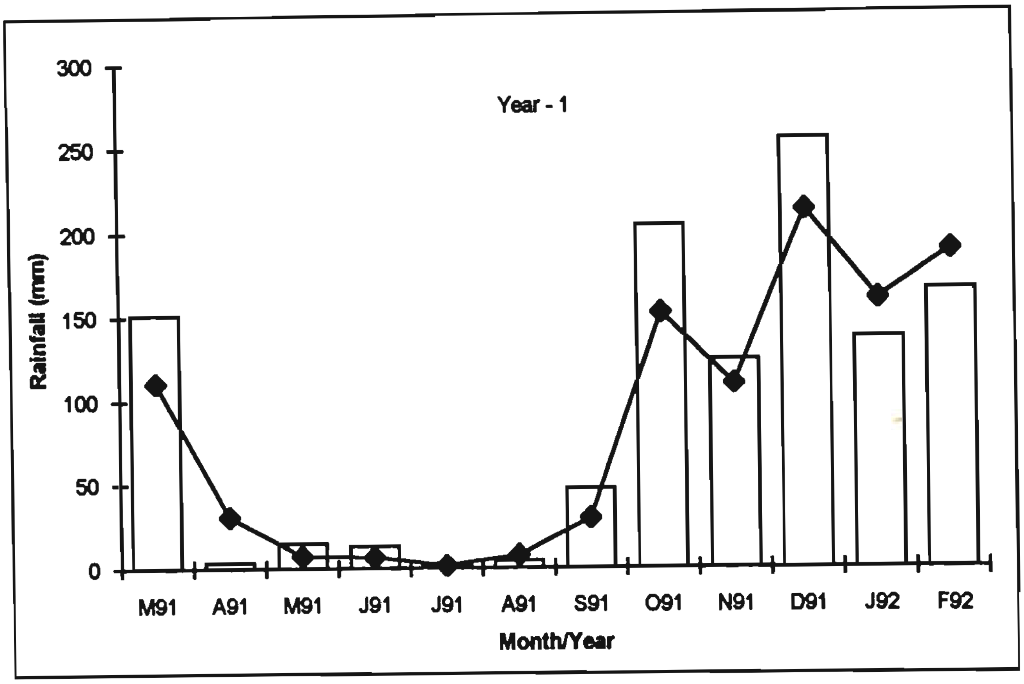


Figure 2: Average monthly temperatures (^{o}C) at Cathedral Peak:- March 1991 - February 1993.

During the first year of the study, the amount of rain that fell per month tended to be above the average for that month (Figure 3 below). Over the first year, 1120.8mm of rain fell as opposed to the yearly average of 1015.8mm recorded during the time of the study. However, from January 1992, the measured rainfall tended to be less that the average for each month, including three months during 1992 when zero rainfall was recorded. During the second year, only 910.4mm of rainfall was recorded as opposed to the yearly average for the entire study period of 1015.8mm.



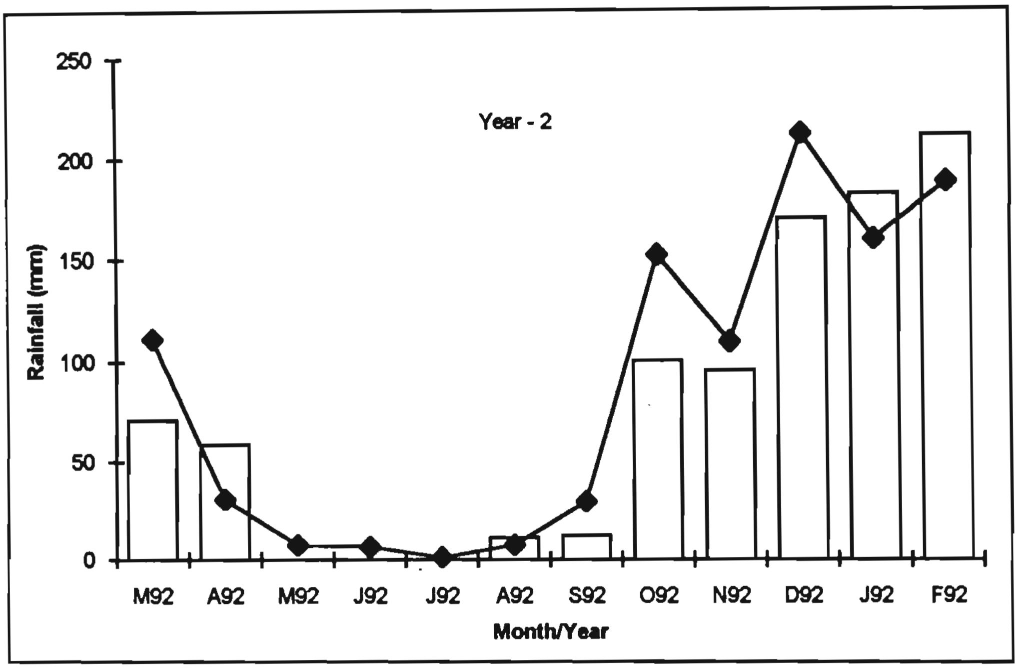


Figure 3: Monthly rainfall (mm) at Cathedral Peak during the first year of this study (top graph) and during the second year of the study (bottom graph). Also plotted is the average monthly rainfall for each month (line graph). Average rainfall is for the period covered by the fieldwork for this study (March 1991 - February 1993). Rainfall data made available by Dr. C. Everson, CSIR FORESTEK, Cathedral Peak.

It was predominantly during the months of below average rainfall (Figure 3, bottom graph) that data were collected on the baboon mothers and infants reported in this study (see Table 3 end of this chapter for schedule of month of year for each infant's monthly age).

2.2 STUDY ANIMALS: THE DRAKENSBERG BABOONS

2.2.1. OVERVIEW OF THE DRAKENSBERG BABOON POPULATION

Given that the Natal Drakensberg conservation area encloses an area of appoximately 3016 km^2 and, on the basis of a working definition of 2.5 animals/km^2 (see Henzi and Lycett 1995 for relevant calculations), it is estimated that the Drakensberg baboon population comprises 7540 animals living in approximately 335 troops (Henzi and Lycett 1995). The mean troop size is 22.49 animals (N=61, median = 22; range: 4-41; Henzi and Lycett 1995). The adult sex ratio within troops is 2.07 females per male, and this remains constant across troop size (N=29, Henzi and Lycett 1995). The ratio of immature animals to adult females (1.17) is representative of the range of troop sizes in the Drakensberg (Henzi and Lycett 1995).

While the Cathedral Peak baboon population has not previously been studied, research has been conducted on Drakensberg baboons at Giants Castle Game Reserve (GCGR) (29^{o}S, 29^{o}E), approximately 45km south of Cathedral Peak

(Byrne, Whiten and Henzi 1989, 1990a,b, Byrne, Whiten, Henzi and McCulloch 1993; Henzi, Dyson and Deenik 1990; Henzi, Byrne and Whiten 1992; Whiten, Byrne and Henzi 1987).

The earlier work on the Drakensberg baboons conducted at GCGR reported a number of distinctive features of this mountain baboon population. Foremost amongst these were low density of animals, small group size, and a decline in troop size with increasing elevation (Whiten *et al*, 1987; Byrne *et al*, 1987). The latter finding reported by Whiten *et al* (1987) does not, however, appear to be a consistent phenomenon over time (Henzi and Lycett 1995). A feature of this baboon population which *does* appear to remain constant over time, is population size. Henzi *et al* (1990) and Henzi and Lycett (1995) report that population growth, over time, appears to be in equilibrium for the period over which census counts have been made (1981 - 1992).

2.2.2 THE FOREST TROOP

Given that the aim of the study was to investigate the trajectories of infant development to independence or competence, the primary criterion on which troop selection was made related to the absence of dependent infants at the initiation of the study. That is, a troop in which the birth of infants could be anticipated was essential. Additionally, a troop which could be considered representative of the Drakensberg baboon population as a whole was a factor.

The composition of the study troop, at the initiation of this study, is presented in Table 1; At that time the Forest Troop (FT) was slightly larger in size (24 animals) than the average Drakensberg baboon troop. The adult sex ratio (1 : 2.25) was average for this baboon population, as was the ratio of immature animals to adult females (1.2). Thus the FT could be considered, certainly in terms of demographic breakdown, to be a representative Drakensberg baboon troop. In terms of the number of infants, at the initiation of the study, the FT had only 2 who were aged at 9-11 months. Accordingly, at least 7 of the females in the troop may have been expected to give birth during the course of the study.

Number of adult males	4
Number of adult females	9
Number of old immatures	1
Number of immatures	8
Number of infants (< 1 year)	2
TOTAL ANIMALS	**24**

Table 1: Composition of the Forest Troop, March 1991

During the course of the study the following demographic events occurred;

July 1991	Infant (PI) disappeared: cause unknown
September 1991	Infant (G2) birth - male
October 1991	Infant (F2) birth - male
December 1991	Infant (J2) birth - male
January 1992	Infant (C2) birth - female
March 1992	Infant (R2) birth - female
July 1992	Adult female (AL) disappeared. Death suspected[1]

Thus, at the end of data collection (February 1993) the FT comprised 27 animals.

Habituation of the FT began in April 1991 although data reported in this study cover the period July 1991 - February 1993. That is, data are considered for analysis only from such time as (a) the animals no longer appeared to be significantly affected by the presence of observers, and (b) most of the troop members could be individually identified.

2.2.3 THE HOUSE TROOP, THE HIGH TROOP, AND THE LOW TROOP

Data on the number and timing of births from additional troops at both Giants Castle and Cathedral Peak Reserves have been included in Chapter 3. Each of these troops were, either during this study or during the previous research conducted at Giants Castle, regularly monitored for the presence of new infants. Data on births were included only if a particular troop

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[1] Prior to the disappearance of this female, she was badly wounded on one of her wrists. In the weeks before she disappeared, she was not able to use this hand in any way, and appeared to be struggling to keep up during troop movements. Also, from her general body condition, she appeared to be very old.

had been regularly monitored for a full calender year, or multiples thereof.

The House Troop at Cathedral Peak was accurately counted for the first time during September 1991 (see A.R. Weingrill, in prep., for a detailed description of the demographic composition of this troop). The troop was encountered each month following this initial count, and any births were recorded. Habitutation of this troop began during April 1993, and they have been under constant observation since that date. Thus data on births for this troop are available for 3 calender years (09.91 - 09.94). At the time of the initial count the troop comprised 27 animals. There was a single black infant in the troop at the time, but its month of birth could not be accurately estimated, and so was excluded from the total number of births recorded for the Drakensberg.

The High and Low troops at Giants Castle Reserve were initially studied over the period August 1982 through January 1984 (Byrne, Whiten and Henzi 1987, 1990*a,b*, Byrne, Whiten, Henzi and McCulloch 1993; Henzi, Dyson and Deenik 1990; Henzi, Byrne and Whiten 1992; Whiten, Byrne and Henzi 1987), with the Low troop having been regularly monitored since that time (Henzi, Dyson and Deenik 1990; Henzi, unpubl. data).

The number of births that each troop contributed to the data set to be presented in Chapter 3 is presented in Table 2. Note that also presented in Table 2 are births for the Forest Troop at

Cathedral Peak that occured after the end of the present study, and so were not included in the description of the troop.

House Troop (CPR)	Forest Troop (CPR)	High & Low Troops (GCGR)
1 x Oct. 92	2 x Nov. 93	1 x Sep. 83
1 x Dec. 92	1 x Dec. 93	1 x Oct. 83
1 x June 93	1 x Mar. 94	1 x Nov. 83
1 x July 93		1 x Feb.
1 x Oct. 93		1 x Sep.
1 x Nov. 93		
1 x Jan. 94		
1 x Feb. 94		

Figure 2: Number of births, and month of birth, for infants in the House and Forest Troops (Cathedral Peak), and the High and Low Troops at Giants Castle. Births for the Forest Troop are those which were noted during the course of ongoing population monitoring after the completion of this study.

2.3 METHODS

The animals were followed on foot at distances of approximately 15m - 30m, depending on the troop's topographical position. The animals were followed for a minimum of five full days a month, and thereafter as often as possible from morning sleeping site to evening sleeping site. The topography of the DM affords excellent observation conditions:- there are few trees in the habitat while the montane belt is characterized by short grassland (see Fig.1 in Whiten *et al* 1987). Data were collected using *Zeiss* 8 x 30 binoculars and were recorded directly onto a pre-determined check-sheet.

2.3.1 SCAN SAMPLING

Scan sampling (Altmann 1974) of the FT took place every 30 minutes of the day while they were being followed. A total of 2678 scan samples were collected, representing approximately 1340 hours of data collection. The number of scan samples for each infant, at each monthly age, are presented in Table 3 (end of this chapter). An average of approximately 69 hours of scan sample data, per infant per month, were collected. The following data were collected using this sampling technique:

(1) the current activity, at the time of the sample, of all observable animals in the troop where, following Altmann (1980), the time budget of mature animals is regarding as being comprised primarily of four standard behaviour categories:-

(1.1) <u>Feeding</u> (or foraging) related to ongoing activity during which an animal was engaged in eating food items, or actively engaged in the harvesting or extraction of food items.

(1.2) An animal was considered to be <u>resting</u> when it was not engaged in activity. That is, when animals were stationary, either seated or lying down, and were not obviously engaging in any of the other behaviour categories.

(1.3) <u>Social</u> activity referred, primarily for adult animals, to grooming interactions. For juvenile and infant animals, but also for adult animals when observed, social activity additionally included <u>social play</u> where an individual was playing with another individual(s).

(1.4) Given that the Drakensberg baboons "travel-feed" (Whiten *et al* 1987), animals were considered to be moving when they were locomoting without stopping to feed. That is, the move category reported on here is close to the move category for other studies in that it excludes movement by the Drakensberg baboons which includes feeding. The Drakensberg baboons tend to feed as they slowly walk through the habitat.

Thus in terms of these definitions, the four categories of behaviour utilized in this study were mutually exclusive.

Insofar as the five infants in the study are concerned, specific distinctions were made with regard to three of the the four primary behaviour categories. Thus:

(1.5) when infants were observed to be feeding, the item they were feeding on at that time was specified (i.e. suckling, grass, leaves, digging);
(1.6) when infants were recorded as moving, it was noted whether they were being carried either dorsally or ventrally, or whether they were moving independently;
(1.7) when an infant was recorded as resting, it was specified whether they were resting in or out of contact with their mothers, as well as whether they were resting in contact with an adult male, and if so, the identity of the male.

(2) the spread of the troop (distance between the two furthest animals in the troop along the longest axis);

(3) the distance, in metres, between adult males. For each scan sample, a focal adult male was designated and the distances between that male and each of the other adult males, if visible, were recorded;

(4) the distance, in metres, between adult males and adult females. As with the distance between adult males, a focal male was designated and the distances between that male and the six adult females closest to him, were recorded. The designated male was the same as for the male-male distances within a scan sample;

(5) the distance, in metres, between adult females, where a focal female was designated and the distances between that female and the six closest adult females to her, were recorded.

Further, the location of the troop at the time of sampling was recorded on a 1:20000 map. The route taken by the troop between scan points was recorded as accurately as possible.

2.3.2 AD LIBITUM DATA

Data that were not easily incorporated into the sampling check-sheet were added as ad libitum data once the scan sample had been completed, or if the behaviour/interaction occurred at a time inbetween scheduled samples. Data collected in this manner included:

(1) the identity (as an age-sex class) of any animal with which an infant played;

(2) the context within which adult male-infant interactions took place (e.g. agonistic buffering, caretaking, infant solicitation for support);

(3) grooming interactions (e.g. initiator, reciprocation, length of grooming bout, identity of animal who breaks grooming bout);

(4) The responsibility within the mother-infant dyad for breaking and re-initiating contact when such contact was broken. That is, during the first few months post-partum when infants tend to cling to mothers, and mothers are restrictive of infant movement, it was recorded whether it was the infant or the mother that increased the spatial distance between the two members of the dyad, and conversely, which of the two closed the spatial gap between the two. After a few months when infants began to move about the environment independently, 'contact' was redefined and did not necessarily refer to physical contact between mother and infant. 'Contact', at this point, referred also to instances when mother and infant were engaged in ongoing activity, but doing so within a metre of each other; contact was considered broken if the spatial distance between the two was increased by one of the dyad.

2.3.3 DATA PRESENTATION AND ANALYSIS

Data have been pooled according to calender months. For the infants, data have been pooled according to monthly age. Similarly, data on maternal activity (Chapter 3) have been pooled by month according to the monthly age of infants. The percentage time expressed for behaviours are weighted as a proportion of the total number of scans available in each month. Data were entered and sorted using the DBXL programme (WordTech Systems, Diamond Release ver. 1.3). All statistical analyses were conducted using the STATGRAPHICS programme (STSC, ver.5 1991). Results were accepted as significant at the 95% level unless otherwise specified.

INFANT	1991				1992												1993	
	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
G2	**B**	1 *144*	2 *138*	3 *117*	4 *162*	5 *154*	6 *142*	7 *151*	8 *157*	9 *132*	10 *126*	11 *156*	12 *172*	13 *144*	14 *168*	15 *94*	16 *124*	17 *168*
F2		**B**	1 *154*	2 *128*	3 *144*	4 *158*	5 *150*	6 *122*	7 *138*	8 *141*	9 *133*	10 *127*	11 *163*	12 *171*	13 *153*	14 *102*	15 *138*	16 *148*
J2				**B**	1 *126*	2 *139*	3 *136*	4 *144*	5 *121*	6 *116*	7 *127*	8 *147*	9 *157*	10 *148*	11 *159*	12 *86*	13 *125*	14 *157*
C2					**B**	1 *148*	2 *153*	3 *116*	4 *124*	5 *118*	6 *133*	7 *138*	8 *149*	9 *131*	10 *144*	11 *110*	12 *136*	13 *123*
R2							**B**	1 *164*	2 *151*	3 *127*	4 *130*	5 *134*	6 *142*	7 *119*	8 *133*	9 *108*	10 *138*	11 *148*

Table 3: Month of birth (**B**) for each infant in the present study, and month of year corresponding to monthly age for each infant. Figures in italics represent the number of scan samples for each infant, per month.

CHAPTER 3

THE ECOLOGICAL CONTEXT OF MOTHERHOOD

3.1. INTRODUCTION

For primates, as for most other mammalian orders, motherhood occurs within the context of a complex physical and social environment. In terms of the physical environment, mothers are responsible for ensuring the safety, survival, and nutritional requirements not only of themselves but also those of their dependent offspring. Simultaneously, as noted by Altmann (1980), at parturition the social life of a female baboon is dramatically changed. Group-living mothers must cope with, and function within, the complexities which arise from living in a social system which is usually comprised of a number of adult females and their offspring, and one or more adult males (Altmann 1984), where mother and infant become a major focus of interest within the group (Altmann 1980; see Lee 1983d).

This chapter will focus on infancy from the perspective of a mother. That is, consideration is to be given to the costs associated with motherhood which in the Drakensberg, it will be argued, are considerable, and that mothers should attempt to minimize these costs. In this regard attention will be given to seasonality of birth which has been regarded as an important means whereby the costs associated with motherhood, for non-seasonally breeding species, might be reduced. This follows the proposition that females might reduce the costs associated with reproduction by timing reproductive events such that they coincide with 'optimal' ecological conditions. Specifically, consideration is to be given to the relationship between varying ecological conditions and the timing of conceptions and birth, and the relationships these have to the quality and quantity of available nutrition especially insofar as the timing of the development of independent feeding for infants is concerned.

Following this it will be shown how the presence of a dependent offspring affects the 'normal behaviour' of baboon females such that constraints are imposed on their activity budgets.

3.2 PARENTAL BEHAVIOUR AND THE COSTS OF REPRODUCTION

Parental behaviour, according to Blurton Jones (1993), evolved because it promotes the reproductive success of the parent(s). Daly and Wilson (1983) propose that the primary functions of parental care are protection of the young from predators as well as from environmental demands such as temperature shock. The form that parental behaviour takes will be selected for in accordance with conditions whereby the individual can leave behind the greatest number of descendants. In this regard, three forms of parental behaviour are of particular importance in terms of the goals each promotes. The first relates to production where parent(s) behave toward a particular offspring in such a way that the parent's ability to produce more children is enhanced (Blurton Jones 1993). Secondly, parents may promote survivorship by countering threats to the infant's survival (*e.g.* by preventing malnutrition, disease, predation, and accidents). A parent's reproductive success will, thirdly, be enhanced through parental behaviour which promotes offspring reproductive success; this third strategy is most commonly associated with humans in that it relates primarily to teaching children, and the accumulation of resources which will promote the offspring's ability to compete for mates (Blurton Jones 1993).

The form parental behaviour takes, and the goal which it promotes -(*vis-á-vis* the three outlined above)- will probably be strongly guided by prevailing ecological conditions within the habitat. Among non-human primates, for example, parental behaviour which promotes *survivorship* will probably be more appropriate in ecologically marginal and impoverished habitats where a *production* strategy may result in high infant mortality. Essentially, parental behaviour directed toward investing in, and increasing the probable survival of each successive infant may, in such (ecological) circumstances, be *as* successful a strategy as that directed toward maximizing production but which carries with it the possibility of high infant mortality. To this end, the benefits derived from a particular form of parental behaviour must be considered in relation to the costs not only of that strategy, but also in contrast to the possible benefits derived from pursuing a different strategy.

3.2.1. THE COSTS OF REPRODUCTION: LACTATION

The costs associated with reproduction are, for females, considerable. Maternal care in mammals is intensive in that it involves both placental nurture prior to birth and suckling after birth (Daly and Wilson 1983). Pereira and Altmann (1985) have argued that for female baboons, relative reproductive success is primarily dependent on a female's success in providing sufficient nutrition to support herself and her offspring through successive periods of gestation and lactation. Given that primates generally produce only one infant at a time, and given further that such offspring are born helpless and thus experience a period of prolonged dependency, ensuring that the infant develops into a functional adult represents a major maternal investment (Altmann, Hausfater and Altmann 1988; Dunbar 1988; Martin 1990). Thus, in order to attain high reproductive success, females should not only conceive offspring but, additionally, should ensure that such conceptions result in offspring *that survive to maturity and reproduce* (Altmann *et al* 1988). The most commonly cited *direct* costs incurred by females in this regard relate to the provision of infant nutritional and locomotor requirements.

Lactation has particular benefits over placental transfer as a means of transferring energy from mother to offspring (Pond 1977). It is a highly efficient means of energy transfer, and it acts as a buffer for young dependent offspring against fluctuations in the quantity and quality of food in the habitat (Pond 1977, but see Portman 1970 for an alternate view as regards the former). Additionally, young inexperienced animals do not of necessity have to gather their own food items which allows for a more specialized adult diet and feeding adaptations while also ensuring that immature animals do not have to compete directly with adult animals for food until they are large and experienced enough to gather food efficiently (Pond 1977; *cited in* Nicolson 1982). However, lactation as a means of providing nutrition is not without its costs. Dunbar and Dunbar (1988) suggest that lactation is the most energetically expensive component of reproduction. During the period of infant nutritional dependence mothers have to provide not only the nutrients required to fuel infant activity but also those for infant growth. Similarly Martin (1984) notes that through lactation the mother's milk should transfer enough energy to sustain the infant's entire basal metabolism, thermoregulation, growth and locomotor activity.

Reporting on an experimental study on hooded rats (*Rattus norvegicus*), Smith (1991) demonstrated that as the energetic costs of lactation increased with pup age, mothers eventually lost body condition which, she argued, affected their ability to provide milk for their young. Similarly, in an experimental study on weaning in the domestic cat (*Felis catus*), Martin (1986) reported a tendency for maternal weight to drop during the first five weeks of nursing. The mothers in his study did, however, recover this weight loss after the fifth week which coincided with the age at which the kittens were first observed to feed for themselves. A substantial energy cost exerted on females through the production of milk has also been reported for baboons. It has been estimated that female energy requirements are increased by 20 to 50% during lactation (Portman 1970; Buss and Voss 1971; *cited in* Nicolson 1982), which is supported by observations that lactating females feed at significantly greater rates than do non-lactating females (Olive baboons, *Papio anubis*: Barton 1990; Saddle-back tamarins, *Saguinus fuscicollis*: Goldizen *et al* 1988). Further, testing Altmann's (1980) prediction that lactating female baboons lose weight while nursing dependent offspring, Bercovitch (1987a) found that the body weight of female olive baboons - in a natural habitat - varied with reproductive condition. Lactating females weighed, on average, 7% less than females that were cycling and approximately 10% less than pregnant females. However, and paradoxically, Rose (1977) and Post *et al* (1980) have both reported that females with young infants spent more time feeding than did other adults. Interpreting this Bercovitch (1987a) posits that lactating females require more food than do other adults in order to maintain body-condition for milk-production and the provision of essential minerals for dependent offspring while, at the same time, replenishing bodily resources which are depleted in the course of nursing (Pond 1977; Williams 1978; *cited in* Bercovitch 1987a). Bercovitch concludes that the apparent paradox of having to eat more whilst losing weight is indicative of the substantial energy cost to lactation; he hypothesizes that the resultant weight loss may have consequences for the timing of weaning in that weight loss resulting from lactation adversely influences the production of milk.

Given these costs to mothers, it might be expected that an optimal time for birth and/or subsequent weaning will have been selected for. That is, it might be expected that selection has operated to favour the timing of birth and/or the development of infant independence such that the costs associated with female reproduction are minimized. Thus Butynski (1988), noting that seasonal reproduction is part of a species' reproductive strategy, suggests that, in theory, natural selection should favour individuals whose reproductive events coincide with varying environmental conditions such that, for example, births occur at the optimal time for the survival of both mother and infant.

3.3 BIRTH SEASONALITY AND BIRTH CLUSTERING

While a number of factors, including photoperiod, rainfall patterns, vegetation cycles, predator avoidance, and social facilitation have been associated with, or have been regarded as important proximate mechanisms which trigger either birth or breeding synchrony (Daly and Wilson 1983; Small and Smith 1986; Melnick and Pearl 1987), food availability has been considered the key factor (Bronson 1989, but see Boinski 1987).

There are, according to Bercovitch and Harding (1994), certain benefits which are derived for species which show clear seasonality or clustering of births at certain points during the year, and which may not accrue to non-seasonal breeding species. In terms of both the direct and indirect benefits for female reproductive success, it has been argued that seasonality might favour infant survival through a reduced risk of predation (Small and Smith 1986; Boinski 1987; Martin 1990), an increase in the number of nonmaternal caretakers (Kavanagh 1983; Small and Smith 1986), and a maximization in the availability of food at specific phases in either infant development or maternal reproductive condition (Altmann 1980; Butynski 1983; Small and Smith 1986; Goldizen *et al* 1988; van Schaik and van Noordwijk 1985; Lee 1987; Martin 1990). Insofar as the latter point is concerned, it has been argued that females living in habitats which experience abrupt transitions between high and low quality food might be constrained in the timing of their birth seasons (Lee 1987; Hauser and Fairbanks 1988; Hauser *in press*). Thus Bercovitch and Harding (1994), noting the advantages of reproductive events which occur during periods of greater food availability, suggest that (a) greater food availability during lactation reduces the metabolic costs associated with nursing an offspring, (b) increases the probability of conception during menstrual cycling and (c) facilitates the storage of body reserves for gestation and lactation.

Among the *Cercopithecinae*, all species with the exception of the grey-cheeked mangabey (*Cercocebus albigena*) and baboons of the genus *Papio* show distinct birth peaks and/or seasonality[1] (Melnick and Pearl 1987). This reported nonseasonality among baboons is confirmed by Bercovitch and

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[1] Butynski (1988), citing Gautier-Hion (*unpublished data*), does however report a birth peak for *Cercocebus albigena* (Table 16.3, p. 298).

Harding (1994). Reviewing data from fourteen baboon studies conducted throughout Africa, they found no evidence for birth seasonality and no clear consistency in birth peaks or clustering across the sites (Olive baboons: *P.anubis:* Laikipia, Kenya:- Berger 1972; Gilgil:- Nicolson 1982, Bercovitch and Harding 1994; Gombe:- Packer 1979a, Ransom 1981; Queen Elizabeth National Park, Uganda:- Rowell 1966; Yellow baboons: *P.cynocephalus:* Amboseli:- Altmann 1980; Amboseli and Nairobi Park: DeVore and Hall 1965; Mikumi:- Rasmussen 1980; Rhine *et al* 1988, 1989, Wasser and Starling 1988; Chacma baboons: *P.cynocephalus ursinus:* Suikerbosrand:- Anderson 1982; Cape Point:- Davidge 1978 Hall 1963; Honnet Reserve (South Africa): Saayman 1970). Non-seasonality of birth is also reported for chacma baboons studied at Mkuzi Game Reserve, South Africa (Henzi *et al*, under review *b*) and olive baboons in Chololo, Kenya (Marsh *pers. comm.*).

Following Bronson (1989), the apparent lack of both conception- and birth-seasonality among baboons is explained with reference to the "pronounced dietary diversity" (Bercovitch and Harding, 1994 p.120) of baboons. They argue that *if* the availability of food influences birth periodicity and *if* dietary diversity increases effective food availability, then birth periodicity should be less constrained under conditions of dietary diversity. Essentially they suggest that the eclectic diet of baboons acts as a buffer against any seasonal variability in the supply of specific food items, which allows for greater opportunism in the timing of reproductive events. This is in contrast to highly specific feeders which must rely on the seasonal occurrence of certain foods and hence will probably reproduce only when such foods are available (Bronson 1989). However, despite finding no clear and consistent evidence for birth-seasonality among savanna baboons, Bercovitch and Harding suggest that where birth-peaks *do* occur, they are likely to be a secondary consequence of a peak in conceptions during months of relative food abundance. Thus, "... birth peaks among baboons [are] probably a secondary consequence of conception peaks resulting from temporarily enhanced food availability" (Bercovitch and Harding, 1994 p.120).

In the section which follows I demonstrate that births are seasonally clustered in the Drakensberg baboon population. Following this I assess the prediction made by Bercovitch and Harding (1994) that birth clustering, as a consequence of conception timing, is related to enhanced food availablity.

3.3.1. THE TIMING OF BIRTHS IN THE DRAKENSBERG MOUNTAINS

Data detailing the number of births, per month, from known troops in the Drakensberg Mountains are presented in Figure 4. The number of births that are presented are those that were recorded for the Forest Troop during the course of the present study, as well as those that were recorded during ongoing monitoring of the troop once the study had been completed. Births have also been included for the House Troop at Cathedral Peak, and from known troops at Giants Castle Game Reserve.

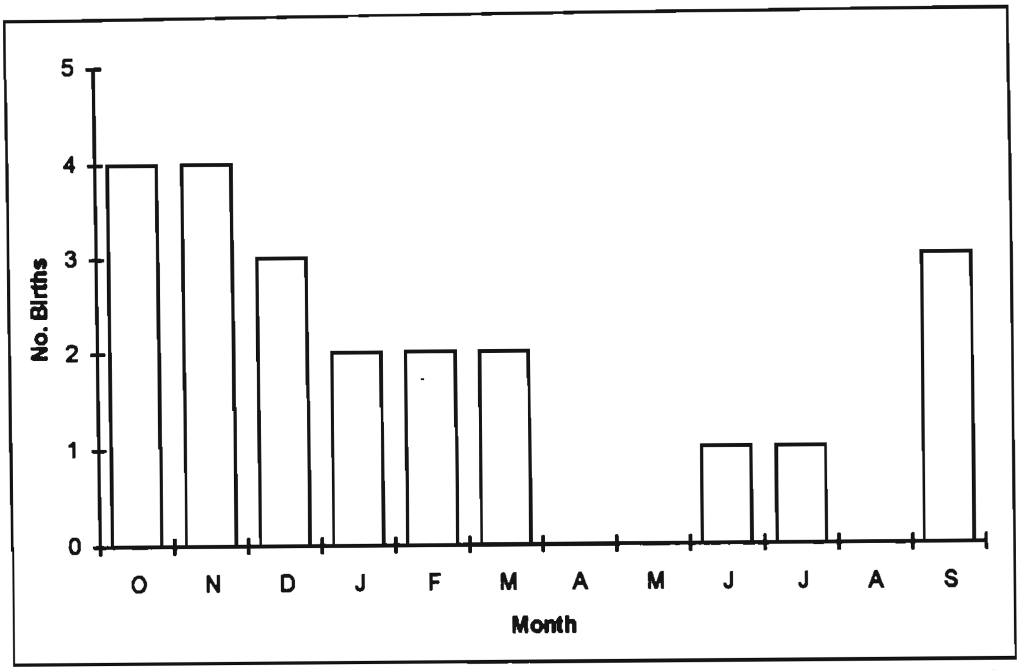

Figure 4: Number of births, by month of year, for known troops of baboons in the Drakensberg Mountains. Number of births taken from 4 study troops (GIANTS CASTLE: HIGH TROOP - monitored for 2 years; LOW TROOP - monitored for 1 year; CATHEDRAL PEAK: FOREST TROOP - monitored for 3 years; HOUSE TROOP: monitored for 3 years; Data sources:- Cathedral Peak - this study; ongoing population monitoring; Giants Castle - Henzi *unpubl. data*). Months are ordered according to the wet (October - March) and dry (April - September) seasons.

While sample size *(n = 22)* is too small to test for the distribution of births across each month of the year, significant differences are revealed if the distribution of births is partitioned between the wet (October - March) and dry (April - September) months. Births occurred disproportionately more during the wet months [N=17] than during the dry months [N=5] ($c^2 = 6.55$, df = 1, $p < 0.02$). No significant differences between the number of births during wet and dry months exist for other baboon study sites (Table 4).

Site	(No.Years)/ No. Infants	No.Wet Months (p.a)	2	Sig. Level	Source
Uganda	(2)/30	6	0.13	N.S. (0.1)	Rowell 1966
Gilgil[1]	(12)/159	4	0.11	N.S (0.1)	Nicolson 1982; Bercovitch & Harding 1994
Mkuzi	(3)/26	6	0.00	N.S (= 1)	Henzi et al, under review
Gombe[2]	(1)/17	7	0.29	N.S (0.59)	Ransom 1981
Amboseli[3]	(2)/16	7	0.46	N.S (0.1)	Altmann 1980

Table 4: Baboon study site with c^2 statistic testing for differences in the distribution of births between wet and dry months of the year. Expected values (number of births) for c^2 weighted according to number of wet months.

[1] Gilgil calculation based on combined data for Pumphouse and Eburru Cliffs Troops.

[2] Gombe data for one ecological year only (October 1967 - September 1968). Births during the remainder of Ransom's study (Oct. 1968 - April 1969) were excluded as their inclusion would have resulted in 2 wet seasons and 1 dry season. Partitioning between the wet and dry months as for Goodall (1986).

[3] Amboseli - number of wet months: *Interrains* (Altmann 1980) included in 'wet season' months.

3.3.2 CONCEPTIONS, BIRTHS, AND RAINFALL

In the absence of any systematic botanical analyses, rainfall is regarded as a useful indicator of ecological conditions (Altmann 1980; Dunbar 1988; Muruthi, Altmann and Altmann 1991; Barrett *et al* 1992; Henzi and Lycett 1995) in that it is a reliable index of both plant biomass and net plant productivity (Dunbar 1992).

For the Drakensberg Mountain baboons, there was a significant and positive relationship between rainfall in a given month and the number of births that occurred during that month ($r = 0.6514$, $p < 0.05$; Figure 5).

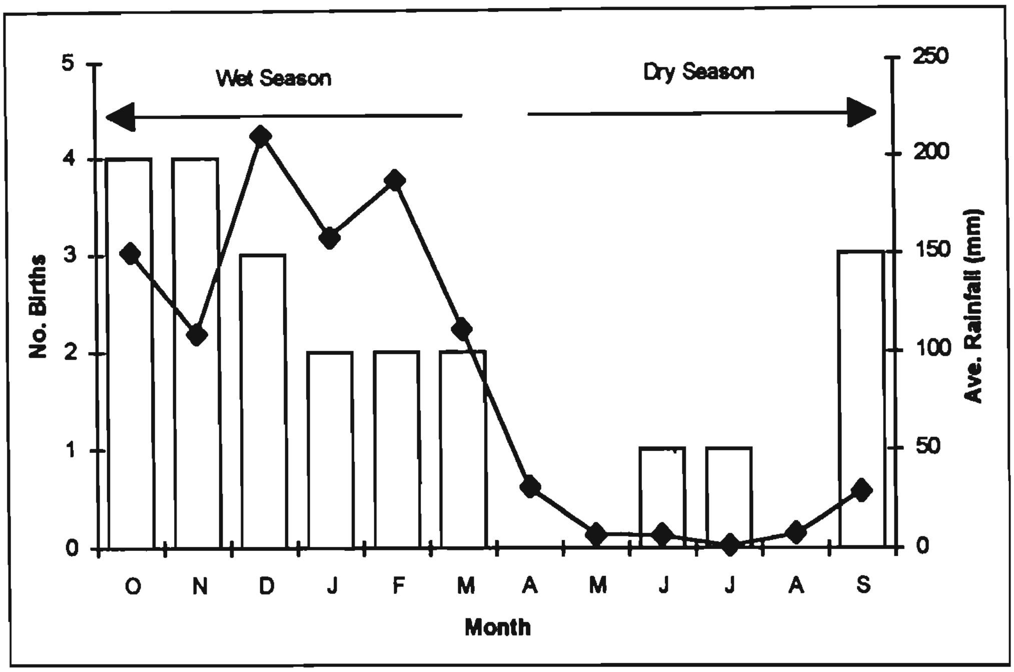

Figure 5: Number of known births by month of year for the Drakensberg baboons and average monthly rainfall (mm - line graph) in the corresponding month. Months of the year are grouped according to the wet season (October - March) and the dry season (April - September).

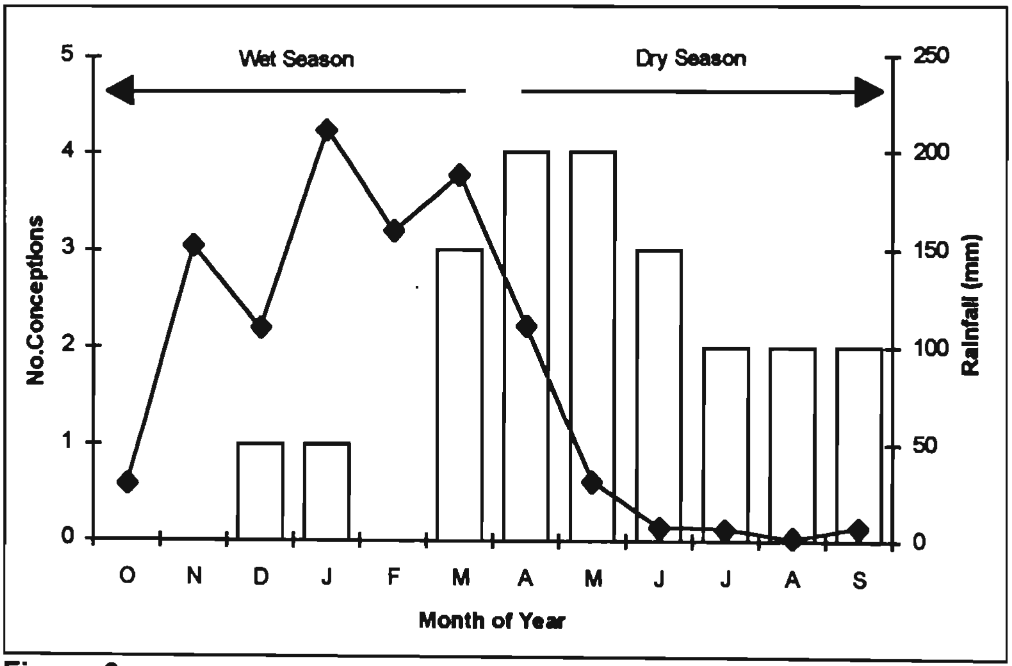

Figure 6: Number of conceptions by month of year for the Drakensberg baboons and the average monthly rainfall (mm - line graph) during the month prior to conception. Months of the year are grouped according to the wet season (October - March) and the dry season (April - September).

Given a gestation of approximately 180 days (Altmann 1980; Dunbar 1988), the number of conceptions that occurred in any month was negatively related to the amount of rainfall during the month prior to conception, although not significantly so (r = -.2725, p > 0.3 Figure 6). This latter finding contrasts with the prediction that conceptions will peak following temporarily enhanced food availability (Bercovitch and Harding 1994).

In terms of comparative data relating to the relationship between rainfall and conceptions, Silk (1986) and Muruthi *et al* (1991) found a significant relationship between the amount of rain in one particularly wet month in Amboseli, Kenya and the number of (baboon) conceptions that occurred in the following month. Lehman *et al* (1994) found that for free-ranging rhesus macaques (*Macaca mulatta*), births were positively correlated with warmer, rainier months while conceptions were associated with cooler, drier months. They note that a multivariate pattern of environmental cues might have indirectly led to a birth season that coincided with conditions where temperatures were at their highest, day length was longest, precipitation was greatest, and plant growth was maximal. Thus the period of lactation, which is the time of greatest metabolic stress for females, coincides with the season when resources and ambient temperatures were at their highest levels (p.122).

3.3.3 FOOD AVAILABILITY AND ITS RELATION TO THE TIMING OF CONCEPTION: CONSEQUENCES FOR THE TIMING OF BIRTHS

Insofar as an attempt is made to identify pressure(s) which might result in the observed clustering of births to a specific time of the year, the benefits which might accrue as a result of reduced predation (Small and Smith 1986; Boinski 1987; Martin 1990) can be discounted. The threat of predation on the Drakensberg baboons is minimal (Whiten *et al* 1987; Henzi *et al* 1992; Henzi *et al* under review *a*). Following Bronson (1989), an alternative explanation is sought in "the key factor", which is food availability and its relation both to conception and birth timing. This follows van Schaik and van Noordwijk (1985) who predict that under conditions where seasonal variation in temperature is small and the predation rate on both parent and offspring is low, seasonal variability in the food supply is expected to determine the timing of reproductive events.

A detailed description of the diet of the FT is not yet available. However, detailed analyses of the diets of both the Low and High Troops at GCGR have been published (Byrne et al 1993). While acknowledging that specific flora might vary between the two study locations, the diet of the GCGR baboons can still be used to illustrate the broad reliance of the DM baboon population on ground-level herbs and grasses, thereby making analyses which use percentage crude grass protein (see below) more meaningful. Using data from the Low Troop (Byrne et al 1993), the diet of these animals was comprised of the following categories of food types (where percentages cited represent the amount of feeding time eating each class of food):- corms

(24.95%); bases (23.12%); leaves (22.9%); flowers (24%); insects (2.95%). While these percentages represent averages for all age-sex classes in the Low Troop, the reliance of adult versus immature animals on each food class is not substantially different (see Figure A: Additional Figures at the end of this chapter). Similarly, the overall diet profile of the Low Troop is not dissimilar from that of the High Troop, with the possible exception of a greater reliance on flowers by the Low Troop (see Figure B: Additional Figures at the end of this chapter).

Month	Average Rainfall	Number Conceptions	Number Births	% Crude Protein
January	159.5mm	1	2	5.50
February	188.3mm	0	2	4.75
March	111.0mm	3	2	4.50
April	30.9mm	4	0	4.25
May	7.5mm	4	0	3.75
June	6.6mm	3	1	3.88
July	1.4mm	2	1	3.00
August	7.6mm	2	0	2.50
September	29.7mm	2	3	2.25
October	151.8mm	0	4	7.25
November	109.5mm	0	4	8.00
December	212.0mm	1	3	7.00

Table 5: Average monthly rain, conceptions and births by month, and % crude grass protein. Crude protein content of grass from Everson 1985.

Conceptions in the Drakensberg tended to be distributed over the dry months of the year, and were not clustered in months which *immediately* followed high-rainfall wet months (see Table 5 above). However, there was a peak in the number of conceptions in the months following a number of high rainfall months. Explaining this, and noting, as an indicator of food quality and quantity in the habitat, that the crude protein content of grass is strongly correlated with rainfall ($F_{1,10}$ = 12.078, p = 5.97%; r^2 = 54.71%), it is hypothesized that females might rely on the summer months when food is comparatively plentiful -(wet-month protein content is significantly higher than during the dry-months: t = 4.28, $p < 0.05$; *see also* Byrne *et al* 1993 Fig. 2)- to 'build' condition before conceiving (*cf.* van Schaik and van Noordwijk 1985). The peak in the number of conceptions during the period March through June (Table 5) followed months with the highest rainfall (October - February). Lee (1987) found a comparable pattern for vervet monkeys (*Cercopithecus aethiops*) in Amboseli. Similar to the trend reported for the present study, she found that the vervet females in her study groups began to conceive three months *after* the peak in the food supply, with the majority of conceptions taking place as much as four to five months after the peak. Thus she noted that ".... females did not appear to conceive as a consequence of *immediate* improvements in overall food quality, ..." (Lee 1987 p.412. Emphasis added). The implications, fortuitous or not, that this had for births and postpartum care of infants were considerable (and which will be referred to in the section below).

3.3.4 THE TIMING OF CONCEPTIONS: CONCLUSIONS

In support of the argument that female baboons in the Drakensberg are conceiving only after a relatively extended period during which high quality resources are available, and given that female mammals do not store energy in anticipation of the energetic costs associated with pregnancy and lactation (Dunbar and Dunbar 1988), there is suggestive and growing evidence that, for some mammals, females are able to ovulate only once a minimal nutritional threshold has been reached (horses: Belonje and van Niekerk 1975; rats: Frisch *et al* 1977; humans: Carael 1978 *in* Nicolson 1982; Frisch 1978; Frisch and McArthur 1974; Dobbing 1985; Ellison *et al* 1986; latter two cited in Blurton Jones 1989. But see Bronson and Manning 1991 for an opposing view). This proposition is in line with the view that the nutritional costs of reproduction are generally considered in terms of elevated protein and energy requirements (Barton 1990).

If females do indeed require the summer months with their associated higher quality food to build condition before conceiving, and assuming a gestation of approximately 180 days (Altmann 1980; Dunbar 1988), the Drakensberg females will then give birth during the following spring and summer months when food is once again of relatively higher quality. Considering the initial state of complete infant dependency on mothers, particularly insofar as nutrition is concerned, the timing of observed conceptions and hence births are such that mothers can take advantage of environmental conditions which would probably reduce the pressures on them. Given that mothers appear to be most nutritionally stressed during the first 4-5 months following parturition (Altmann 1980; Lee 1987; Dunbar and Dunbar 1988; Bronson 1989; *see below*), summer-births would allow mothers to take advantage of higher quality resources when they most need them. This point was demonstrated by Lee (1987) who argued that while the food supply may not have been directly implicated in the timing of conceptions for her vervet monkeys, the abundance and quality of food may have been crucial in female success at lactation. She hypothesized that, from the maternal perspective of optimizing investment in offspring, peak lactation should coincide with enhanced food availability and quality such that females can meet the energetic costs of lactation. The data supported this; she reported that the period of peak lactational frequencies and infant growth coincided with peaks in gross estimates of food quality (p.419).

The timing of births for the Drakensberg infants may also fortuitously serve to reduce the costs sustained by mothers in terms of the provision of transport for infants. For the Drakensberg baboons, day journey length decreases as food availability increases (Henzi *et al* 1992). Similarly, Altmann (1980) reported that the daily travel distance for the Amboseli baboons was the shortest during wet months. Given the fact that baboon mothers carry their infants most of the time for the first few months post-partum (Altmann 1980; Nicolson 1982; Rhine *et al* 1984; Altmann and Samuels 1992; Marsh 1992; This study, below), births during the summer rainfall months would translate into reduced stress on the mother through (a) more readily available food quantity and quality and (b) decreased costs associated with carrying an infant than would be the case if births occurred during the low-rainfall months when food quality and quantity are declining and average distance travelled per day increases.

While it may be that baboon births in the Drakensberg occur at a favourable time for mothers, and hence there is an 'optimal birth-period' in the sense that costs to the mother might be reduced, it is probable that this birth-period is a fortuitous consequence of the timing of conceptions which take place following an extended period of high quality resource availability. While Bercovitch and Harding (1994) argue that such peaks may result from "... *temporarily* enhanced food availability" (p.120, Emphasis added), it appears here that conception peaks arise from *extended* enhanced food availability. Nonetheless, given the timing of conceptions and births, it then needs to be seen what the actual pressures and costs of having a dependent infant are for females. The costs to females, particularly with reference to the provision of nutrition to the infant, were outlined above. To assess more directly how the presence of an infant affects the ability of a female to function within the ecological arena, it is necessary to ascertain what constitutes the normal constraints on a female's time budget. These are considered in the sections which follow.

3.4 FEMALE TIME BUDGETS

Any attempt to assess the effect that a dependent infant has on the activity of its mother should necessarily begin with a description of the normal baseline activity budgets of females prior to birth or pregnancy.

The time budget for females without infants, for the present study, is presented in Figure 7. Given the observation that the Drakensberg baboons 'travel-feed' (see Whiten *et al* 1987), the 'move' category here is strictly limited to occasions where individual animals were walking or running without stopping to feed, and thus excludes movement involving 'travel-feed'.

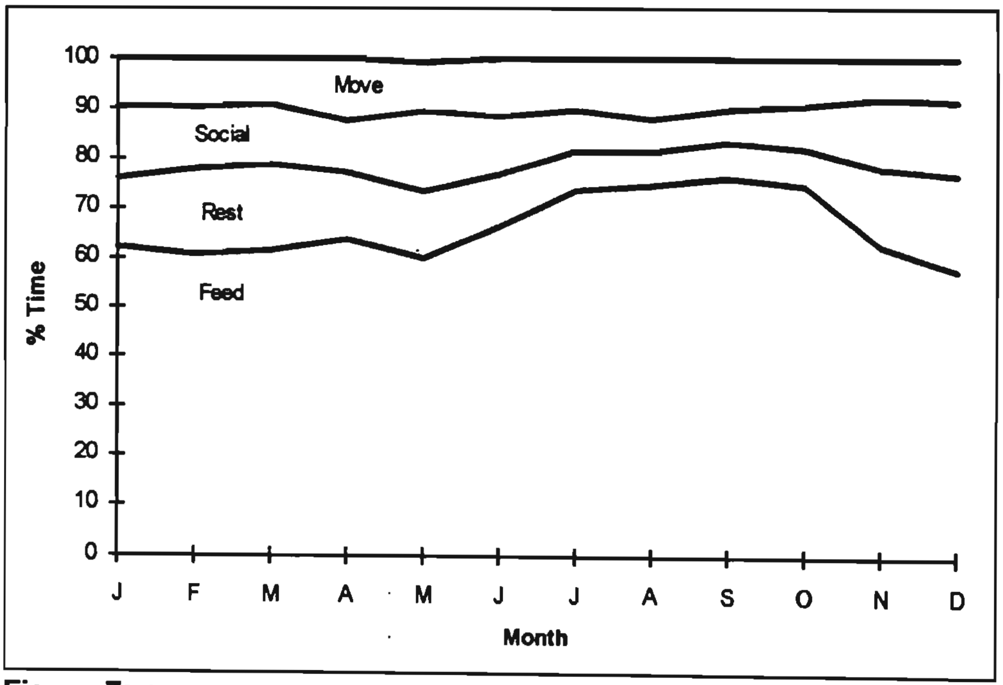

Figure 7: Activity profile for females without infants (n=4). Graph based on 1283 scan samples representing approximately 640 hours of observation.

It is clear from the graph that female feeding time increases steadily during the dry, winter months (April - September). The amount of time females in this study spent feeding is very similar to the values reported for the "Low Troop" females at Giants Castle Game Reserve (Byrne *et al* 1993) which ranged at approximately the same altitude (Figure 8). The striking similarity in the results of the two studies, separated both spatially and temporally, in the amount of time dedicated to feeding provides some measure of confidence that the values presented are both reliable and representative.

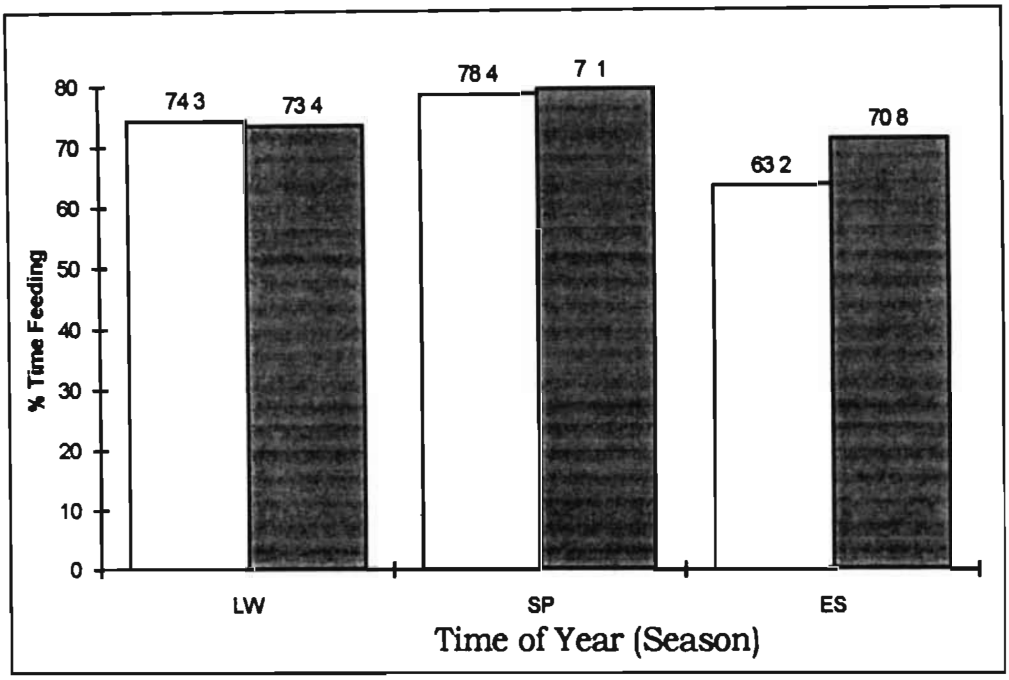

Figure 8: Comparison between the amount of time spent feeding, during three time blocks of the year, by adult females in this study (clear blocks) and at Giants Castle (filled blocks). LW = Late Winter; SP = Spring; ES = Early Summer. Giants Castle data from Byrne *et al* (1993). See Byrne *et al* (1993) for time of the year covered by each time block.

The increase in non-maternal feeding time during the period May through September corresponds with the decline in forage quality as measured by the content of both protein and fibre. Grass protein declines through the dry, winter months, while the fibre content increases (Everson 1985). It has been argued that dry season conditions are usually associated with an increase in the fibre content of plants with a consequent decline in digestibility (Braun 1973; van Soest 1982; *cited in* Dunbar 1992). Dunbar (1992) suggests that this increased fibre content should translate into an increased demand for feeding time given that the animals will need to eat more in order to achieve the same nutrient intake as that obtained during the wet season. The month during which (non-maternal) female feeding peaks -(September)- also corresponds with the "nutritional bottleneck" identified by Byrne *et al* (1990*b*; 1993). Whiten *et al* (1987) noted that during the period leading up to this nutritional bottleneck, surface vegetation dies back almost entirely with the consequence that the baboons must alter their foraging strategy to the harvesting of underground food items (corms, tubers, *etc.*) which take more time to harvest. Byrne *et al* (1993) have shown that, for their GCGR study troops, adult reliance on underground food sources is pronounced, particularly during the period they describe as 'late winter'. At this time females in their 'Low Troop' spent approximately 40% of their feeding time budget extracting such foods. They further report that, certainly within the area in which their study was conducted, the range of food items in the Drakensberg available to baboons is greater in the spring/early summer than in the late winter.

As the amount of time spent feeding increases through the dry months, time dedicated to resting and socializing decreases, while time spent moving remains relatively constant throughout the year. The amount of time females without infants spent resting and socializing were both negatively correlated with the amount of time spent feeding (r = -0.9467,

$p < 0.01$, $N = 12$; and $r = -0.9202$, $p < 0.01$, $N = 12$; respectively). While time spent moving tended to increase as the amount of time dedicated to feeding increased, the relationship between the two was not significant ($r = 0.4253$, $p > 0.1$). Females spent more time moving during the dry months than in the wet months ($t = 4.46$, $p < 0.05$).

These data make it possible to examine the effect the presence of offspring have on females and their maintenance activities. Altmann (1980) attempted to investigate this exact issue. Her model of maternal feeding was the first to quantify the costs associated with a dependent offspring incurred by mothers.

3.5 ALTMANN'S (1980) MODEL OF MATERNAL FEEDING

Altmann (1980) attempted to explicate some of the consequences for female baboons of having a dependent offspring, particularly in terms of the allocation of time to their various maintenance activities. Starting with the premise that female mammals do not anticipate the energetic costs of reproduction during pregnancy and thus do not store fat, it follows that the energy demands of growing infants are met by increasing maternal food intake as required (Dunbar and Dunbar 1988). That this is probably so is supported by observations which report that lactating female primates spend more time foraging than do non-lactating females (Rose 1977; Post *et al* 1980; Goldizen *et al* 1988). Further, Dunbar and Dunbar (1988) argue that infant energy demands are not constant but vary with age and, as a consequence, the energy costs to females should vary accordingly. Given this, Altmann's (1980) model of maternal time budgeting attempts to show how females reallocate their time to various maintenance activities in order to accommodate the expected and predicted increase in time dedicated to foraging.

Essentially, Altmann (1980) conceived a female's time budget as consisting of four major categories of behavior (i.e. feeding, moving, resting, and social activities) where both moving and resting time are treated as constant and fixed as these are primarily 'imposed' upon the female as a result of her participation in a social group which largely determines the amount of time spent in each of these categories of behaviour (Dunbar and Dunbar 1988). Accordingly, Altmann (1980) assumed that moving and resting time will be conserved while any additional feeding time will necessarily have to be taken from social time which would result in decreased participation in social interactions.

To assess the consequences of having a dependent infant for female activity budgets, Altmann (1980) derived the following equation which predicts, for each month of infant age, the levels at which mothers *should* feed in order to meet both her and her infant's energetic requirements:

$$f_t = A\,m^{0.75} + \frac{A\,(i_o + t\Delta i)^{0.75}}{E}$$

where: ft is the predicted amount of time a female should spend feeding,
A is the coefficient of energy ingestion during lactation,
m is maternal weight in kilograms,
i_0 is the infant weight at birth, in kilograms,
Δi is the rate of change in infant weight,
and, E is the energy coefficient of lactation,

In the sections which follow, Altmann's (1980) model and the predictions contained therein, will be applied to the mothers in the present study. As comparative data to demonstrate how the seasonal timing of birth impacts on maternal feeding, the model will be applied to the Gilgil olive baboons (data extracted from Nicolson 1982), the Amboseli yellow baboons (Altmann 1980), and to gelada baboons (Dunbar and Dunbar 1988). For the Gilgil and Amboseli studies, the seasonal effect of birth timing is masked whereas for the gelada study the effect is similar to that for the present study.

In applying the model to the different study sites, Altmann's assumptions have been retained, as have her values for the variables used in the above equation with the exception of maternal and infant body weights which differ across study sites, as well as the values for *A* which have been calculated on the basis of activity budgets reported for each specific study. In applying the model to the four different sites, and given the differing ecological circumstances within which each study was conducted, it is possible to assess the effect local ecology may have on maternal activity and for mother-infant strategies.

3.5.1 CHACMA BABOONS (THIS STUDY)

In Figure 9 is presented the application of Altmann's (1980) model of maternal feeding for the mothers in this study. Plotted, as horizontal lines, are the basic time budget allocations for Drakensberg baboon females without infants (average for a year:- 66.23% feeding, 12.37% resting, 11.33% social activity, and 10.01 moving). Also plotted are the mean observed values of time spent feeding by mothers at each month of infant age, as well as the model's predicted levels at which they should feed (calculated using Altmann's formula assuming a 10g and 5g infant weight-gain per day, and using female weights for Drakensberg females (15,00kg, Henzi, *unpubl. data*) and infant weights for *P. cynocephalus* (0.854kg) provided by Harvey *et al* 1987.

There are two features of the graph which are of immediate relevance. The first relates to the extent to which observed maternal feeding is consistently above the levels predicted by the model, and the second relates to the observation that maternal feeding showed only a relatively slight decline following the peak around month 5, and even then remained considerably above the normal feeding time (of non-mothers) through month-12. That is, while maternal feeding time declined slowly to levels below those predicted by the model between months 10-11, the observed feeding time nonetheless remained consistently above the average feeding time for non-lactating females. Each of these observations is considered below.

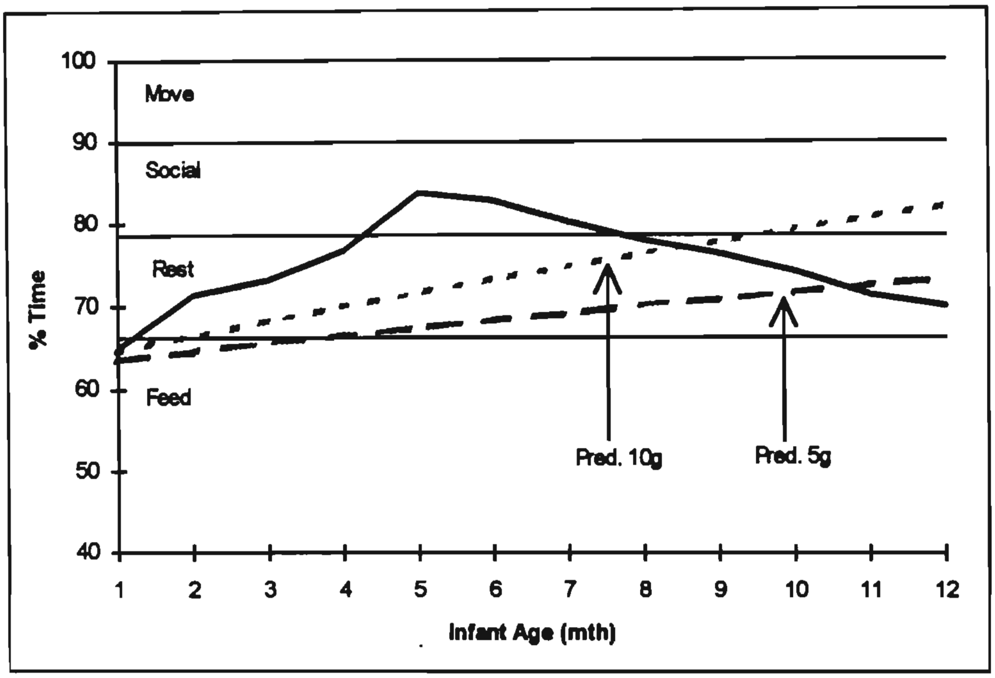

Figure 9: Maternal time budget plotted against infant age for the Drakensberg baboons. The thick line represents the observed amount of time mothers spent feeding. The dashed lines represent the levels of maternal feeding predicted by Altmann's (1980) model assuming a 5g (short dash) and 10g (long dash) infant weight gain per day. The horizontal lines at 62.63%, 77.93%, 90.31%, and 100% demarcate the average amount of time females *without* infants spent feeding, resting, socializing, and moving. The amount of time spent in each category of behaviour -(for these females)- has been cumulatively totalled.

Maternal feeding time, as expected (Altmann 1980; Dunbar and Dunbar 1988), increased with infant age, rising steeply during months-1 through month-5, and declining gradually thereafter. What is immediately apparent from the graph is the fact that from month-1 through month-8 the mothers in this study were observed to feed at levels considerably above those predicted by the model, and then from month-8 through month-11 within predicted levels. In explaining this, reference is made to the previously reported distribution of births in this study. Given that all births occurred during the summer months, the first months post-partum for mothers tended to occur during the drier, winter period. As a consequence of the timing of births, it is probable that the differential between the amount of time mothers were observed to feed and the expected levels is partly due to a combination of at least two factors: *firstly*, the decline in forage quality (as indicated by grass protein content) which all animals, regardless of whether or not they are mothers, experience in the dry period leading up to the nutritional "bottle-neck" (Byrne *et al* 1990b) and *secondly*, the increase in thermoregulatory requirements resulting from declining mean ambient temperature (R.I.M Dunbar, *pers. comm.*). The relationships between the amount of time each month that mothers spent feeding, the average monthly temperature, and grass protein content are presented in Table 6.

MOTHER	FEED/TEMP.	FEED/PROTEIN
GO	0.4713 NS (N=12)	-0.5428 NS (N=12)
FO	-0.2578 NS (N=12)	-0.6888* (N=12)
JO	-0.8175* (N=12)	-0.6532* (N=12)
CH	-0.9078* (N=12)	-0.7030* (N=12)
RI	-0.7172* (N=11)	-0.5355 NS (N=11)

Table 6: Correlation coefficients for each mother for (i) maternal feeding and average monthly temperature and (ii) maternal feeding and grass protein content. (*) = results are significant at $p<0.05$.

With the exception of the correlation between feeding and temperature for female GO, the amount of time mothers spent feeding was negatively related to both average monthly temperature, and grass protein content. That is, as both declined, mothers dedicated more time to feeding. This pattern is similar to the observed and predicted feeding rates for the gelada (Dunbar 1988; Dunbar and Dunbar 1988; *see below*). The gelada analyses demonstrated that the months during which the gelada fed above predicted values were the dry months when forage quality was declining with time and thus Dunbar (1988) argued that females will have to eat proportionately more food to extract the same quantity of nutrients.

Considering the shape of the graph (Figure 9), the timing of the peak in maternal feeding at months 5-6 corresponds to the claim by Altmann (1980) that an infant will need to begin providing for its own nutritional needs at this age given that the mother will no longer be able to meet *all* the infant's requirements. She suggests that, even given the conservative estimates of energetic demands used in the formulation of her model, mothers would not be able to provide all the caloric needs of both herself and an infant beyond 6-8 months of infant age. If she is correct, then it would be expected that once infants begin to feed independently, mothers would be able to reduce the time dedicated to feeding (*cf.* gelada baboons, Dunbar and Dunbar (1988) Fig.2; and yellow baboons, Altmann (1980) Fig.14). However, if infants are to begin feeding independently, then appropriate weaning foods must be readily available. For two of the infants in this study the fifth month of life coincided with the end of the summer months (February and March) when green-grass cover was still relatively abundant;- Altmann (1980) has identified grass as a favoured infant weaning food for Amboseli infants given its digestibility and the ease with which it is obtained and harvested (*cf.* Rhine *et al* 1989). For the other three infants, their fifth months of life occurred during dry winter months (May, June and August).

Thus, even though it may have been possible for the two oldest infants in the study to begin independent feeding during their fifth month, such feeding would have been curtailed by the onset of winter when surface vegetation dies back (Whiten *et al* 1987; Rhine *et al* 1989 - Mikumi) and the diet of the animals must shift to the extraction of underground items. Given the inability -probably due to physical 'deficits' *cf:* Altmann 1980; see below- of infants to utilize such food sources, mothers, by necessity, remained the principle source of nutrition during this time. This explains two features of the graph of observed maternal feeding: *firstly*, unlike Dunbar and Dunbar's (1988) gelada and Altmann's (1980) yellow baboons, maternal feeding time in this study declined only slightly after month-5 and *secondly*, while some decline in feeding time was observed, the observed levels remained above those predicted by the model.

If births are timed such that mothers are able to take advantage of readily available food sources during the first few months of intense infant dependency (Altmann 1980; Nicolson 1982; Dunbar and Dunbar 1988; Bronson 1989), then infants in the present study appear to be missing the predicted optimal period at which independent feeding should begin.

Altmann (1980) argued that the independent harvesting of food by infants at 5-6 months of age is dependent on the presence and availability of the "... right foods ..." (p.57) in the habitat. For the infants in this study, those food items (*e.g.* grass, leaves, flower petals - Altmann 1980) were not available at that age. The adult alternative, utilizing underground food sources, was an option which too was not readily available to infants. No infant was observed to *successfully* harvest underground food sources in the first 12 months of life (see next chapter). In Altmann's (1980) terms, infants are probably prevented from taking advantage of these underground food items by both 'knowledge-deficits' as well as 'physical-deficits' where (a) the cues which mark the presence of these foods in the Drakensberg mountain are cryptic (Whiten *et al* 1987) and hence are probably not known to infants, and (b) the infants have probably not yet developed the strength and skills required to extract and harvest the foods (*cf.* Rhine *et al* 1988).

The remaining alternative strategy, in the absence of favourable weaning foods and in light of the inability of infants to utilize underground food items, is for mothers to continue nursing infants through the winter period until appropriate weaning foods are once again seasonally available. This form of parental behaviour promotes *survivorship* rather than *production* (Blurton Jones 1993; see above). The reliance of infants on their mothers for nutrition, within the context of weaning and the promotion of infant independence, will be considered in the next chapter. It will be argued that the length of the nursing period for the Drakensberg infants is a function of the relationship between timing of birth (which is a consequence of conception timing) and ecological conditions which prevail at that time and in the following months, and that this is at least partially responsible for the observation reported above that mothers feed considerably above the levels at which other females do. The nature of the relationship between timing of birth and observed feeding in the following months of infant dependency, for each individual mother in this study, will now be considered.

3.6 MATERNAL FEEDING AND TIMING OF BIRTH

The proposition that mothers are constrained by both ecological conditions and the timing of births in the allocation of time to their various maintenance activities is made clearer if consideration is given to the relationships between individual maternal feeding and the feeding time of non-mothers represented in the five graphs below (Figures 10a,b,c,d,e; and see summary graph at the end of this chapter Figure 16).

3.6.1 FEMALE "GO"

Mother GO (Figure 10a) gave birth during September 1991. The mean amount of time that she spent feeding each month increased steadily during the first 5 months following birth, reaching asymptote at month-6 (March 1992). It is at this age that an infant should begin considerable independent feeding (Altmann 1980). However, as has been argued above in relation to the application of Altmann's (1980) model to the mothers in this study, March marks the end of the wet season and the beginning of the dry months. It will be shown in the next chapter that GO's infant did not begin to feed significantly for himself until October/November 1992 and thus remained almost entirely reliant on GO for nutrition through to that time. While some decline in the amount of time GO spent feeding is evident during months 7-8, it should be noted that this still remained consistently above the levels at which non-mothers were feeding. The amount of time non-mothers spent feeding increased through the period June-August 1992 to the levels at which GO was feeding.

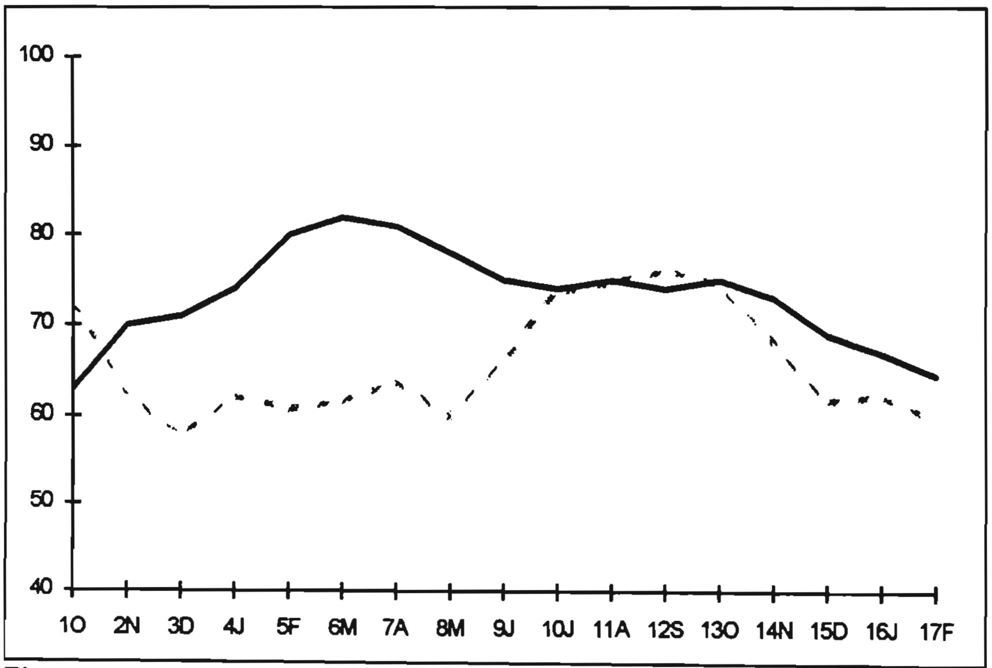

Figure 10a: The mean amount of time, per month of infant age, mother GO spent feeding (solid line). Also plotted is the mean amount of time for the corresponding months that non-mothers in the study troop spent feeding (dashed line). Plotted along the x-axis is infant age specifying month of year for that age, while the y-axis represents mean percentage time feeding.

3.6.2 MOTHER "FO"

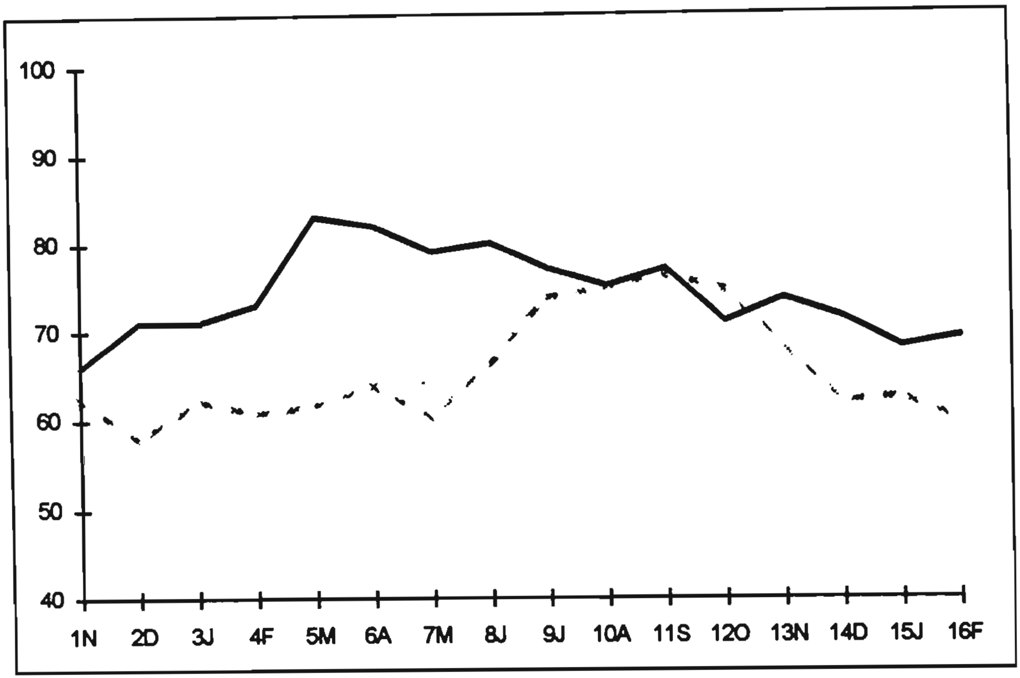

Figure 10b: The mean amount of time, per month of infant age, mother FO spent feeding (solid line). Dashed line and axes as for Figure 10a.

The infant of female FO (Figure 10b) was born in October 1991. For this mother, time spent feeding peaked during the infant's fifth month of life. Maternal feeding time increased slowly through months 1-4, and then suddenly during the fifth month (March 1992). As with mother GO, the amount of time spent feeding decreased only slightly after month-5 and also remained consistently above the levels at which non-mothers fed. The point at which the amount of time spent feeding coincided for non-mothers and FO (month-10, August 1992) was the month during which non-maternal feeding reached asymptote. That is, rather than FO having significantly reduced feeding time, the coincidence appears to have been primarily due to the peak in non-maternal feeding during the late-winter season.

3.6.3 MOTHER "JO"

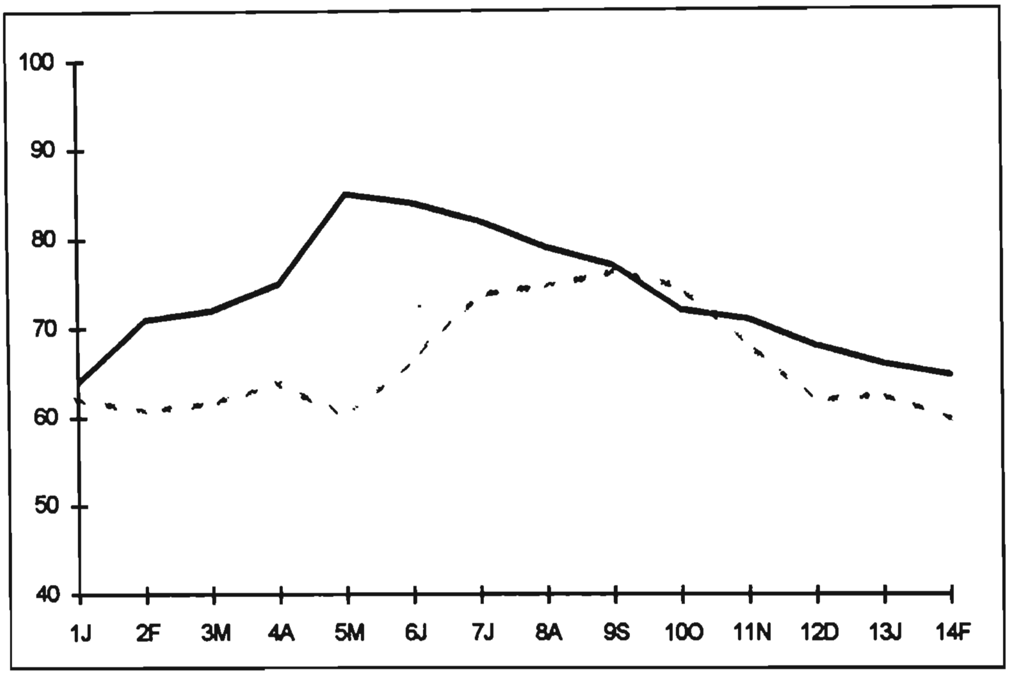

Figure 10c: The mean amount of time, per month of infant age, mother JO spent feeding (solid line). Dashed line and axes as for Figure 10a.

Mother JO gave birth to her infant (J2) during December 1991. The first 3 months post-partum corresponded with the last 3 months of the wet season. Following month-4 (April 1992), the amount of time that JO spent feeding increased sharply, reaching asymptote during month-5 (May 1992), and then declined slowly after this. As with mothers GO and FO, the amount of time that JO dedicated to feeding remained consistently above the feeding levels of non-mothers (Figure 10c). However, unlike the two other mothers considered above, JO's feeding time showed a consistently steady decline from approximately month-6.

3.6.4 MOTHER "CH"

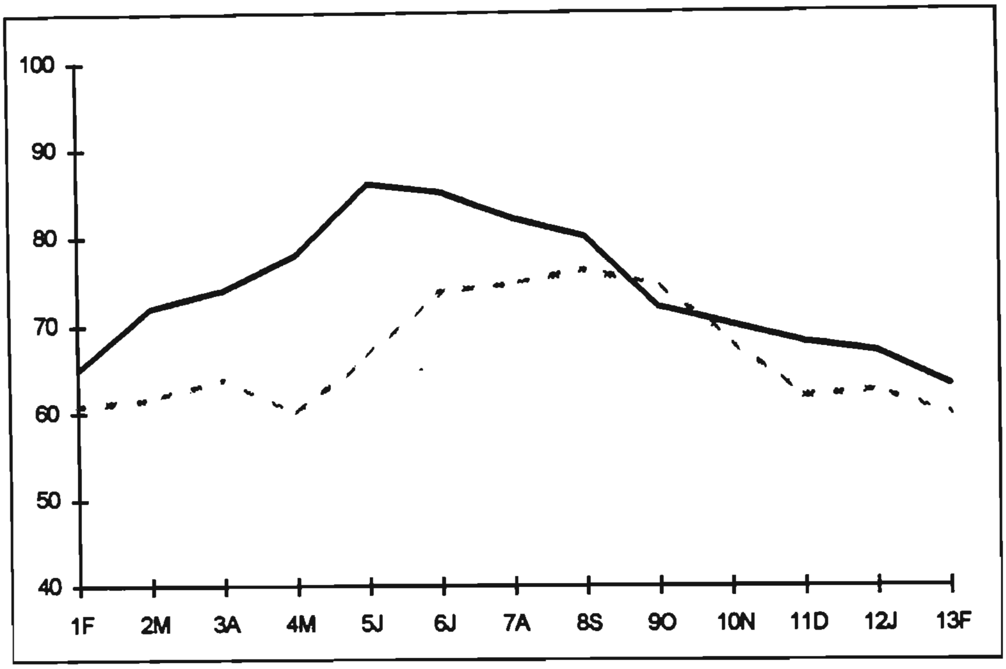

Figure 10d: The mean amount of time, per month of infant age, mother CH spent feeding (solid line). Dashed line and axes as for Figure 10a.

Female CH gave birth to her infant during January 1992. Time spent feeding increased steadily through to the infant's fifth month, and thereafter declined slowly to reach non-maternal levels as these peaked during September (infant age: 8.5 months). The period April - September (months 3-8) during which CH fed above non-maternal levels corresponded with the dry season which, as has already been noted, is the time when the above-ground food resources of the Drakensberg baboons become progressively less available, and hence there occurs a concommitant increase in the amount of time the animals dedicate to feeding. In the light of this, it might thus seem unexpected that CH (as well as JO above) decreased the amount of time she fed. However, while a decrease in feeding time is evident, it nonetheless remains above non-maternal levels. It is only after October, which marks the beginning of the wet season, that the level of feeding for CH begins to decline toward 'normal' non-maternal levels.

3.6.5 MOTHER "RI"

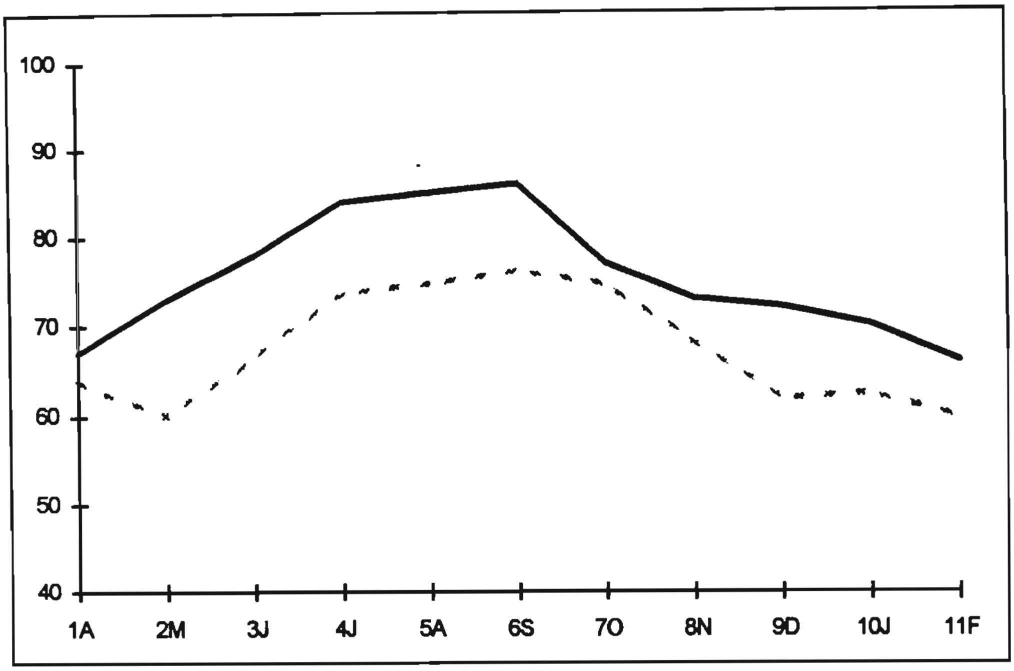

Figure 10e: The mean amount of time, per month of infant age, mother RI spent feeding (solid line). Dashed line and axes as for Figure 10a.

The fifth mother in this study, RI, gave birth during the last month of the wet season (March 1992), and thus at each month of infant age this female encountered dry, winter conditions. The amount of time she spent feeding increased sharply through months 1-6, peaking during the sixth month (September). The shape of the graph representing her feeding time mirrors quite closely that of non-mothers, but at higher levels. The decline in the amount of time RI spent feeding following month-7 coincides with *(a)* the onset of the wet months and *(b)* the beginning of independent feeding by her infant (R2). However, whereas non-mothers reduced quite quickly the amount of time spent feeding, RI continued feeding through month-11 at levels above non-mothers, which coincided with the continued suckling of R2 at the same time that she had begun independent feeding.

3.7 ALTMANN'S MODEL - COMPARATIVE DATA: OLIVE, YELLOW, AND GELADA BABOONS

For the three comparative data sets, only limited conclusions can be made in the absence of complete details. However, from the graphical presentation of the data from the three sites (Figures 11,12,13 below) it is immediately apparent that for both the olive baboons at Gilgil and the Amboseli yellow baboons, maternal feeding time remained consistently below the levels predicted by the model.

For the Gilgil mothers, in particular, at no time during the first 16 months of infant life did the mothers in Nicolson's (1982) study feed at predicted levels. For the Amboseli baboons, Altmann (1980) noted that the mothers did in fact increase the amount of time they spent feeding above normal levels which led her to conclude that a female's time budget is indeed affected by the presence and age of a dependent offspring. However, while the effect of a dependent offspring on maternal activity was evident, it was noted that the effect was less than predicted:- with the exception of months 5-6, the mothers fed at levels consistently below those predicted by the model. A possible explanation for these observations will be considered within the context of the proposition that Altmann's model does not account for seasonal effects of the timing of birth on maternal activity. (For further details regarding both the Gilgil and Amboseli studies, see ADDITIONAL NOTES at the end of this chapter).

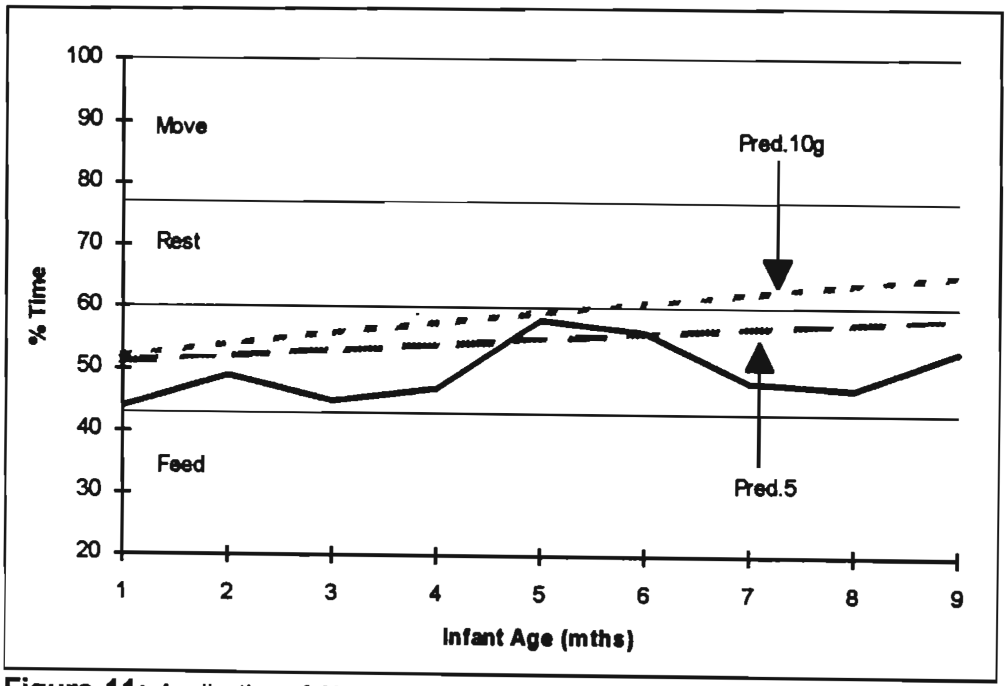

Figure 11: Application of Almann's (1980) model of maternal feeding to the AMBOSELI YELLOW BABOONS. Maternal time budget plotted against infant age for the first 9 months of infant life. All data taken from Altmann (1980 Fig.14) except observed maternal feeding during month 9 (calculated from Altmann 1980 Fig.13). Observed maternal feeding represented by thick line; predicted levels represented by dashed lines (short dash:- 10g infant weight gain/day; long dash:- 5g infant weight gain/day). See Altmann (1980 Fig. 14 and text for details). Note the scaling on the Y-axis.

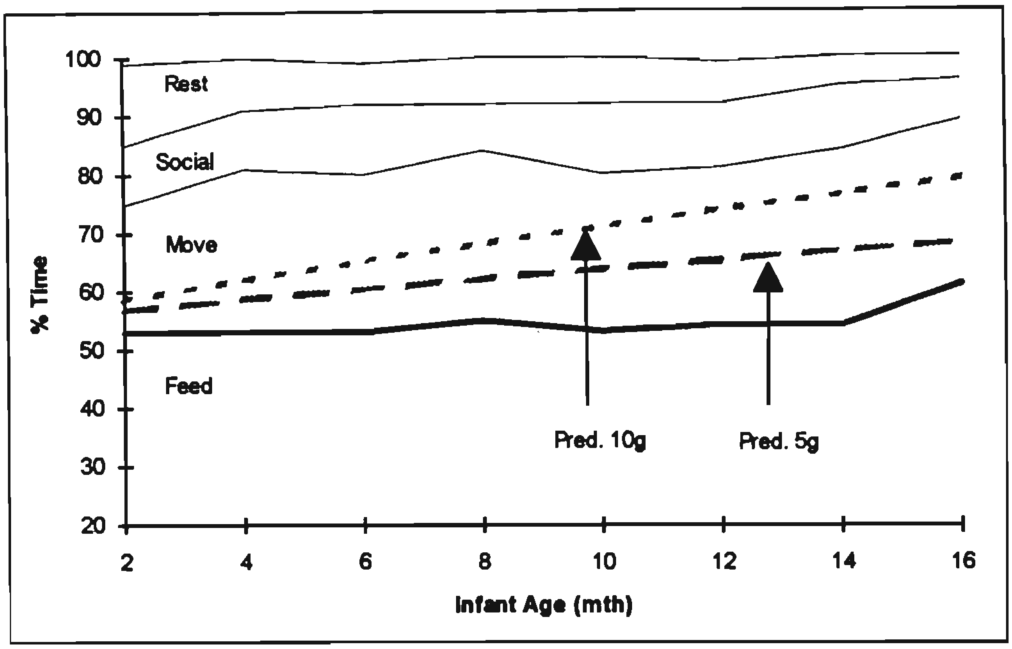

Figure 12: Application of Almann's (1980) model of maternal feeding to the GILGIL OLIVE BABOONS. Maternal time budget plotted against infant age for the first 16 months of infant life. Amount of time spent in each category of behaviour at each infant age taken from Nicolson (1982 Table 36b). Observed maternal feeding represented by thick line; predicted levels represented by dashed lines (short dash:- 10g infant weight gain/day; long dash:- 5g infant weight gain/day). Female and infant birth weights used to calculate predicted levels are those for olive baboons provided by Harvey *et al* (1987). Note the scaling on the Y-axis.

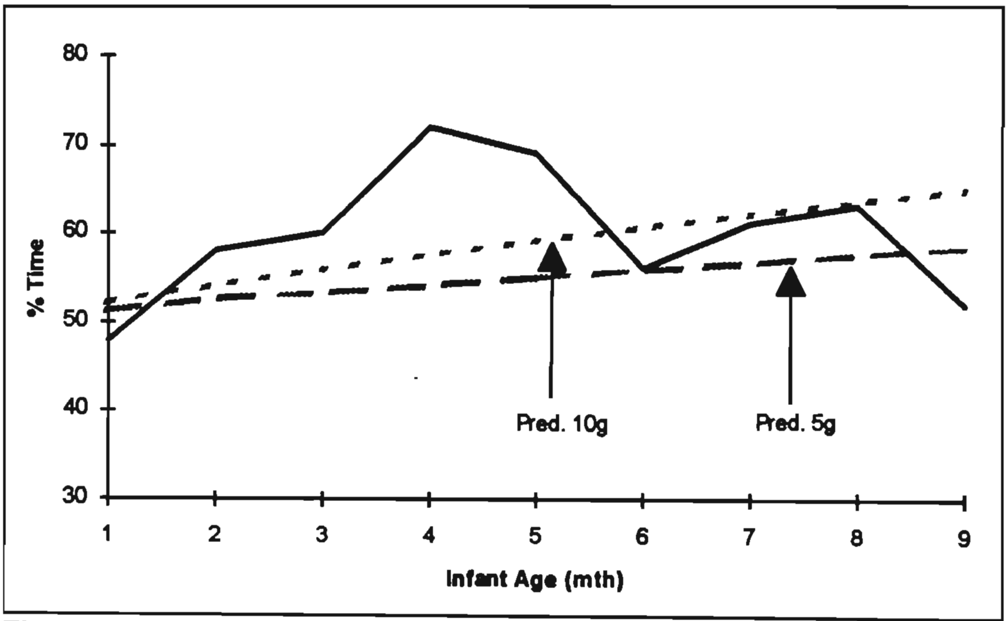

Figure 13: Application of Almann's (1980) model of maternal feeding to GELADA BABOONS. Maternal feeding time plotted against infant age for the first 9 months of infant life. Observed maternal feeding represented by thick line; predicted levels represented by dashed lines (short dash:- 10g infant weight gain/day; long dash:- 5g infant weight gain/day). Observed values redrawn from Dunbar and Dunbar (1988). Female and infant weights used to calculate predicted levels taken from Harvey *et al* (1987). See footnote No.2 below. Note the scaling on the Y-axis.

In contrast to both of these studies, and similar to the data for this study, Dunbar and Dunbar's (1988) gelada mothers, at least until their infants were 6-months old, fed at levels consistently above predicted levels, even given a recalculation of predicted levels of maternal feeding based on revised adult female and infant-birth weight estimates[2].

With the limited background (or contextual) information available, it is possible to speculate as to why mothers in these three studies fed at levels below and above, where applicable, levels expected by the Altmann (1980) model by extrapolating from ecological conditions, where the data are available.

Certainly for the Gilgil baboons, Nicolson (1982) reported that the animals inhabited an area which was characterized by relatively stable temperatures throughout the year, relatively stable water supplies which were complemented by an unusually wet period during which the study was conducted, and what Nicolson (1982) terms an "... apparently abundant year-round food supply ..." (p.134). Thus, if seasonally variable ecological conditions exacerbate the effect a dependent offspring has on maternal time budgets as was suggested in

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[2] The predicted levels of maternal feeding for the Dunbar and Dunbar (1988) study were calculated using female and infant-birth weights for Altmann's (1980) yellow baboons which, Dunbar and Dunbar (1988) assumed, were negligibly different from those for gelada. However, when using gelada weights (Harvey, Martin and Clutton-Brock 1987) the predicted levels of maternal feeding are increased such that observed maternal feeding time falls within, and then below predicted levels at month-6 as opposed to doing so only around month-8 when using the yellow baboon weights as for Dunbar and Dunbar (1988) (Compare Figure 13 this chapter and Fig.2, Dunbar and Dunbar 1988).

relation to the baboons in the present study, then it would not be unexpected that Nicolson's mothers, who presumably did not experience *extreme* conditions, did not show concommitant extreme fluctuations in the time devoted to the various activities which comprise their time budgets. For Altmann's (1980) mothers, and noting that the presence of an infant did affect time budgeting of mothers, the distribution of time to various maintenance activities, particularly feeding, confirmed the hypothesis that by the time infants are 5-6 months old, mothers would reach the maximum amount of time they could dedicate to feeding without seriously jeopardizing their allocation of time to other activities, and thereby incurring further energetic cost. Altmann (1980) thus proposed that at this age infants should begin independent feeding if the appropriate weaning foods are available. While the data confirming whether or not infants had started feeding for themselves at this age are not available, mothers did in fact reduce the amount of time dedicated to feeding following month-6 of infant age.

One of the difficulties in accurately assessing the effect a dependent offspring has on a mother in both the Altmann (1980) and Nicolson (1982) studies is the fact that the effect of the timing of birth, for individual mothers, is masked in their presentation of the data. That is, while it has already been noted that both of these study sites do not experience seasonality or clustering of births, it remains possible that births at certain times of the year (e.g. low rain, low plant productivity) will incur for such mothers greater energetic cost in providing infant care than would be the case for females who give birth during more 'favourable' times of the year. In contrast, as has been shown for the present study, and will be shown for the gelada, where clustering of births does occur, it is possible to more accurately explain the observed levels at which mothers feed in relation to levels predicted by Altmann's (1980) model.

Considering the shape of the graph of observed maternal feeding for the gelada (Figure 13), the decline in maternal feeding to within the range predicted by the model might be argued as follows:- given that the observed peak in maternal feeding during month-4 coincided with the age at which infants were first observed to feed independently, the slight decline in maternal feeding time between months 4-5 might have occured as a consequence of reduced pressure on mothers following such independent feeding. The steep decline in maternal feeding time to within predicted levels following month-5 was probably facilitated by a combination of at least 2 factors where;

(i) continued and increased independent feeding by infants would presumably further reduce maternal pressure, where gelada infants start to feed <u>significantly</u> for themselves during their sixth month (Dunbar 1984, p.102; Dunbar and Dunbar 1988), and

(ii) an increase in food production and hence protein following the onset of the rainy season (see Barrett *at al*, 1992 for rainfall figures in the study area) where grass production is positively correlated with rainfall (Everson 1985; Barrett *et al* 1992).

A more direct example of how ecological conditions affect maternal feeding behaviour is provided by the data reported by Dunbar and Dunbar (1988). The majority of their infants (9/10) were born within a month of each other, and thus those mother-infant dyads presumably exerienced similar ecological conditions at the same time. For those animals the first 4 months of infant life corresponded with the driest trimester of the year[3], and thus, probably, the time of year with the least amount of available food. The point being made is that the mother of the 10th 'late-born' infant[4] was, following the onset of the rainy season, able to effectively reduce her foraging time during a time of relative food abundance (Dunbar and Dunbar 1988) while the other mothers, at corresponding infant ages, maintained higher levels of feeding (see Dunbar and Dunbar 1988, Fig.4).

With regards the application of the model of maternal feeding to the four different baboon studies, it appears that for the two savanna baboon populations (Amboseli and Gilgil), observed maternal feeding remains, by and large, less than predicted by the model. For the Amboseli study it is clear from the shape of the maternal feeding graph that the presence of an infant does indeed affect the time budget of mothers. For the Gilgil study,

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[3] Average monthly rainfall: Jan-April: 5mm; May-Aug: 314.5mm; Sep-Dec: 55.75mm (from Barrett *et al* 1992).

[4] The 10th infant was born 4 months after the median birth date for the other 9 infants, and two months after the last born of these (Dunbar and Dunbar 1988).

however, the effect is not immediately apparent and this may be a consequence of the relatively stable ecological conditions which Nicolson (1982) described for the period covered by her study. For the present study and that for the gelada, seasonal variation in ecological conditions combined with the clustering of births to circumscribed times of the year may have resulted in the observations that mothers expended more time feeding than Altmann's (1980) model predicts.

3.8 CONSEQUENCES FOR FEMALE REPRODUCTIVE SUCCESS: INTERBIRTH INTERVALS

In Triverian terms, the ultimate cost of mothering must be the inability of a female to invest in a subsequent offspring. Citing Trivers (1974), Altmann (1980) has argued that a female's reproductive success might be enhanced through the early weaning of a currently dependent infant, thereby making it possible for her to begin investing in her next offspring. However, the early weaning of an infant is a viable option only if the risk of infant mortality is low.

If, as has been argued in this chapter, mothers in the Drakensberg Mountains are constrained in their reproductive output in the sense that they are compelled to allow infants to remain nutritionally dependent for what is a comparatively long period, then this should be reflected in the interval between successive births. While the mothers in the present study had not fallen pregnant by the time field work ended, and thus no actual interbirth intervals can be reported, it is nonetheless possible to provide some estimate. The measure of interbirth-interval (IBI) is derived by dividing the number of female years by the number of infants born, where the number of female years represents the number of females studied multiplied by the number of years that those females were studied and/or monitored (sensu: Dittus 1975; Henzi and Lucas 1980). A similar method for estimating the IBI of a gelada population was used by Dunbar and Dunbar (1975). They reported 58 births to 117 females during a 12 month study which, they argued, suggested an IBI of 24 months. Using this method[5], the following apply for the Drakensberg baboons (Table 7).

Troop	No. of Females	No. Years Monitored	No. of Female Years
GC: High	3	2	6
GC: Low	3	1	3
CP: FT	9 8	1 2	25
CP: HT	12	3	36
TOTAL			**70**

Table 7: Number of females, and number of years studied/monitored for baboons in the Drakensberg Mountains at Giants Castle (GC) and Cathedral Peak (CP). The 2 values presented for the FT at CP result from 1 female dying after the first year of the study. The number of years studied/monitored for the 2 CP troops include the period covered by the field work reported here (2 years) as well as ongoing population monitoring.

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[5] It is possible that this means of calculating the estimate of IBI may, in fact, overestimate the IBI in that "partial" infants (i.e. those that have been conceived but have not yet been born) are not included in the calculation. At the same time, however, the actual mean interbirth interval which is provided in most studies fails to account for females who have not, for whatever reason, fallen pregnant a subsequent time.

Thus, in terms of the calculation method described above, and using the 22 known births reported earlier in this chapter, the average IBI for the Drakensberg baboons is 3.2 years (38.4 months). While this method of estimation is neither as suitable nor as accurate as actual IBIs, it nonetheless provides a reasonable estimate when data are truncated and complete life histories are not known. Some indication of the reliability of the estimate is provided by a single actual IBI for one of the mothers in the present study. Female GO, whose first (known) infant was born during September 1991, gave birth to her second during November 1994. This IBI of 38 months is the same as the estimated IBI for the DM females reported above. Of the four remaining females in the study, none had given birth for a second time as at February 1995. Even if each gave birth during February 1995, the individual IBIs would be as follows:- FO (40 months), JO (38 months), CH (37 months), and RI (35 months). These values provide a mean IBI of 37.5 months. If this (minimum) value is combined with the actual IBI for female GO, then the mean IBI for these five FT females is 37.6 months[6]. Given that this value assumes four births during February 1995 which may, in fact, take place later in the year, then the above IBI estimation method appears to be underestimating the IBI for the Drakensberg baboon females.

In terms of maximizing female reproductive output, the (estimated) length of this interval compares unfavourably with

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[6] The estimated IBI remains unchanged even once (i) an extra five years are added to the number of female years and (ii) an extra infant (the second of female GO) is added to the sample in order to accommodate the extension of the study period through to February 1995.

that of other study sites, with the exception of the 37 month interval for the Gich gelada population (Table 8 and Figure 14).

SITE	SPECIES	IBI	SOURCE
Mikumi	P. cynocephalus	21.0	Rhine (1992)
Amboseli	P. cynocephalus	24.0	Altmann (1980)
Okavango	P. cynocephalus	23.5	Collins et al (1984)
Mkuzi	P.c. ursinus	20.2	Henzi et al (under review b)
Gilgil (EC Troop)	P. anubis	26.5	Nicolson (1982)
Gombe	P. anubis	25.0	Collins et al (1984)
Chololo	P. anubis	20.0	R. Barton (pers. comm.)
Erer, Ethiopia	P. hamadryas	24.0	Sigg et al (1982)
Ethiopia:	T. gelada		
Bole		24.0	Ohsawa and Dunbar (1984)
Sankaber (1971)		24.0	Ohsawa and Dunbar (1984)
Sankaber (1974)		28.0	Ohsawa and Dunbar (1984)
Gich		37.0	Ohsawa and Dunbar (1984)

Table 8: Interbirth Interval (IBI), in months, for comparative baboon study sites. IBIs for females whose infants survived the first year.

Similar to the Drakensberg baboons, the Gich gelada population experiences seasonal variation in ecological conditions and, when latitude is accounted for, range at approximately the same functional altitude as the Drakensberg animals (R.I.M. Dunbar, pers. comm.). However, if the comparison is confined only to *Papio*, the IBI for the Drakensberg animals exceeds by 11.9 months the next longest IBI (i.e. that of the females in the Gilgil Eburru Cliffs troop).

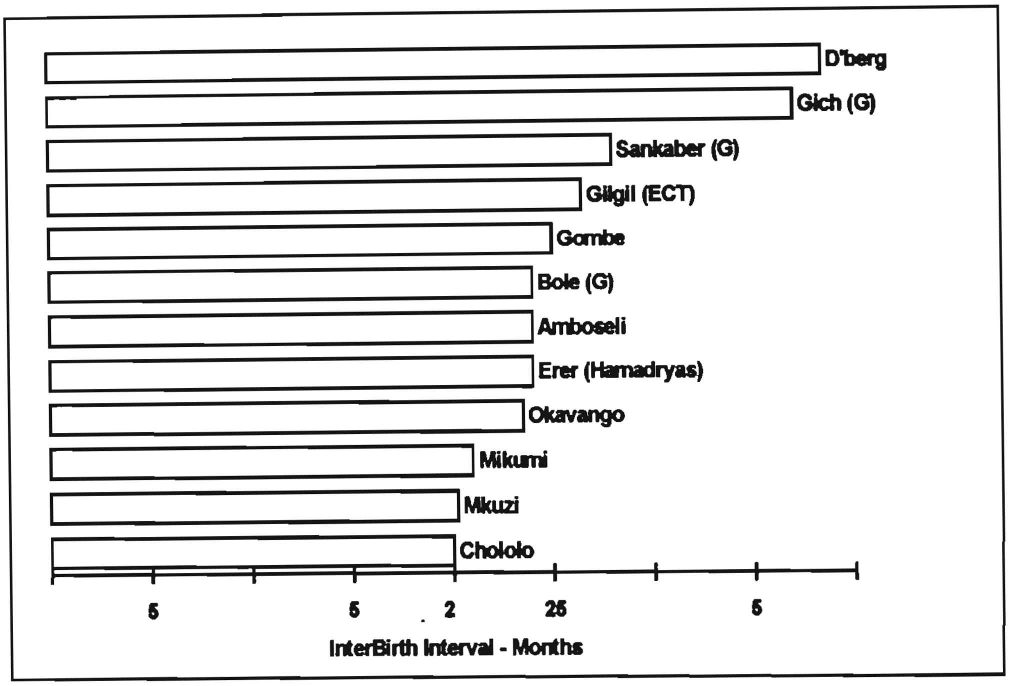

Figure 14: Comparison of interbirth intervals (months) for this study and other baboon study sites. Gelada study sites indicated by (G). The Gilgil data applies to the Eburru Cliffs Troop (ECT). Sources for comparative data as listed in Table 8.

The length of the IBI for the animals in this study is not entirely unexpected given (a) the timing of births in the Drakensberg, (b) the necessity for mothers to allow infants to remain dependent longer than would normally be expected, and (c) the claim made above that females in the Drakensberg Mountains require an *extended* period of high quality food availability to rebuild condition before conception takes place. This is in line with assertion by both Altmann (1980) and Lee (1987, citing Short 1985) that a delay in future reproduction might be brought about by the hormonal effects of extended suckling (Konner and Worthman 1980, cited in Altmann 1980) or through nutritional and other stresses (Frisch and Revelle 1971, cited in Altmann 1980), including weight loss during lactation (Bercovitch 1987a).

3.9 INTERBIRTH INTERVALS AND INFANT SURVIVAL

It is possible to argue that a mother's willingness to allow her infant continued access to care, such as suckling, beyond a normally expected age, will reflect a strategy or style of parental care which ultimately will maximize the female's reproductive success. For the present study it is probable that infants would not have survived the first year of life had mothers restricted their access to the nipple at the time mothers are expected to. That is, infant age 5-6 months coincided with dry winter conditions, and the timing of this would not have facilitated infant survivorship where infant survivorship is expected to be enhanced when weaning coincides with maximum food availability in the habitat (Nicolson 1982; Bercovitch and Harding 1994). Thus Lee (1987) suggests that vervet monkey mothers may monitor, or assess, the needs of a current infant and, where necessary, ".... some mothers may continue to suckle at higher rates ensuring infant growth and survival while delaying their reproduction until the subsequent year" (p.419).

So, in terms of the forms of parental care introduced in the beginning of this chapter, mothers in the Drakensberg population appear to forego a production strategy (see Section 3.2 above) in favour of a survivorship strategy where the probable survival of each successive infant is increased through parental efforts to counter threats to offspring survival. The relative success of whatever form of parenting is adopted will, necessarily, be found in rates of infant survival. Plotted in Figure 15 is the calculated rate of infant survival (and mortality) during the first year of life for the Drakensberg baboons, as well as those reported for other baboon study sites.

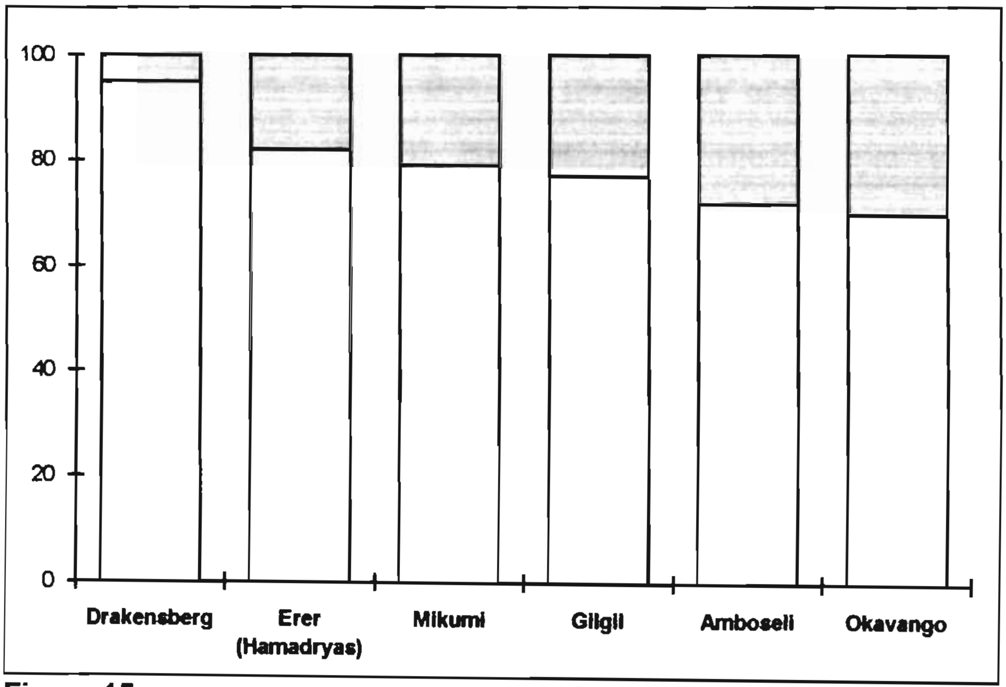

Figure 15: Infant survival rates during the first 12 months of life. Filled sections represent infant mortality. Data sources: Erer: Sigg *et al* (1982); Gilgil: Nicolson (1982); Amboseli: Altmann (1980); Okavango: Collins, Busse, and Goodall (1984); Mikumi[7] (Ramon Rhine pers.comm.).

The Drakensberg survival rate of 95%, calculated from one known death from 22 infants, is considerably higher than the rates for the other sites. Effectively, mothers in the Drakensberg appear to invest heavily in each infant in order to ensure the survival of each, rather than maximizing output but

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[7] The infant mortality rate for Mikumi is based on the probability that a live born infant survived through to it's 12th month for the first 10-years of the Mikumi study. This figure may have changed given a population crash in the area in recent years (Ramon Rhine, pers. comm.).

with the possibility of relatively high infant mortality. For the six study sites for which the necessary data are available[8], IBI of mothers whose infants survived to 12 months of age is positively correlated with infant survival rates in the respective populations (r = .8207 $p < 0.05$, N=6). Thus, as interbirth interval increases, survivorship increases. Bearing in mind that in populations where the mean IBI for mothers with surviving offspring is low, then the probability of infant death before 12 months of age will be high, the relationship (correlation) between IBI and infant survivorship is intuitively correct. If females expend considerable time and effort in providing care for an infant, then mortality would be expected to be low. The corollary, however, is that if mothers invest heavily to ensure the survival of a current offspring, then their ability to invest in a subsequent offspring is postponed, and this will be reflected in interbirth interval.

3.10 SUMMARY

This chapter has reported, for the first time as best I am aware, a significant seasonal effect in relation to the timing of births among *Papio* baboons. Baboon births in the Drakensberg Mountains occur significantly more often during the time of the year when the energetic costs of lactation for females will be lessened. The probability remains, however, that the timing of births is a fortuitous consequence of conception timing which,

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[8] Drakensberg (this study), Gilgil (Nicolson 1982), Amboseli (Altmann 1980), Okavango (Collins et al 1984), Ethiopia - Hamadryas (Sigg et al 1982), Mikumi (Rhine 1992; pers.comm.).

in turn, is related to the seasonal availability of food resources which impact on the length of infant dependency on mothers. It was shown that, as a consequence of extended infant dependency, female baboons in the Drakensberg Mountains experience longer intervals between successive births when compared with other baboon studies, but that this had positive implications for infant survival prospects.

In the chapter which follows, specific emphasis will be given to the trajectories of infant dependence, the development of independence, and the relationship between the two.

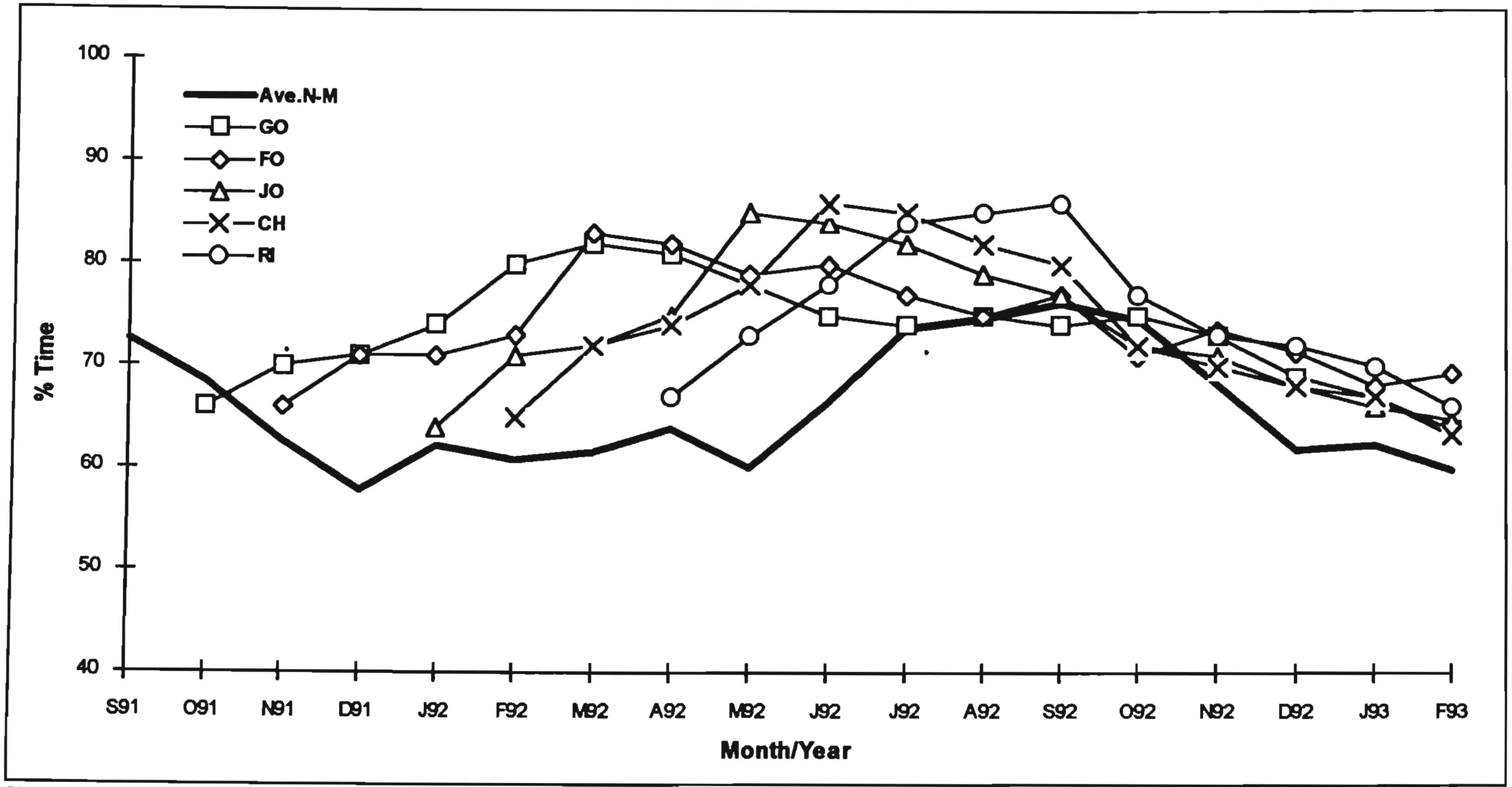

Figure 16: The amount of time that each mother in this study spent foraging at each monthly infant age. Also plotted (thick solid line) is the amount of time that females without infants (n = 4) in the study troop spent foraging during the corresponding months.

ADDITIONAL FIGURES

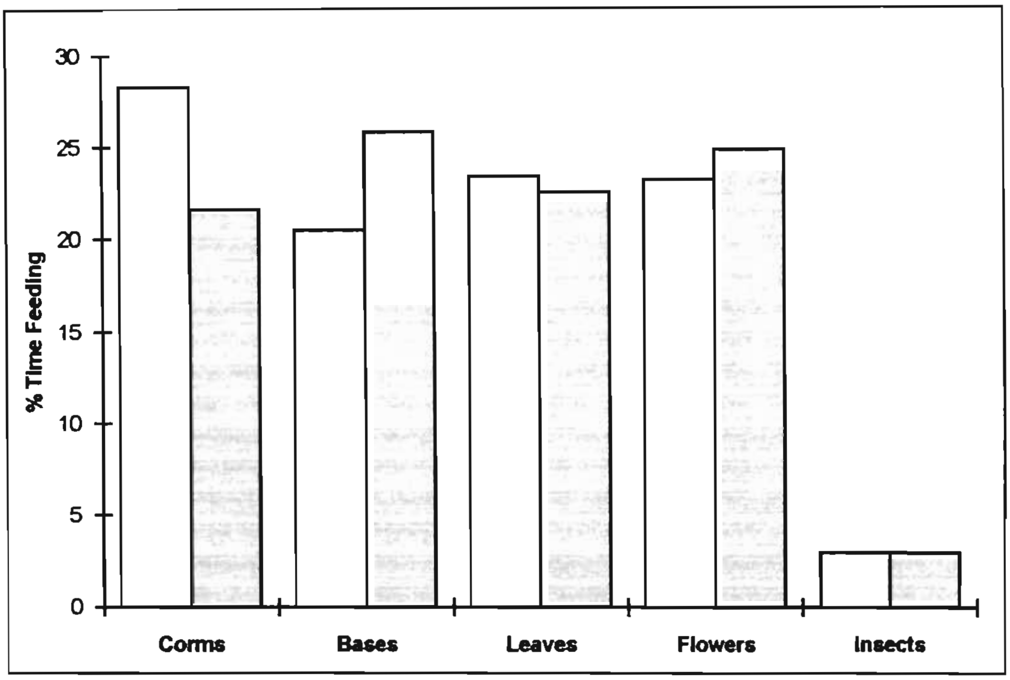

Figure A: Percentage time that adult (clear columns) and immature (filled columns) animals in the GCGR Low Troop spent feeding on different classes of food. Data from Byrne et al (1993).

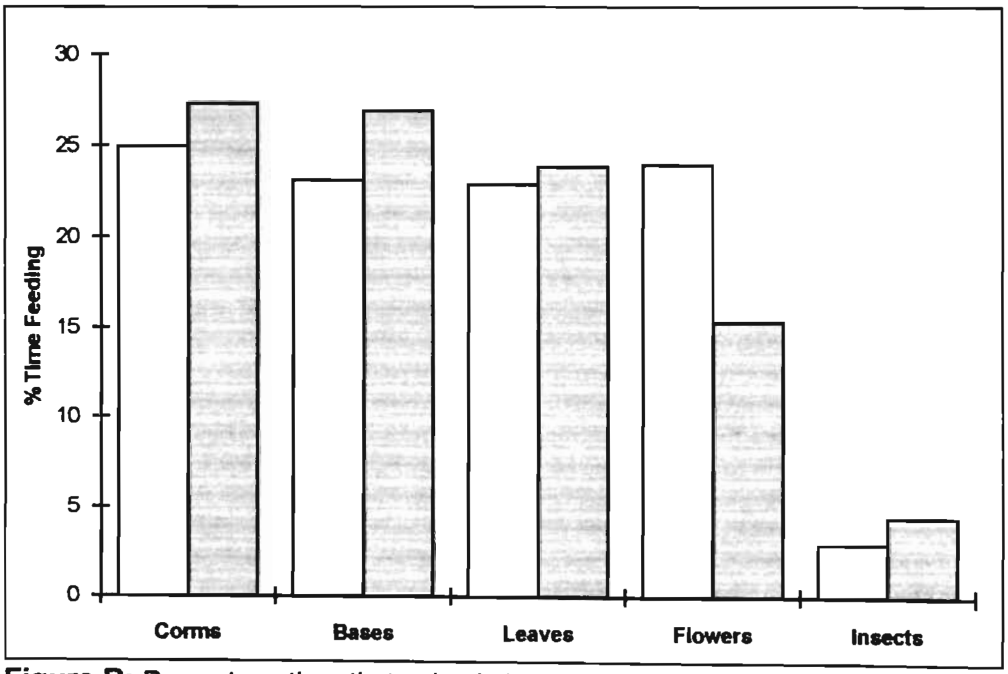

Figure B: Percentage time that animals in the Low Troop (clear columns) and the High Troop (filled columns) in the GCGR spent feeding on different classes of food. Note that percentages are the average for all age-sex classes in each troop. Data from Byrne et al (1993).

ADDITIONAL NOTES

MODEL OF MATERNAL FEEDING: GILGIL AND AMBOSELI:-

(i) GILGIL

Nicolson (1982) did not provide data on the time budgets of non-mothers in the Eburru Cliffs troop, and thus no direct comparison between the amount of time mothers and non-mothers spent feeding is possible. As a result, no 'base-line' measure by which to guage the effect an infant will have on the activity budget of a mother is possible. However, Bercovitch (1983) provides activity data for the Pumphouse troop at Gilgil. Comparing the daily time budgets of females engaged in consortships with those females that were not, he reported that females engaged in consortships spent approximately 54% of the time feeding (41% 'feeding' and 13% 'foraging', where feed and forage were operationally defined as "ingesting food or water from a stationary position, including eating food stored in cheek pouches" and " combination of feeding concurrent with locomotion", respectively. For purposes of comparison with this study, Bercovitch's feed and forage are combined). Females not involved in consortships were reported to 'feed' 52% of the time, and to 'forage' 13% of the time (total: 65%) (all data from Bercovitch 1983, Fig's 2 and 3).

If one assumes that females that are lactating (i.e. those that have a currently dependent offspring) are excluded from his analysis, then his sample should consist of those females who do not have infants and possibly some females whose infants are almost completely independent, and thus do not place considerable demands on their mothers. Given this assumption, it is then possible to accept the average time non-mothers spent feeding as the average between consort and non-consort females, which is 59.5%. This represents a greater amount of time spent feeding than reported for Nicolson's (1982) mothers in the Eburru Cliffs troop (except during the 16th month post-partum when feeding comprised 61% of the activity budget).

(ii) AMBOSELI

The base-line measure in Altmann's model against which an increase in maternal feeding is measured the amount of time that a mother should spend feeding in order to meet her own energetic requirements. One of the factors which Altmann considered in deriving this level was the assumption that a female in late pregnancy has the same energetic requirement as a non-pregnant, non-lactating female of the same total weight. However, more recent work by Bercovitch (1987a) calls into question the assumption that weight differentials will be small and therefore negligible. He found that pregnant females weighed more than non-pregnant, non-lactating females. Although the difference in weight was not significant, Bercovitch suggested that this may have been due to sampling error where "... the magnitude of possible weight differences between pregnant and cycling females would be diminished if pregnant females were not near term" (p.190-191).

CHAPTER 4

THE ECOLOGICAL CONTEXT OF INFANCY: I

4.1 INTRODUCTION

Primate survival and reproductive success is, according to Rhine *et al* (1984), fundamentally conditional upon an animal's successful transition from dependence upon others to more independent behaviour. These states of dependency and independence represent two stages of infant development which are respectively characterized by (i) a period during which the infant is totally dependent on its parent(s) for nutritional requirements, care, and transport, and (ii) the second period during which time the infant is no longer dependent on parents for food and transport yet, nonetheless, relies on its mother and other close relatives for social support against other group members and predators (Dunbar 1988). The length of the initial period of intense infant dependence varies among primates, with larger bodied animals requiring longer periods of nurturance (Goodall 1967; Ingram 1977; Wright 1986; *cited in* Dunbar 1988). Further, there is a proportional increase in the infant's care-requirements with its increase in weight (Altmann 1980).

Relative to other orders, primate infants experience a prolonged period of dependency between birth and maturity (Lancaster 1972; Kaufman 1976; McGrew 1977; Altmann 1980; Lee 1983a, 1984*a*; Berman 1983; Attili 1985; Walters 1987; Hauser *in press*). Hauser posits that among nonhuman primates there occured strong selection pressure for an extended period of immaturity during which a variety of skills are developed and fine-tuned. He suggests that such dependency is necessary given the fact that primate infants are initially fed a diet of milk and thus obtain only an indirect introduction to the foraging environment. Given this, he claims that learning plays an important role in the acquisition of foraging skills and the development of an adult-like diet. Further, in order to fully comprehend the transition to foraging independence, Hauser (*in press*) argues that a thorough understanding of the precise form the weaning process takes is necessary in that it determines when the infant begins to learn about potential food sources.

In the previous chapter infancy was considered from the perspective of the mother. Attention was given to the costs incurred by females who have dependent infants. It was shown that the presence of an infant has significant consequences for female baboons in general, and specifically for the Drakensberg females. It was argued that the presence of an infant affects the amount of time a female can allocate to her various maintenance activities, with the primary consequence being an increase in feeding time to meet the energetic requirements of both mother and infant. It was shown that mothers in the present study not only spent more time feeding than non-mothers, but also that they continued to feed above these non-maternal levels for a longer period of time than may have been expected from comparative studies. Additionally, mothers in the present study fed at levels above those that would be expected given the assumptions underlying Altmann's (1980) model of maternal feeding.

Throughout the previous chapter, general reference was made to '*the costs of reproduction*' for females. However, little specific mention was made of the categories of care mothers provide for infants, and the costs to the mother of each. This chapter begins by describing these categories of care, and how the measured decline in each has, and can be, utilized to chart the development of infant independence. Consideration is given to the concept of weaning as it relates to the infant transition from dependency to more independent behaviour. Data describing the trajectories of infant development toward independence are presented and discussed.

4.2. INFANT DEPENDENCY: CATEGORIES OF CARE AND THE COSTS INCURRED BY MOTHERS

An 'appropriate' maternal strategy should be one in which females provide only sufficient care for an offspring such that it can survive a reallocation of her care from a current to a future offspring. There are, as identified by Altmann (1980), four primary categories of maternal care that baboon mothers provide;- these relate to (i) the provision of nutrition through nursing, (ii) the provision of transport, (iii) protection from disease and ectoparasites through grooming and restricting early infant exploration and social contact, and (iv) protection from predators which may be achieved by carrying infants away from danger. Each of these is briefly considered below

4.2.1. THE COST OF TRANSPORTING A DEPENDENT INFANT

Insofar as locomotory care is concerned, it has been argued that the energetic cost of transporting an infant is proportional to the additional weight involved (Givoni and Goldman 1971; Soule *et al* 1978; *cited in* Altmann 1980). It would thus be predicted that mothers should no longer provide transport once the infant is able to stay with the group on its own. However, if the mother is still the sole provider of infant nutrition, then the cost in terms of energy expended in infant locomotory independence may exceed the cost incurred by the mother were she to continue carrying it. That is, infant locomotory independence will have certain consequences in terms of providing nutritional care.

4.2.2. THE COST OF INFANT NUTRITIONAL CARE

Apart from normal-growth caloric requirements, increased infant activity levels will result in heightened infant nutritional requirements which the mother must provide through nursing. Altmann (1980) thus speculates that, from the mother's perspective, it would be preferable for a nutritionally dependent offspring to remain in passive contact. In support of this, van Schaik and van Noordwijk (1985) found that, among Sumatran long-tailed maçaques (*Macaca fuscicularis*), females with young infants (2-5 months old) spent less energy in activities related to foraging than did females with older infants (5 - 9 months) where, presumably, younger infants spent more time in contact with mothers and were transported by mothers

(Berman 1978 *in* Altmann 1980). However, would such maternal restriction on infant movement be necessary if the infant was independently out of contact *and* harvesting some of its own food items? Altmann (1980) believes that such would be the case *only* if the caloric costs to the mother are less than the calories assimilated by the infant from independent feeding. In practice, however, it may occur that as a result of either infant knowledge or physical-deficits, appropriate food items may neither be available nor accessible for harvesting and incorporation into the infant diet. These deficits, as they may impede the transition from a dependent to an independent diet, are noted by S. Altmann (1991) when he points out that "... an infant's success at making this transition depends heavily on the timely acquisition of a considerable repertoire of selective foraging and harvesting skills" (p.420). Thus Altmann (1980) concludes that both infant physical development and the availability of 'weaning foods' will be important factors in the determination of the rate and age of infant self-sufficiency, thereby contributing toward the maximization of female reproductive effort.

4.2.3. THE COST OF PROTECTING INFANTS FROM DISEASE AND PREDATORS

A semi-independent infant which spends the day moving through and playing in shrubs and grass will, according to Altmann (1980), have a higher density of ectoparasites, and hence will be more susceptible to disease, than will one which is carried and restrained by its mother. Therefore, given a particular infant weight and body size, mothers will probably need to spend more time grooming and cleaning semi-independent infants than those that are dependent. Similarly, the effort required by mothers to protect dependent, and 'in-contact' offspring from predators will be significantly less than protecting infants that are out of contact. Within the context of the present study, only the former two types of maternal care are considered. As mentioned in Chapter 3, predation on baboons in the Drakensberg Mountains is negligible, while data on ectoparasitism are not available.

In short, mothers should weigh the cost incurred by providing a specified amount of each category of care against the benefit she derives from doing so. When the costs begin to outweigh the benefits, mothers should cease to provide such care at such levels. The point at which a reallocation in the amount of maternal care provided occurs has been referred to as the "weaning period".

4.3 WEANING

The term *weaning* has, at best, been ill-defined with varied meanings having become attached to it (Martin 1984*a*). As a result, he claims, the term has frequently been left undefined. Weaning has classically been thought of as a gradual process through which parous mammals decrease the dependence of their offspring on milk, often involving maternal aggressive acts toward offspring which might range from subtle signals to active fighting (Berger 1979*a*). In terms of this perspective, weaning is confined to mammals and thus is exclusively associated with animals that suckle their young (Counsilman and Lim 1985). While Martin (1984*a*) concedes that the measure of energy transfer through lactation is probably the most promising means of describing weaning, Galef (1981) and Martin (1984a, 1986) nonetheless advocate the use of a broader sense of the term that extends beyond lactation. They base this on their belief that weaning encompasses an entire array of behavioural, nutritional, morphological and physiological changes that, taken together, represent the transition to an independent adult existence. Thus they qualify the 'classical' approach to weaning by contending that not only is it a gradual and progressive reduction in the rate of milk transfer from mother to young which is accompanied by an increased intake of solid food by the offspring, but further that it entails profound behavioural changes in the parent-offspring relationship. Such a transition, they argue, may span an extensive period in ontogeny. Following from this point is the one made by Martin (1984*a*, 1985) and Collinge (1987) who suggest that due to the complex and gradual nature of weaning it is more usefully considered as a process rather than as a denoted point in time.

4.3.1 WEANING AND THE DEVELOPMENT OF INDEPENDENCE

Apart from definitional and terminological confusion, the issue of weaning has further generated debate in that it has been questioned whether emergent infant independence is promoted or retarded through weaning. Focus has been directed toward the relationship between, on the one hand, maternal rejection and aggression toward the infant and, on the other, the promotion of infant independence (Nicolson 1982). Hauser (*in press*) suggests that weaning forces infants to search for alternative sources of nutrition and energy in the face of declining resources imposed by mothers which, implicitly, supports the line of argument which claims that for normal development of independent functioning to proceed maternal rejection is necessary (Hansen 1966; Hinde 1969; Rowell 1972). In contrast, Rosenblum (1971) and Kaufman (1974) have argued that maternal punishment is likely to result in increased rather than decreased dependence on the mother. The dichotomy between the two view-points hinges on whether or not it is the mother or the infant that is responsible for initiating infant independence. The former emphasizes the role of the mother while the latter focusses on the importance of the infant's maturing motor and social capabilities which gradually allow the infant greater access to the physical and social environment (Nicolson 1982).

In evolutionary terms the proposal by Trivers (1972, 1974) has been influential. He argued that a genetic 'conflict of interest' between mother and infant is resolved through behavioural conflict between the two. Beginning with the premise that a mother has been selected to maximize parental investment[1] in all her offspring, current and future, and given that she is equally related to each, she then comes into conflict with a *currently dependent* offspring who attempts to maximize

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[1] Parental investment is defined by Trivers as "anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring" (Trivers 1974, p.249).

parental investment in itself. The argument follows that any particular current offspring is more related to itself than to its siblings, and thus should attempt to maximize the amount of parental investment in itself in order to enhance its own reproductive prospects, at the expense of any siblings. Once a mother reallocates her energy toward future progeny, the energy she is currently investing in an infant is decreased for that infant with a decrease in milk being the major proximate result. Consequently the current offspring is faced with a dwindling resource base and must turn elsewhere - independent foraging- to alleviate hunger (Berger 1979*a*). However, and importantly, the timing of this reallocation of resources should necessarily coincide with the availability of appropriate "weaning foods" as these will affect the length of lactation and hence the rate of infant development (Altmann 1980; Burger 1981; Pereira and Altmann 1985; Bercovitch 1987a; Lee 1987; and see Chapter 3). Thus, and within the framework of the parent-offspring conflict model, the covarying effects of food quality and interbirth interval should be considered when attempting to explicate the role of parent-offspring conflict in promoting independence (Hauser and Fairbanks 1988).

A number of points raised in the previous chapter are of relevance in this regard. It was noted that the Drakensberg females experience substantially longer intervals between successive births than do female baboons at other study sites. It was also argued that due to the seasonal variation of food quality in the Drakensberg, infants cannot be weaned at the expected time (cf: Altmann 1980), and that this has consequences for the length of infant dependence particularly insofar as the provision of nutrition is concerned.

In the sections which follow immediately, I will present data detailing mother-infant behaviours related to infant feeding. I will first consider the relationship between infant suckling and the development of independent feeding, and how the relationship between these two has further implications insofar as mother-infant contact is concerned. In this regard, preliminary data will be presented which relate to the infant transition to independent locomotion as this relates to mother-infant contact.

The chapter will conclude by returning to the concept of weaning. Following from the premise that mothers must at some time reallocate care away from a currently dependent offspring, and that this change in the mother-infant relationship has usually been considered in terms of weaning and how it relates to emergent infant independence, it is then possible to utilize a measure which will demonstrate the decline in maternal care. The data from this study, as well as comparative data from other studies will be presented to assess Martin's (1984a) model by which, he claimed, it is possible to delineate the weaning period with reference to the rate of decline in parental investment.

4.4 INFANT SUCKLING AND THE DEVELOPMENT OF INDEPENDENT FEEDING

4.4.1 INFANT SUCKLING ACTIVITY

Given the difficulty in distinguishing whether an infant was actually suckling when observed with the mother's nipple in its mouth, or whether it was simply using the nipple for comfort or as a fifth anchor-point (*cf:* Altmann 1980; Marsh 1992), the measures of suckling activity discussed below represent *opportunity* to suckle (sensu Nicolson 1982). The mean percentage time, per month of infant age, that infants spent at the mother's nipple is presented in Figure 17. Comparable data from five other baboons study sites are presented.

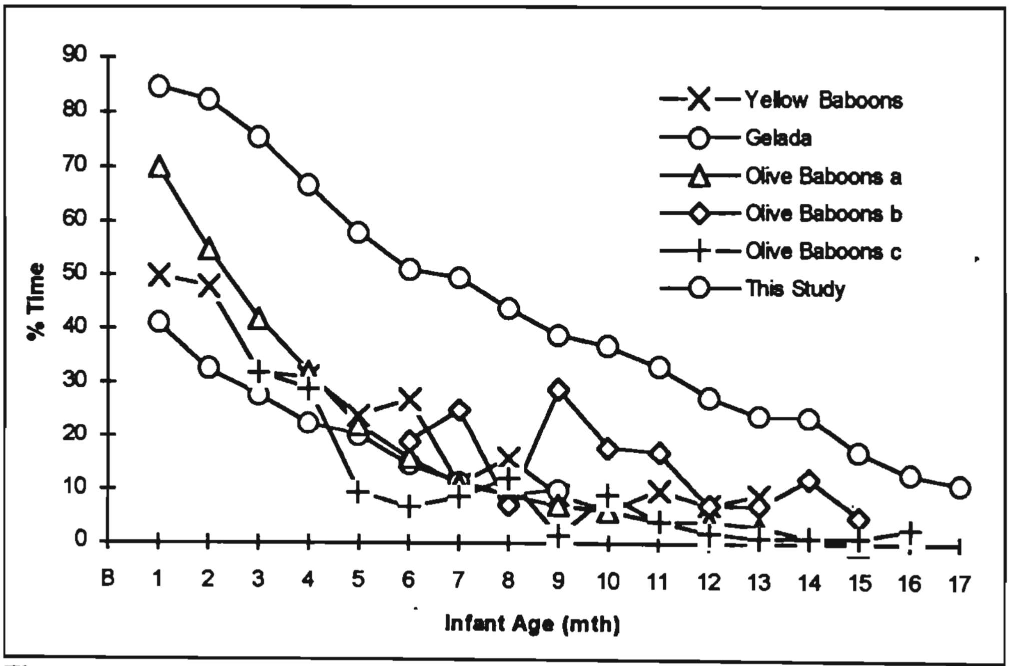

Figure 17: Percentage time infants spent on the nipple per month of infant age. The present study compared with infants from other study sites (Sources:- redrawn from - Nicolson 1982 (olive baboons, a); Nash 1978 (olive baboons, b); Marsh 1992 (olive baboons, c); Dunbar 1984 (gelada); Rhine *et al* 1985 (yellow baboons).

The mean percentage time infants in the present study spent at the nipple declined steadily with increasing infant age from a high of 84.68% (SE 1.12, N=5) at month-1 to 27.50% (SE 3.34, N=4) at month-12, to 12.81% (SE 0.8, N=2) at month-16 when the last data were collected[2]. A similar pattern of decline with increasing infant age is evident for the five comparable data sets presented in Figure 17. Apart from the similar value observed at month-9 by Nash (1978), the mean percentage time that infants in the present study spent at the nipple is consistenly higher, at each monthly age, than for the other studies.

Infant age had a significant effect on the amount of time spent at the nipple (ANOVA, $F = 52.01$, $p = 0.001$). Post-hoc analyses revealed that, in each of the month-by-month changes in amount of time spent at the nipple, only the changes during months 3-4 and 4-5 were statistically significantly (multiple range tests: See end of this chapter - Table A). Although the mean decline, for all infants, in time at the nipple was greatest during month 3-4 and 4-5, there was individual variability among infants as to the months of greatest decline[3] for each (G2 - months 11-12; F2 - months 3-4; J2 - months 8-9; C2 - months 7-8; R2 - months 5-6. See Figures 19a,b,c,d,e which plot, for each individual infant, the relationship between time at nipple and independent feeding).

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[2] Data on time spent suckling are available for one infant during it's 17th month. That infant was observed at the nipple 11.5% of the time.

[3] The month(s) of greatest decline was calculated by comparing the percentage change, from month to month, in a specified category of behaviour. Thus, for example, declining infant-mother contact with increasing infant age is the "general pattern" for baboons, yet the rate of decline will vary from month-to-month.

These differences between infants are considered in relation to the development of independent feeding.

4.4.2 THE DEVELOPMENT OF INDEPENDENT FEEDING

As would be expected (Nicolson 1982; Marsh 1992), the amount of time infants spent at the nipple is negatively related to the amount of time taken up by the independent harvesting of food items (Table 9). So, as their dependence on mothers for nutrition decreases, infants necessarily have to replace this by finding their own food. Further, the amount of time infants spent feeding is affected by increasing age where feeding time increases with age (ANOVA, $F = 37.45$, $p = 0.001$).

INFANT	NIPPLE AND FEED	
	r	p <
G2	-.9354	0.01
F2	-.8905	0.01
J2	-.8793	0.01
C2	-.9170	0.01
R2	-.8453	0.01

Table 9: Correlation coefficient for each infant in this study between time spent at the nipple and independent feeding.

The relationship between dependent and independent feeding for the infants in this study is plotted in Figure 18. Comparative data for time spent independently feeding for infants in two studies of olive baboons (Nicolson 1982; Marsh 1992) are also presented.

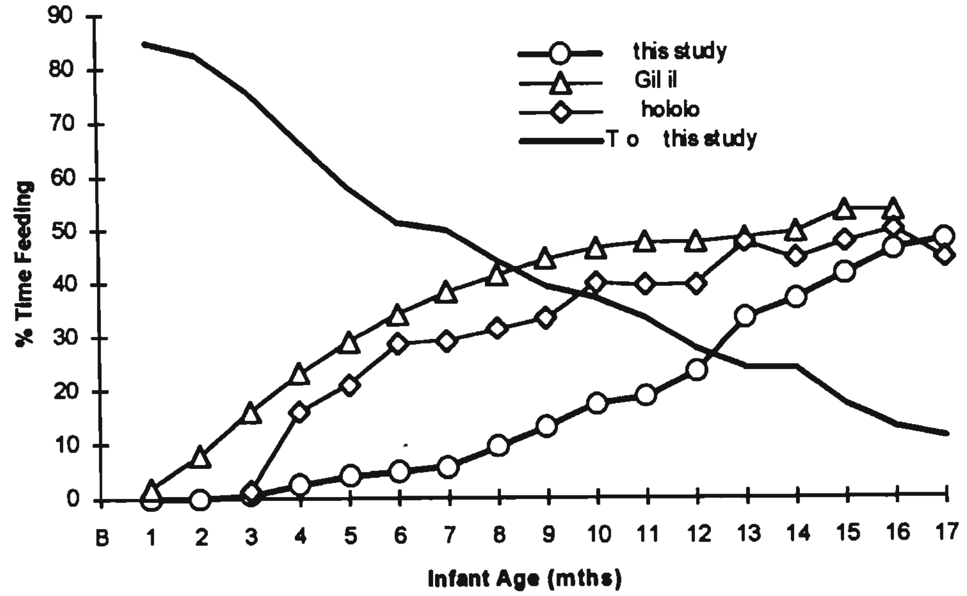

Figure 18: Mean percentage of time per month that infants in this study spent at the nipple (T-o-N) (solid line - no marker) and independently feeding (I-F). Also plotted is the mean percentage time spent independently feeding for infants at Gilgil (redrawn from Nicolson 1982) and Chololo (redrawn from Marsh 1992).

For the infants in this study, the mean amount of time spent independently feeding each month remained below 10% until the 9th month. Following this, feeding time increased rapidly;- by their 16th month, the infants for which data are available were harvesting their own food 45.8% (SE 1.6, N=2) of the time, although this figure remains considerably below the average feeding time for both juvenile and adult animals at Cathedral Peak (adult females[4] - 64.5%; juveniles - 61.8%). The development of this independent feeding will be examined

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[4] Note that the value of 64.5% is for adult females only, both mothers and non-mothers, and represents the amount of time females spent feeding during the month of February 1993 which was when the last data were collected for infants G2 and F2. Similarly, the value for juvenile feeding at Cathedral Peak is confined to this same month.

in relation to ecological conditions and constraints following birth.

When comparing the development of independent feeding for the infants across the three study sites, what is immediately apparent is the comparatively late age at which infants in this study started feeding at any substantial rate. At just about each infant age, the Drakensberg infants spent considerably less time harvesting their own food than did the infants in the two other studies. For Nicolson's (1982) infants, the amount of time spent independently feeding increased from approximately 2% during month-1 through 29% at month-5 to 47% at the 12th month. Independent feeding reached asymptote at month-15 when the infants were spending as much time feeding as were the adults in the troop (53%). A similar pattern was reported for the infants studied by Marsh (1992). She reported that the mean percentage of time her infants fed independently increased from 1.5% at month-3 through 21% at month-5 to 39.3% during the 12th month. The infants were reported to allocate the same amount of time to feeding as mothers did (52%) during their 19th month.

The idea that infants were not able to begin significant independent feeding during the dry months of the year was introduced in Chapter 3. Central to this argument is the recognition that surface vegetation, which constitutes 'appropriate weaning food' (Altmann 1980), dies back progressively during the dry winter months in the Drakensberg. Also referred to in the previous chapter was the finding of Whiten *et al* (1987) that, as a consequence of this decline in the availability of surface vegetation during these months, the Drakensberg baboons alter their foraging strategy to utilize underground food items.

To assess more directly the relationship between food availability and the development of independent feeding by infants, the protein content of grass was correlated with the mean amount of time, at each monthly age, that each infant was observed to be feeding independently. As pointed out in Chapter 3, the protein content of grass can be used as an indicator of the quality of surface (weaning) food available to infants.

INFANT	ALL MONTHS		INDEPENDENT FEEDING MONTHS	
	r	p <	r	p <
G2	0.1676	.5202	0.5476	.0427
F2	0.1922	.4757	0.4527	.1041
J2	0.4891	.0759	0.5772	.0494
C2	0.5079	.0764	0.5565	.0754
R2	0.4932	.1232	0.4380	.2777

Table 10: Correlation coefficient for the relationship between mean amount of time per month that each infant fed independently and the percentage grass protein. The coefficient for each infant for ALL MONTHS include data for every month following birth, while the coefficient for INDEPENDENT FEEDING MONTHS includes only the monthly observations which followed the timing of first observed infant independent feeding. : significant ($p < 0.1$)

When all monthly feeding observations were included in the analysis, only the feeding data for two infants were significantly related to grass protein content (Table 10).

However, when the first 2 or 3 months of complete infant dependence on mothers were excluded from the analysis, the relationship for three of the infants reached significance while that of a fourth infant (F2) just missed significance (Table 10). Thus, as grass protein content declined, so too did the amount of time infants spent independently feeding. The fact that the relationship between feeding and protein content became positive only in the latter set of correlations is not unexpected given that during first 2-3 months of life baboon infants are overwhelmingly dependent on their mothers for nutrition (Altmann 1980; Nicolson 1982) and hence would not be expected to be engaged in independent feeding.

In relation to the two features of foraging during the dry period that were referred to above, it was hypothesized that infant baboons in the Drakensberg may experience knowledge and physical-deficits which prevent them from exploiting the same resources that adult animals do. That is, if for whatever reason young animals are not able to exploit the same food sources that adults do during the winter, and if alternate foods in the habitat are not available, then young animals should necessarily display little independent feeding. That infants are probably constrained in this manner is highlighted when one considers the differences in the trajectories of independent feeding for each infant and which are described below (Figures 19a,b,c,d,e).

For the two infants born early in the summer months -(infants G2 and F2 - born September and October 1991 respectively;

Figures 19a and 19b)- some feeding was observed for the first time during their respective fourth and third months, although the amount was extremely small.

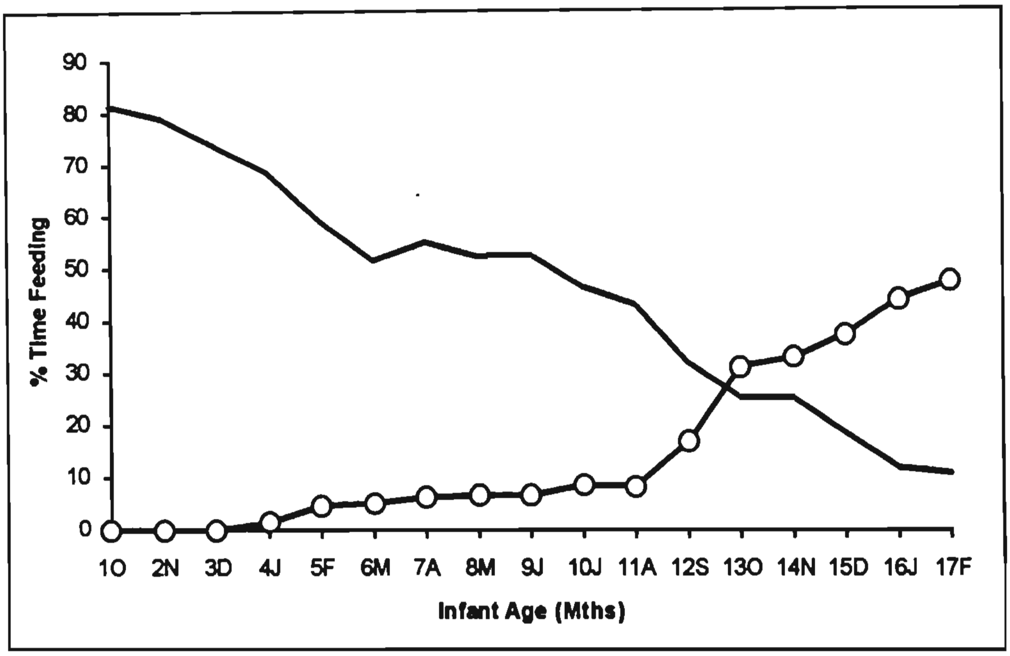

Figure 19a: Mean percentage time per month that infant G2 spent independently feeding (marked line), as well as mean percentage time per month that he spent at the nipple (unmarked line). Letters at each monthly age correspond to month of year where '1O' refers to Month-1 during October.

For infant G2, over the period 4-11 months of age, the average time per month dedicated to the harvesting of food was 6.02% (range: 1.5% - 8.66%), with the first attempt at independent feeding first observed during his fourth month. After month-11 (August 1992) there was an increase in feeding time, rising through 16.81% at month-12 to 47.55% at month-17 when the last data were collected. It was over the period 12-13 months that the increase in the month-to-month change in time spent independently feeding was the greatest for this infant. The timing of this followed the sharpest decline in the amount of time he spent at the nipple (months 11-12). Months 12 and 13 of this infant's life coincided with the beginning of the wet summer months (September and October). The months which preceded this increase in infant feeding time, when G2's feeding time remained at low levels, covered the dry winter period during which, it has been shown, easily obtainable surface food resources are not present in the habitat.

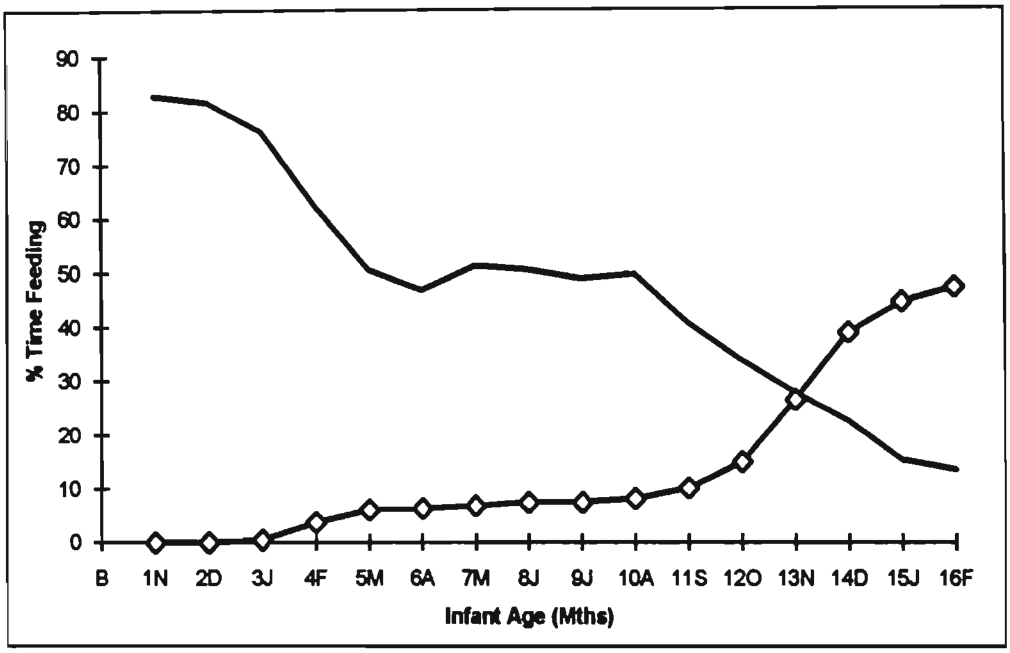

Figure 19b: Mean percentage time per month that infant F2 spent independently feeding (marked line), as well as the mean percentage time per month that he spent at the nipple (unmarked line). Letters at each monthly age correspond to month of year where '1N' refers to Month-1 during November.

A similar pattern is evident for infant F2 (Figure 19b). For this infant, the average amount of time per month dedicated to feeding over the period 3-10 months was 5.83% (range: 0.5% - 8.16%) which increased through 10.12% at month-11 to 47.3% at month-16 when the last data were collected on this infant. As with infant G2, the month during which independent feeding was first observed for infant F2 (month-3) is consistent with the reported timing of independent feeding (± 3 months) for the infants studied by both Nicolson (1982) and Marsh (1992). The sharpest increase in the month-to-month change in F2's feeding time occured during months 13-14 (November - December) which, although later than observed for infant G2, also corresponded with wet summer months and their associated changes in the quality and quantity of available foods in the habitat.

For the two infants born during the middle of the summer - (infants J2 and C2 - born December 1991 and January 1992 respectively; Figures 19c and 19d)- a similar pattern of low rates of feeding during winter months, with a subsequent increase during the wet summer months is apparent.

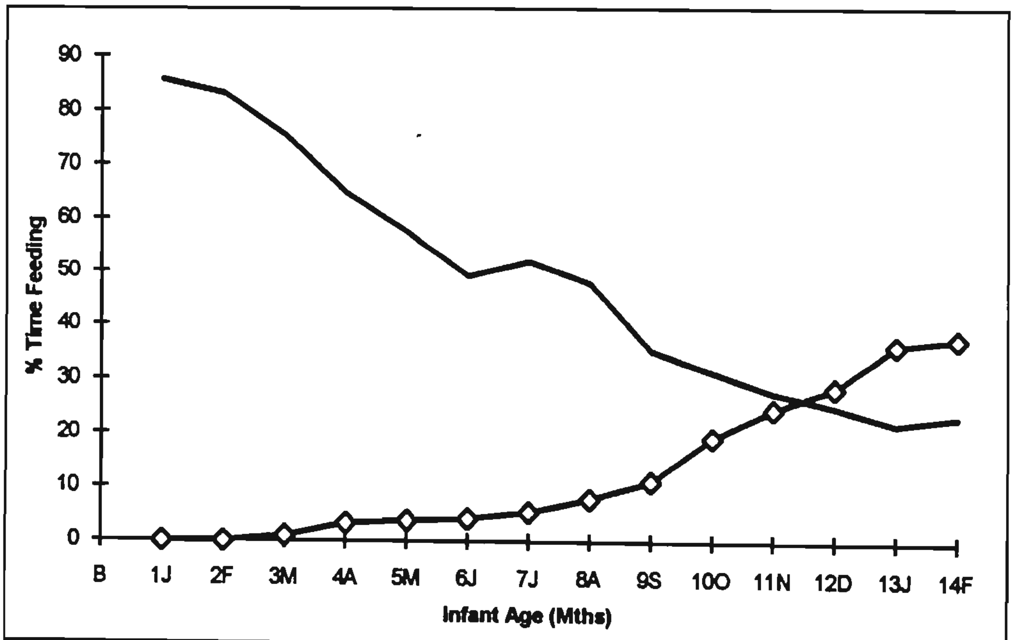

Figure 19c: Mean percentage time per month that infant J2 spent independently feeding (marked line), as well as the mean percentage time per month that he spent at the nipple (unmarked line). Letters at each monthly age correspond to month of year where '1J' refers to Month-1 during January.

As with infants G2, F2, and those in the Nicolson (1982) and Marsh (1992) studies, the first time both J2 and C2 were observed to feed independently was during their third month of life (March and April respectively). Yet, as with the two early born infants, the amount of time per month that J2 and C2 spent feeding did not appreciably increase until their respective tenth and ninth months (Figures 19c and 19d). At the end of J2's fourteenth month when data collection ended, he was feeding 37.42% of the time, while at the end of C2's thirteenth month, she was feeding for herself 37.77% of the time.

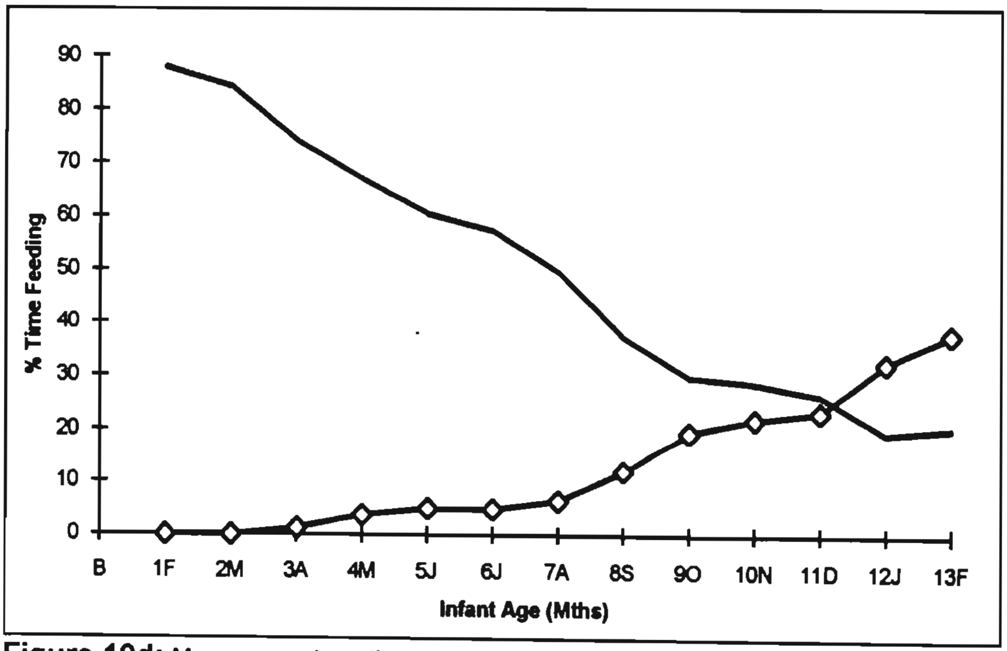

Figure 19d: Mean percentage time per month that infant C2 spent independently feeding (marked line), as well as the mean percentage time per month that she spent at the nipple (unmarked line). Letters at each monthly age correspond to month of year where '1F' refers to Month-1 during February.

For the fifth, late born infant -(R2 - born March 1992; Figure 19e)-, independent feeding was first observed during her fourth month (July 1992). For this infant, feeding time increased slowly during the following months, with an appreciable increase occurring during and after month-8 (October 1992). When the last data were collected for this infant at the end of her eleventh month, she was spending 26.02% of the time feeding. The age at which she began to significantly increase the amount of time harvesting her own food was earlier than that for the other four infants in the study. In comparison with the other four infants, by her eleventh month R2 was feeding more of the time than any of the other infants (R2 = 25.2%; G2 = 8.42%; F2 = 10.12%; J2 = 24.42%; C2 = 23.32%). Whether she was able to sustain this increase during the winter months which followed the end of data collection, or whether she again became reliant on her mother is not known. There was a slight decrease in her feeding time between months 10-11 when she was spending approximately the same amount of time feeding independently as she was at the nipple. It is possible, but by no means certain, that she would not have been able to further increase the amount of food she harvested independently. This latter assertion is made within the context of the aforementioned increased reliance by adult animals on underground food sources during the winter months, combined with the observation that none of the other four infants were observed before their twelfth month to successfully harvest underground food items.

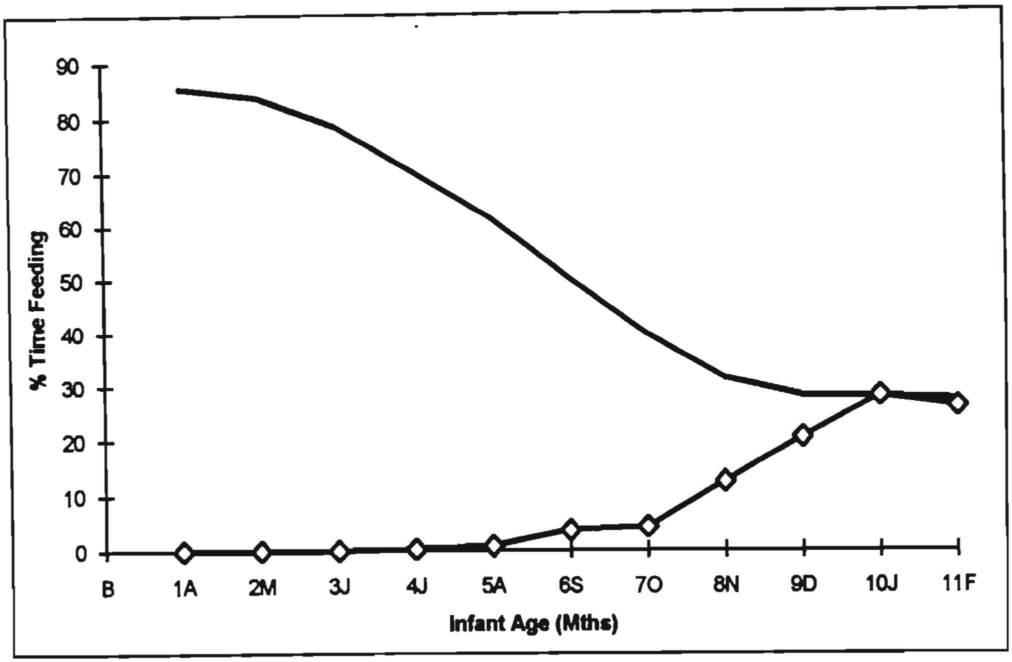

Figure 19e: Mean percentage time per month that infant R2 spent independently feeding (marked line), as well as the mean percentage time per month that she spent at the nipple (unmarked line). Letters at each monthly age correspond to month of year where '1A' refers to Month-1 during April.

The characteristic feature of each of the five trajectories of independent feeding is that time spent feeding increased, for all infants, during the summer period. So, whereas adult animals are, during the same time, able to decrease the amount of time they allocate to feeding (Byrne *et al* 1990b, 1993; Whiten *et al* 1987; this study - Chapter 3), infants increase their feeding time. Thus, it is possible that some of the same factors which allow adult animals to decrease feeding time (viz. abundant surface vegetation with (comparatively) high protein content) enable increased independent infant feeding.

It should be noted that even though it has been suggested here that infant feeding effectively begins around infant age 5 months, albeit at low levels, infants in this study were observed as early as their second months to interact with food items. However, they did not appear to be ingesting the food. They were seen to pick at grass and/or the remains of food that adult animals had discarded, and then (often) place the food in their mouths. This was followed by active spitting of the food from the mouth. It remains a possibility that through interaction with food in this way they were obtaining some nutritive value, but the amount of any possible benefit cannot be known. Nonetheless, even if some benefit was obtained, such events comprised a negligible proportion of feeding related activity.

If, as has been suggested in relation to the development of independent feeding, infants are constrained by variable ecological conditions in the timing at which they can demonstrate some significant degree of nutritional self reliance, then their dependence on mothers for food should be reflected in patterns of contact between the mother and infant. Mother-infant contact patterns are presented in the section which follows.

4.5 CHANGES IN MOTHER - INFANT CONTACT

Given the generally reported observation (Altmann 1980; Nicolson 1982; Marsh 1992) that young baboons initially spend the first few months postpartum in close spatial proximity to their mothers, and that this proximity declines with increasing age, the section which follows focusses on mother-infant contact. Particular emphasis is given to the changing nature of contact in relation to both age and infant feeding patterns. That is, it has been argued that infants in the Drakensberg are constrained by local ecological conditions in the timing of the development of independent feeding. If this is correct, then their reliance on mothers as the only alternate source of nutrition should be reflected in their spatial relationships with mothers.

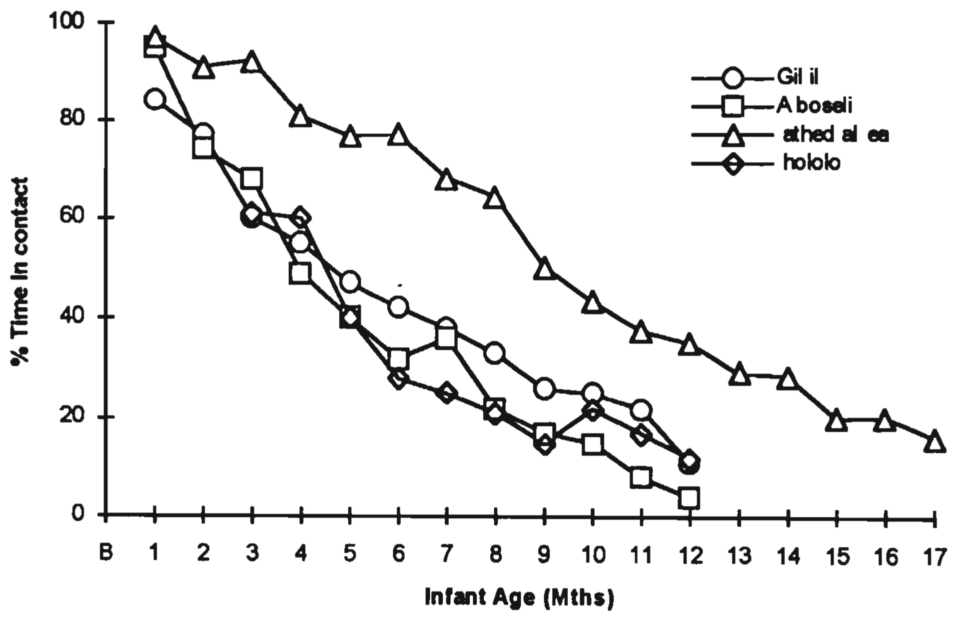

Figure 20: Comparison of percentage time infants spent in contact with their mothers at Cathedral Peak (this study), Chololo (redrawn from Marsh 1992), Gilgil and Amboseli (both redrawn from Nicolson 1982).

The mean percentage time, at each monthly infant age, that infants spent in contact with their mothers, regardless of infant behaviour (e.g. at the nipple, dorsal riding, resting, grooming), is plotted in Figure 20. Also plotted are comparative data from three other baboon study sites. As with infant time at the nipple (Figure 17), the general pattern of declining contact time with increasing infant age is similar across study sites.

Mother-infant contact for the animals in this study declined from a high of 97% (SE 0.75, N=5) during the first month of life to 35.1% (SE 1.80, N=4) at month-12, to 20.4% at month-16 when the last data were collected (and 16.2% for infant G2 during his 17th month). The rate of decline in contact time was the greatest during months 8-9 of infant life. Similar to the pattern reported above for infant time at the nipple, mother-infant contact for the animals in this study was observed at levels consistently above those reported from the comparative studies. That is, mothers and infants in this study spent, at each monthly age, more time in contact than did the mother-infant dyads in the other studies. It will be shown that these comparatively high levels of contact are at least partially accounted for by extended infant reliance on their mothers for nutrition.

The high levels of mother-infant contact during the first few months of life are not unexpected given that mothers not only carry infants for much of the first few months post-partum, but also that mothers usually keep infants in ventral contact while resting and during stationary social activities. However, as infants begin to independently move about the habitat, particularly when mothers and the troop are stationary, the amount of contact time within the mother-infant dyad would be expected to decrease.

With increasing age, infants not only spent less time in contact with their mothers (see above), but the nature of the contact changed in terms of activities, or type of interaction, that the dyads engaged in during contact periods. Plotted in Figure 21 is the proportion of total contact time taken up by various mother-infant interactions.

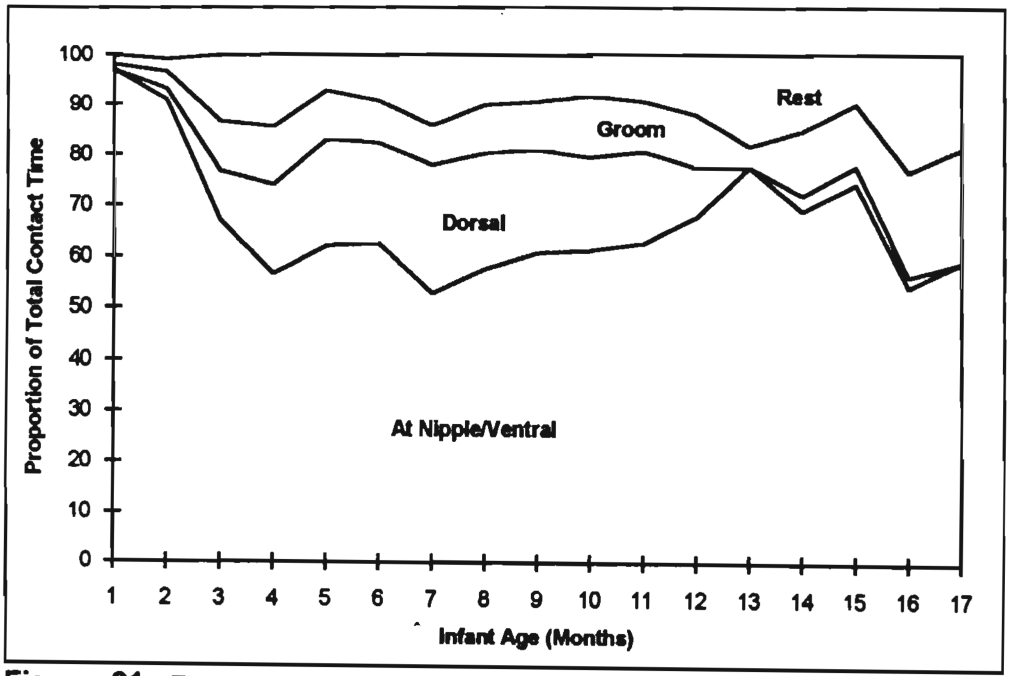

Figure 21: The proportion of total mother-infant contact time taken up by various behaviours. 'At Nipple/Ventral' includes infant ventral contact; 'Rest' and 'Groom" contact refers to resting and grooming contact that occured outside of the ventral position.

Infant time spent 'At Nipple/Ventral' (see additional notes at the end of this chapter) accounted for a relatively stable proportion of all mother-infant contact. On average, throughout the 17 months over which data were collected, 66.7% of total contact time was taken up by this category of contact. The sharp decline in 'At Nipple/Ventral' time during months 3-5 reflects the decrease in time that infants were carried in the ventral position, and hence the increase in the proportion of time that they were in contact with their mothers in the dorsal position (see below).

Both 'Rest' and 'Groom' contact refer only to mother-infant contact which occured while infants were not in the ventral position. As a proportion of total contact, these categories of contact comprised, on average, relatively small proportions of total contact ('Rest' = 9.4%; 'Groom' = 9.0%). While these values may appear less than expected, it should be noted that any resting or grooming that took place while the infant was in the ventral position was subsumed under the 'At Nipple/Ventral' category of contact and thus the extent of both 'Rest' and 'Groom' contact may be under-represented, while 'At Nipple/Ventral' contact may be over-represented.

The decline in the proportion of 'At Nipple/Ventral' contact at month-13 coincides with the sharpest increase in the rate at which infants fed independently, and thus probably when they spent less time relying on their mothers for nutrition (and hence were in the ventral position). At the same time, the proportion of contact time categorized as 'Rest' and 'Groom' increased where, with the decline in 'At Nipple/Ventral' contact, resting and grooming interactions became less subsumed under the 'At Nipple/Ventral' category.

From about three months of age, dorsal contact increased as a proportion of all contact as infants changed from a ventral-carrying position to one of dorsal-riding (Figure 22a). With increasing age, dorsal riding decreased as a proportion of total contact as infants began to move independently (Figure 21).

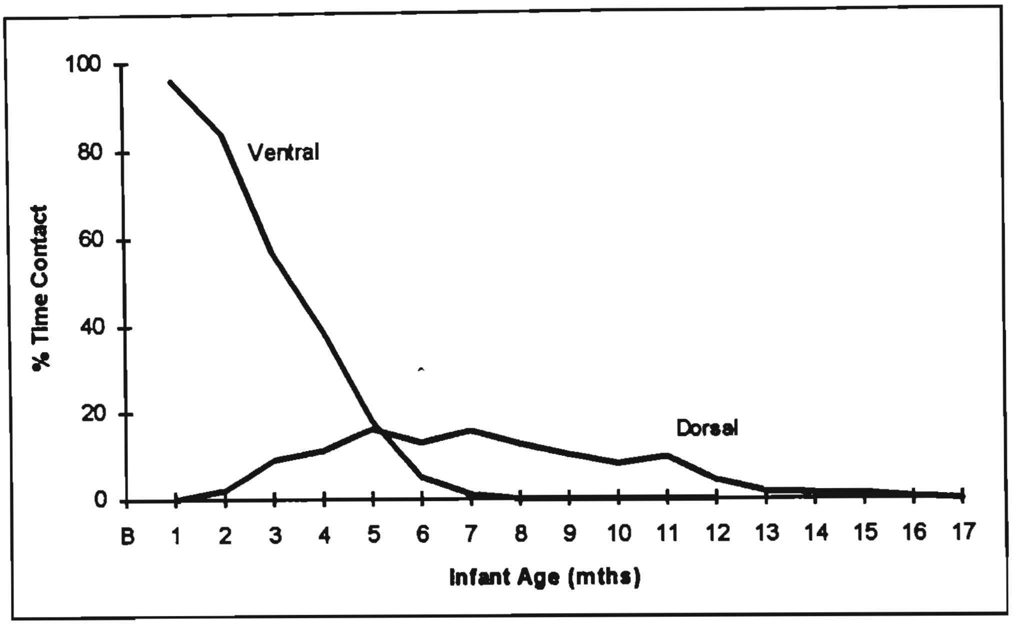

Figure 22a: Mean percentage of time per month infants spent in ventral and dorsal contact with mothers.

The appearance of dorsal riding at around 2 months of age is similar to the age at which it was observed for infants in the studies of Altmann (1980) and Nicolson (1982). Marsh's (1992) study focused on infants from 3 months of age, and so the initial appearance of dorsal riding for her infants is not recorded. However, by 3 months of age her infants were observed in 'other' contact (which included dorsal contact) approximately 26% of the time which is higher than the 9% observed in this study during month-3. Nicolson's infants, at three months of age, were observed in dorsal contact approximately 18% of the time, while Rhine *et al*'s (1984)

Mikumi infants at the same age were riding dorsally approximately 10% of the time. These comparative data are presented in Figure 22b.

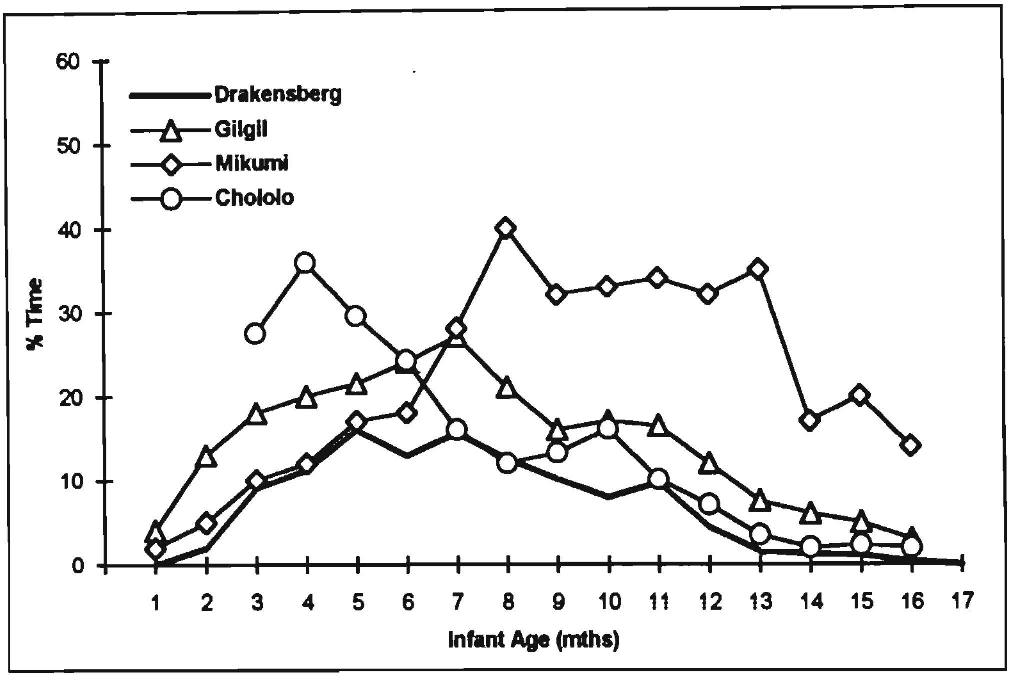

Figure 22b: Comparison of the mean amount of time spent in dorsal contact by infants in Drakensberg (this study), Gilgil (Nicolson 1982), Chololo (Marsh 1992) and Mikumi (Rhine *et al* 1984). Note that the Chololo data are those for 'other' contact, which included dorsal riding.

Differences across the study sites are apparent in the amount of time infants spent in the dorsal position. The average amount of time, across the infant ages presented in Figure 22b, that infants at the comparative study sites spent in dorsal contact were all higher than that for the Drakensberg infants (Drakensberg, 1-17 months: $\bar{x}$ = 6.7%; Gilgil 1-16 months: $\bar{x}$ = 14.47%; Mikumi 1-16 months: $\bar{x}$ = 21.81%; Chololo, 3-16 months: $\bar{x}$ = 14.37%). However, while the amount of time infants spent in dorsal contact may vary across studies, the general pattern of increasing and then declining contact is the same for each study. The 6.7% average figure for the Drakensberg infants is not, in any case, unexpected if it is noted that adult animals in the Drakensberg spent approximately only 10% of their time moving, and it is primarily during troop progressions or during troop flight that infants ride dorsally.

In summary, what has been shown thus far is that, with increasing age, infants show a change in the nature of their contact relationships with their mothers. Not only does the amount of contact time decline with increasing age, but the nature of contact that continues changes as well. Infants spend proportionately more contact time at the nipple, proportionately less time being carried in the ventral position, and proportionately more time being carried in a dorsal position, although this too declines with increasing age. This decline in reliance on mothers for transport corresponds with increased independent mobility by infants which will be described in the following chapter. The point is that nutritional reliance on mothers, and to a lesser extent transport reliance, are the most energetically expensive forms of maternal care, and thus mothers would be predicted to attempt to minimize the extent that infants are dependent on them in these areas as early as possible. That is, mothers should *wean* infants as soon as they are able to.

In the remainder of this chapter, I will be attempting to delineate the weaning process (or period) for the infants in this study. In order to do this, a model of weaning will be applied to the data observed for this study, and also to the data from comparative studies where they are available.

4.6 DELINEATING WEANING

Martin (1984a), following Trivers (1972; 1974), argued that during the post-natal period of parental care, parental investment rises steeply and that with increasing infant age the cost to the mother of providing such care increases. He suggested that given this relation between the rate of parental investment and offspring age, the phase of parental care during which the rate of parental investment drops most sharply, can be considered *weaning.* Martin's (1984) model has recently received attention in the literature, and has been used to guide interpretation of behaviours relating to parental investment in offspring (Gomendio 1991; Smith 1991; Bateson 1994). In terms of any attempt to identify or delineate weaning (or the weaning period), Martin's (1984) definition shifts the emphasis away from the last day of parental care (Smith 1991), and instead focusses on a phase of infant development during which parental investment is gradually withdrawn from the infant. Such a focus assumes that it is the parent who is guiding the time course of emergent infant independence in the sense that emphasis is placed on the parent and when it begins to decrease care given to a dependent offspring.

Presented in Table 11 are comparative data from a number of baboon study sites specifying measures of parental investment and the months of infant age during which the decline in the rate of investment was the sharpest.

Measure of Maternal Investment	(1)	(2)	(3)	(4)	(5)	(6)
Mother-infant contact	4-5	4-5	2-3	N-A	1-2	1-2
Infant ventral contact	2-3	4-5	1-2	1-2	N-A	
Infant time on nipple	3-4 4-5	4-5	1-2 2-3	2-3 6-7	N-A	1-2
Infant: Independent feeding[3]	12-13	3-4	1-2	6-7	N-A	5-6
Infant:Independent locomotion[3]	3-4	5-6		3-4	N-A	N-A
Mother: Infant carry (ventral + dorsal)	4-5	4-5	2-3	6-7	6-7[1] 3-4[2] 5-6[2]	
Infant: "Temper tantrums"[4]	N-O	6-7	5-6	N-A	N-A	5-6[5]

Table 11: Months of infant life during which the rate of decline for measures of maternal investment were the greatest for baboon infants at: **(1)**:- Cathedral Peak (this study), **(2)**:- Chololo (from Marsh 1992), **(3)**:- Gilgil (from Nicolson 1982), **(4)**:- Mikumi (from Rhine *et al* 1984, 1985), **(5)**:- Amboseli (from Altmann 1980; Altmann and Samuels 1992), and **(6)**:- Gelada infants (from Dunbar 1984; Dunbar and Dunbar 1988; Barrett, Dunbar and Dunbar, in press).

Where two time periods within a single measure of maternal investment are given (for any of the studies) , the rate of decline is the same for both.

(N-A) = data are not available; (N-O) = behaviour did not occur.

Notes: (1) For Alto's Group (from Altmann and Samuels 1992)

(2) For Hook's Group (from Altmann and Samuels 1992)

(3) These measures represent the rate of *increase* in independent *infant* behaviour.

(4) Months during which the *increase* in the rate of infant tantrums was the greatest.

(5) For the gelada, the data presented refer to the increase in the number, per infant, of rejections received. The number of rejections should correspond closely with the incidence in infant tantrums which, presumably, will result from rejections.

For two of the measures provided (*viz.*, infant independent feeding and infant independent locomotion) the category of behaviour should correspond with a 'maternally-driven' measure;- for example, the month(s) during which the rate of <u>increase</u> in infant independent feeding was the greatest should correspond relatively closely with the month(s) during which the <u>decline</u> in infant time on mother's nipple was the sharpest. This follows from the assumption that if mothers are reducing maternal investment in an infant, then the infant should necessarily turn elsewhere for the care that the mother was providing until that point.

4.6.1 DELINEATING WEANING: THIS STUDY

For the infants in the present study there appeared to be no consistent trend insofar as the months of sharpest decline on the various measures are concerned. The different measures of maternal investment, as well as the corresponding measures of infant independence, show little, if any, synchrony in the timing of rate of decrease (or increase, where appropriate). In terms of Martin's (1984a) model, the implication is that it is not possible, at least insofar as this study is concerned, to delineate 'the weaning period'. This lack of consistency between the measures is understandable within the context of the developmental trajectories described above, and which are interpreted below.

Insofar as the relationship between infant nutritional dependence and independence is concerned, it may well be argued that if Martin's (1984) model has any predictive value, then the period/months with the sharpest decrease in infant dependence on mothers for nutrition should correspond quite closely with the period/months during which infants substantially increased levels of independent feeding. From Table 11 it can be seen that this is not the case. Infant time at the nipple ("nutritional dependence") showed the sharpest decrease during the period months 3-4 and 4-5, whereas the sharpest increase in the amount of time infants spent feeding themselves ("nutritional independence") occurred only during months 12-13[5].

Now, if the model is correct in the sense that the decline in infant time at the nipple is indicative of decreased parental investment, given that it assumes that infant access to, and time at the nipple is a maternally-controlled measure of investment, then the probable conclusion to be drawn from the data for this study is that the significant decreases (see Multiple Range Tests: Table A at the end of this chapter) in infant time at the nipple at ages 3-4 and 4-5 months suggest that mothers were decreasing care in their infants at those times, and thus that this might represent the weaning period. However, such a conclusion has limited validity in that although infant time at the nipple may have been significantly reduced at those times, infants nonetheless continued to spend time at the nipple during the following months and, for those infants for which data are available, continued to do so until 16 or 17 months of age. In a sense, the discrepancy in the

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[5] If the month-by-month change in infant (independent) feeding time is confined to only the first 11 months (i.e. when data are available for all five infants in the sample), then the sharpest increase in infant feeding time occurred during months 10-11, which remains later than the sharpest decline in infant time at the nipple (months 3-4 and 4-5).

timing between the decline in infant time at the nipple and the increase in independent feeding leaves open the question as to what the infants did for nutrition after the 'weaning phase' and the time that they began to feed at any substantial rate for themselves. In answer, it has been shown that they continued to spend more time at the nipple than they may have been expected to from comparative study data.

In terms of the maternal provision of infant transport through carrying, parent-offspring conflict theory would predict that mothers should attempt to wean infants from riding (Nicolson 1982) and thus provide the impetus for infants to become independently mobile. While the data on the trajectory of independent movement by infants will be presented only in the following chapter, it should be noted here that the greatest change in the month-by-month amount of time infants moved by themselves (3-4 months) *preceded* the sharpest monthly reduction in the amount of time that infants were carried by their mothers, either ventrally or dorsally (4-5 months). Thus, certainly in terms of the relationship between riding and moving independently, changes in maternally driven measures of investment are not, as may have been expected, seeming to result in the impetus for infants to become independent. Rather, infants appear themselves to initiate behaviour (for example, independent movement), the consequence of which may be that mothers are no longer needed by the infant. Of course the possibility remains that, insofar as the development of movement is concerned, mothers may have reduced infant carrying *only once* infants had demonstrated their ability to move by themselves. However, if this were the case, then it would be expected that as soon as infants have demonstrated such an ability, mothers should refuse to carry infants at all, except perhaps during troop flight. This was not the case, as was shown above. Mothers continued to carry infants some of the time through to month-16 by which age, it will be shown in the next chapter, infants were spending as much time moving independently as were adult animals.

There is a sense in which the timing and presence of weaning, as it is usually conceived of (i.e. maternal restriction on infant attempts to obtain more care than mothers are prepared to provide), can be identified with some ease. That is, evidence of weaning processes should be provided by infant resistance to maternally imposed changes in care, where such infant resistance is manifested in weaning or infant tantrums. Infant tantrums will be considered once the comparative data have been considered in terms of the model of weaning.

4.6.2 DELINEATING WEANING: COMPARATIVE DATA

In contrast to the data in the present study, those for most of the comparative studies for which data are available indicate that 'maternally-driven' measures of declining investment appear to be consistent within a single study. That is, for example, the data reported by Marsh (1992 - column 2 Table 11) show that the rate of decline for 3 measures of maternal investment, and 1 measure of (increased) infant independence, was the greatest during months 4-5. Thus, mother-infant contact, infant ventral contact, and infant time at the nipple all showed the sharpest decline in the same months, which followed the greatest increase in the amount of time infants spent independently feeding (months 3-4). During the same months as contact and nipple time decreased, infant independent locomotion showed the sharpest increase. As with the data for the present study, this increased locomotion by her infants preceded the sharpest decline in the amount of time mothers carried infants.

The data reported by Nicolson (1982) for the Gilgil infants similarly show that rate of decline (as well as the rate of increase in infant measures) are clustered within a month or two of each other (column 3 Table 11). What is striking about her data are the early declines (and increases) on all the measures. Her data show that the greatest increase in independent feeding time for her infants occured during months 1-2. At face value, what this suggests is that her infants went from complete dependence on maternal milk to a significant reliance on solid foods. In reality, however, this cannot have been the case. What should be looked at in some detail in the future, are the magnitude of these monthly changes. For most of the Gilgil measures, the trajectories showed slow, but steady decline, with very little variability on a month-by-month basis.

As far as the Mikumi data are concerned (column 4, Table 11), a similar pattern for the Chololo and the Drakensberg infants in the transition from riding to independent movement is apparent. The Mikumi infants showed the largest increase in independent movement (3-4 months) before the sharpest decline in maternal carrying of infants (6-7 months). That this should be so for three studies for which the necessary data are available raises questions which a systematic study of the transition from dependent to independent locomotion may answer. There were two periods when the rate of change in infant time at the nipple declined the most for the Mikumi infants. The first (2-3 months) preceded the sharpest increase in the amount of independent feeding (6-7 months), while the second occured at the same time as significantly increased feeding.

In terms of comparisons of measures across study sites, there was seemingly little consistency in the timing of declining maternal investment. Thus, where some consistency was evident in a study, this did not necessarily coinicide with the consistency in measure evident for another study. This variability in the timing of the development of infant independence between studies is, in part, probably due to the differing ecological circumstances in which each of the studies were conducted as suggested in the previous chapter. Even so, the approach taken here which focusses on measures within studies, can profitably be used to look for trends in the pattern of mother-infant relations across studies. As a consequence, variability across studies in the timing of developmental events, once highlighted, may focus attention back to individual studies in order to understand more completely the the relationship between different aspects of infant development. This may be no more clear than in the case of the timing (or age) of infant temper tantrums, and their relation to measures of infant independence.

4.6.3 INFANT TANTRUMS: EVIDENCE OF WEANING CONFLICT?

Infant temper tantrums have usually been associated with maternal rejection of infant attempts to gain access to the nipple, to riding, and less usually, to infant contact with mothers (chimpanzees, Pan troglodytes: Clark 1977; yellow baboons, Papio cynocephalus: Altmann 1980; Japanese macaques, Macaca fuscata: Hiraiwa 1981; olive baboons, Papio anubis: Nicolson 1982, Marsh 1992; gelada, Theropithecus gelada: Barrett *et al, in press*). While there is disagreement as to the underlying dynamics which elicit tantrum responses (see section below), it is, for the present, sufficient to accept that *some* form of conflict between mother and infant is inherent in the relationship.

For the infants in the present study, it is particularly noteworthy that infant tantrums were not observed at any age. If infant tantrum behaviour has been correctly interpreted as *some* form of conflict between mother an infant (see discussion below; Altmann 1980; Nicolson 1982; Marsh 1992; Barrett *et al, in press*), then the obvious conclusion to be drawn from the fact that maternal rejections and associated infant tantrums were never observed during the course of this study, is that little, or no conflict between mother and infant occurred. It has been argued that maternal rejection of infant attempts to suckle or ride need not necessarily be overt, and indeed may be hard to distinguish from normal maternal behaviour where conflict is often inferred from the infant's tantrum response (Altmann 1980). It is therefore possible that rejection by mothers in the present study may have taken place, but in a form that was not accompanied by obvious infant distress. The observation reported for this study that maternal restriction on infant access to the mother and the care she provides was not actively enforced is suggested by the inconsistency in the data for this study presented in Table 11. That is, for example, while the <u>decline</u> in infant time at the nipple was the greatest during months 3-4 and 4-5, the sharpest <u>increase</u> in the amount of time that infants harvested their own food occurred only during months 12-13. In this regard it has been shown that the average amount of time that infants spent independently feeding remained less than 10% of the time until month-9 which, in the absence of any observations that infants were acquiring food elsewhere, necessarily implies that mothers must have remained the principle source of food for the infants until that age. That mothers did remain the primary source of nutrition for infants until that age stands in contrast to data reported for the other studies where infant suckling declined earlier and at faster rates than for this study.

For the three comparative studies for which data are available, the months during which.the rate of <u>increase</u> in tantrums was the greatest did not correspond with the months during which the rate of <u>decline</u> on maternally-driven measures was the greatest. For Marsh's (1992) study, tantrums increased the most during months 6-7 while infant time at the nipple as well as mother-infant contact declined most during months 4-5. Nicolson's (1982) infants demonstrated increased tantrums during months 5-6 while time at the nipple and mother-infant contact decreased most rapidly during months 1-2/2-3 and 2-3 respectively. The third study for which a measure of weaning conflict is available reported the sharpest increase in tantrums during months 5-6 which coincided with the months during which infants were observed to substantially increase the rate at which they harvested their own food (Barrett *et al*, *in press*; see note [5] Table 11). However, as with the Nicolson (1982) and Marsh (1992) studies, the months with the greatest decline in infant time at the nipple and mother-infant contact preceded the timing of these increased tantrums. That this is so seems surprising given that the occurrence of tantrums should provide some indication as to when mothers were most rejecting of attempts to gain access to some category of maternal care. This apparent paradox in the timing of tantrums remains valid even if tantrum behaviour is interpreted as conflict over the timing of access to categories of maternal care (see below).

More recent work has questioned the suitability of Trivers' theory in explaining the phenomenon of weaning conflict. Where Trivers supposed that weaning tantrums were the infant manifestation of maternal restriction on the amount of investment, or parental care, the infant can obtain, Altmann (1980) and Dunbar (1988) have argued that the conflict is less a dispute over the amount of care as it is over the timing of infant access to a category of maternal care. Their data demonstrate that for both yellow baboons (Altmann 1980) and gelada baboons (Dunbar 1988; Barrett *et al*, *in press*), mother-infant conflict arises from the imposition of constraints by the mother which makes infant access to care contingent on the current activity of the mother. In terms of this argument, at some point during infant development mothers should 'condition' infants to time their approaches for care to those times when such approaches will be acceptable to mothers. That is, infant access to the nipple and physical contact should be confined to those times when mothers are resting or socializing, rather than during those times when the mother is feeding or moving and hence the presence of a ventrally attached infant would hinder maternal activity.

Extending this, it might well be argued that *if* contact starts to become contingent at a specified age, and *if* weaning conflict is the outcome of disagreement over the *scheduling* of contact bouts, then rejection behaviours with, presumably, associated infant reactions to such rejection (i.e. tantrums) should be most evident at that age. Following from this, such tantrums should thereafter decrease in frequency as the infant becomes more accustomed to suckling at the appropriate time. While the data to test this argument are not available for the yellow baboons, they are for the gelada. Barrett *et al* (*in press*) report that gelada infant contact probabilities become contingent on maternal activity as early as 8 weeks of age. However, the rejection data that they provide show that maternal rejections[6] first appeared at infant age 3-months and then increased during the following months to peak during the 6th and then again during the 8th. Given that these peaks occur a number of months after infant contact probabilities became contingent on maternal activity, and given further that by month-6 infants were no longer attempting to approach mothers while they fed or moved, then it is not clear why mothers would be most rejecting of infants at this age if the infants were already behaving "appropriately".

4.7 SUMMARY

It was reported in the previous chapter that female baboons in the Drakensberg Mountains show extended interbirth intervals, and the point was made that this was due, in part to extended infant dependency, primarily in terms of maternal provision of nutrition. This chapter presented data to show that Drakensberg infants do indeed remain nutritionally dependent on their mothers for what is a comparatively long time. It was argued that, in line with the prediction of Altmann (1980) and others, that the timing of the development of independent infant feeding should optimally coincide with the availability of favourable weaning foods. For the Drakensberg infants, such foods are seasonally available, and so in the absence of alternate food sources, mothers necessarily

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[6] Note that the frequency of rejections referred to here relate specifically to those rejections experienced by infants when they attempted to gain access to mothers while mothers were feeding.

remained the principle source of nutrition. The consequences this may have, if any, will be considered in the next chapter which continues to describe infant trajectories of development toward the adult behavioural model. In particular, infant behavioural development will be considered in terms of the lack of any serious constraints on activity budgets as a result of delayed independent feeding which has been demonstrated in this chapter.

ADDITIONAL NOTES

During the first few months post-partum, it was difficult to distinguish whether infants were on/at the nipple or merely in the ventral position but not attached to the nipple. This was particularly true when a mother-infant dyad was engaged in activity at some distance from the observer and it could not be accurately ascertained what category of contact should be recorded. Accordingly, during these first few months, data recorded as being of one or the other category were pooled in order to minimize over- or under-representation of either.

TABLE A: MULTIPLE RANGE TEST FOR INFANT TIME AT THE NIPPLE AND MONTHLY INFANT AGE

	DIFFERENCE	± LIMITS	SIG.?
1 - 2	2.40000	7.92056	NS
2 - 3	6.72000	7.92056	NS
3 - 4	9.00000	7.92056	S
4 - 5	8.70000	7.92056	S
5 - 6	6.85000	7.92056	NS
6 - 7	1.45000	7.92506	NS
7 - 8	5.68000	7.92056	NS
8 - 9	4.95000	7.92056	NS
9 - 10	2.11000	7.92056	NS
10 - 11	3.80000	7.92056	NS
11 - 12	5.52000	8.40102	NS
12 - 13	3.72000	8.85545	NS
13 - 14	0.09667	9.56498	NS
14 - 15	6.69333	11.4323	NS
15 - 16	4.18000	12.5235	NS
16 - 17	1.76000	15.3381	NS

TABLE B: MULTIPLE RANGE TEST FOR INFANT INDEPENDENT FEEDING AND MONTHLY INFANT AGE

	DIFFERENCE	± LIMITS	SIG.?
1 - 2	0.00000	5.88200	NS
2 - 3	-0.52000	5.88200	NS
3 - 4	-1.98000	5.88200	NS
4 - 5	-1.54000	5.88200	NS
5 - 6	-0.78000	5.88200	NS
6 - 7	-0.98000	5.88200	NS
7 - 8	-3.49000	5.88200	NS
8 - 9	-3.71000	5.88200	NS
9 - 10	-4.16000	5.88200	NS
10 - 11	-1.30000	5.88200	NS
11 - 12	-4.67500	6.23881	NS
12 - 13	-9.81000	6.57628	S
13 - 14	-3.50833	7.10319	NS
14 - 15	-4.64667	8.48994	NS
15 - 16	-4.65000	9.30026	NS
16 - 17	-1.80000	11.3904	NS

CHAPTER 5

THE ECOLOGICAL CONTEXT OF INFANCY: II

5.1 INTRODUCTION

In the previous chapter the development of infant independence was considered primarily in terms of the decline in dependence on mothers for nutrition. To a lesser extent, changes in the nature of mother-infant contact were introduced. It was demonstrated that the development of nutritional independence differed in terms both of direct comparisons between other studies of baboon infants, as well as between infants in this study. These differences were explained with reference to the ecological conditions which prevailed at the time of birth and during the months thereafter.

While certainly the most energetically expensive forms of parental care, the provision of nutrition through lactation and the transport of infants through carrying are not the only domains of dependency that infants experience. To survive, infants have to make additional transitions. Thus Nicolson (1982, 1987) has drawn attention to the necessity for infants to successfully complete the transition from attachment to the mother to social independence. Essentially, during the first few months postpartum infants are spatially attached to mothers but gradually, with age, they break this contact and independently enter the wider social group in which they live and will function. The transition to social independence is characterized by the social interactions of the infant shifting increasingly away from mothers to other kin, peers, and unrelated members of the social group (Walters 1987). It is this transition which is one of the focii of this chapter. A detailed description will be provided of infant behavioural development. That is, as infants become less attached to their mothers, and as they become more independently mobile, they begin to explore their environment, both social and physical. However, and at the same time, as infants begin to spend time engaging in one or more particular activity(s), they must necessarily adjust the time they can spend in others. The data on behavioural development are, as far as possible, to be considered in relation to that of adult animals who, logically, are competent in the balancing of their activity budgets.

This chapter is structured in the following way. In the section which follows immediately, I will describe the changing nature of the infant's primary relationship with its mother. I will show that, with increasing age, the nature of its attachment to its mother changes and that as it spends increasing amounts of time away from her, so it encounters other members of the social group. Following this I will present data on the development of the different infant activities. Of specific interest will be the standard behaviour categories (viz. movement, resting, socializing, and play). The chapter concludes with a presentation and discussion of the integrated behavioural profile of infants and how, if at all, the amount of time allocated to particular activities is adjusted to account for participation in additional behaviours.

5.2 THE TRANSITION TO SOCIAL INDEPENDENCE

According to Altmann (1980), the world of the young baboon infant can usefully be viewed as a circle with its mother at the centre. Illustrating the dialectical nature of this relationship, she suggests that an infant is born into the mother's world and is thus immediately affected by the things which affect her while, at the same time, the presence of the infant influences and intensifies the things and events which influence her. This is most evident in that the infant exerts pressure on the mother's maintenance activities (Chapter 3) and attracts the attention of other group members.

The importance of mother-infant contact in promoting the "healthy psychological" development of infants was demonstrated by Harlow and his co-workers (Harlow 1958; Harlow and Harlow 1965). They claimed that infant contact with the mother's body provided the infant with reassurance, warmth, and a safe base from which to explore (Nicolson 1987). More recently it has been suggested that the learning of essential survival techniques is facilitated through the primary relationship that an infant has with its mother (Attilli 1985). Echoing Harlow, and considering Bowlby's (1963, 1973) mother-infant attachment theory, Attilli (1985) has emphasized the security and comfort provided by mothers, which has implications in terms of providing safe opportunities for infants to explore and experiment.

With the mother as a secure base to whom the infant can return, and from where it can start exploring, the infant begins to interact with animals other those than it encountered within the context of the mother-infant dyad. Similarly, the range of activities that the infant engages in increases as it interacts with other animals, as do the contexts of interaction. These contexts of interaction are often different, and probably separate from the interactions with other animals that infants experienced as a result of their attachment to their mothers.

5.2.1 CHANGES IN MOTHER-INFANT SPATIAL PROXIMITY

It was shown in the previous chapter that as infants get older, so the amount of time that they spend in contact with their mothers declines (Figure 20, Chapter 4). It was further shown that the function served by such declining contact also changes, with infants spending proportionately more time suckling when in contact with their mothers (Figure 21, Chapter 4).

The logical and obvious corollary of spending decreasing amounts of time in contact is that infants are necessarily spending increasing amounts of time apart from mothers. The changing nature of spatial proximity between mother-infant dyads, with increasing age, is presented in Figure 23.

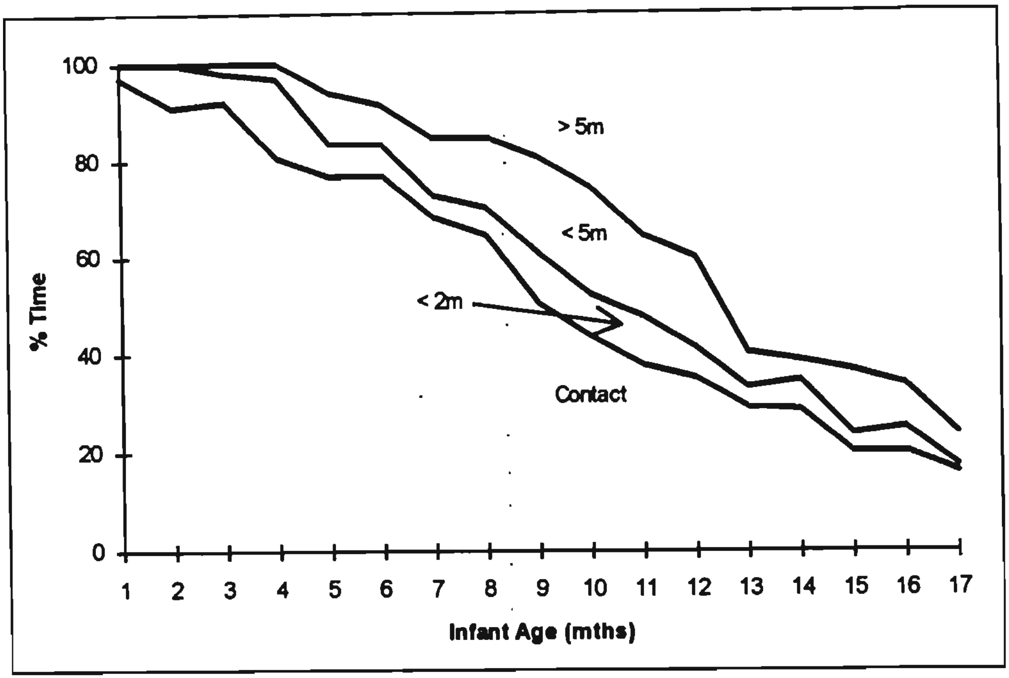

FIGURE 23: Distance between mother and infant per month with increasing infant age. Each line represents the cumulative total of time spent at that distance plus those below it.

Not only did the infants in this study spend increasing time out of contact from their mothers, but such time was spent at greater distances from mothers. By month 8-9 they were spending as much time out of contact as they were in contact. As they got older, the amount of time infants spent out of contact but within 2 metres represented a decreasing proportion of the total time spent out of contact (Figure 24). Time spent at a distance of greater than 2 metres but within 5 metres of mothers represented an increasing proportion of the total amount of time out of contact through to month-11, and then began to decrease as a proportion, while time spent at distances greater than 5 metres began to increase substantially around month-10. This is consistent with the nature of changing spatial proximity between mothers and infants reported for other infant baboon studies (Altmann

1980; Nicolson 1982). For the infants in this study, the substantial increase around month-10 in the proportion of out-of-contact time that is spent beyond 5 metres from mothers precedes by about two months the largest increase in the month-by-month change in the amount of time infants were feeding independently (Table 11, column 1: Chapter 4).

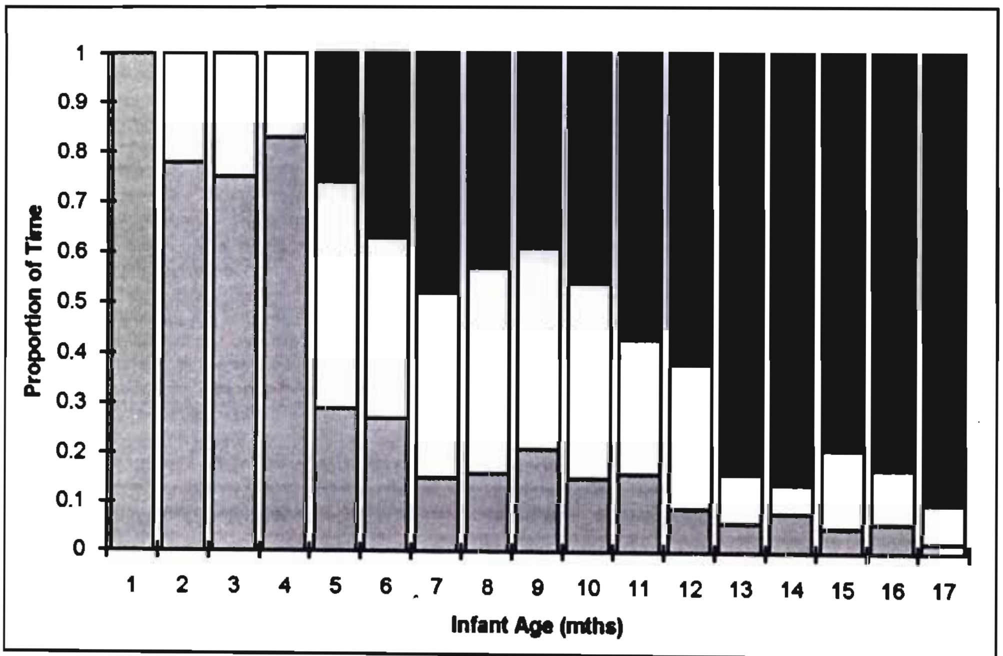

Figure 24: Proportion of time that infants spent, at each monthly age, at different distances from their mothers when not in contact . Dotted section: out of contact but within 2 metres of mother; Blank section: beyond 2 metres of mother but within 5 metres; Horizontal lined section: beyond 5 metres of mother.

Given that infants were spending increasing time out of contact from their mothers as they got older, the issue arises as to which of the dyad partners was primarily responsible for the maintenance of contact. These data are presented below.

5.2.2 RESPONSIBILITY FOR THE MAINTENANCE OF CONTACT

During the course of observation when a break in mother-infant contact occurred, I recorded whether it was the mother or the infant who initiated the break, and who reinitiated contact if it occurred. Following Altmann (1980) and Nicolson (1982) the methods of Hinde and co-workers (Hinde and Spencer-Booth 1967, Hinde and Atkinson 1970; White and Hinde 1975) are used to establish responsibility for proximity. Plotted separately in Figure 25a are the percentage "approaches" (within 1 metre of their mothers) as well as the percentage "leaves" (beyond 1 metre of their mothers) that infants made at each monthly age.

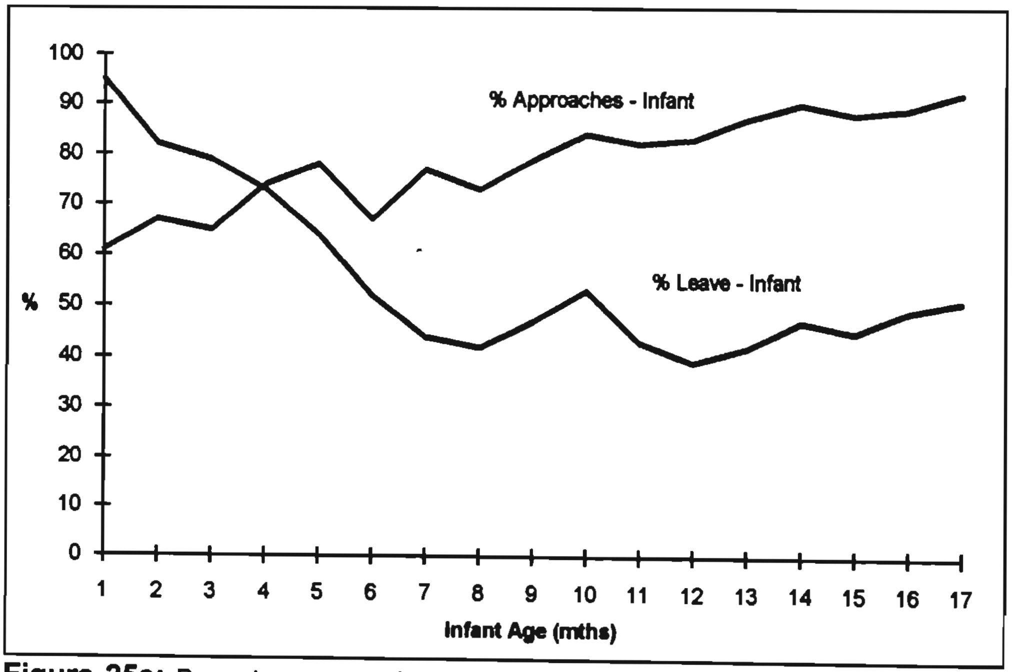

Figure 25a: Percentage approaches and percentage departures to and from 1 metre of mothers made by infants at each monthly age.

Over the first 17 months, infants increased the distance between the two an average of 55.7% of the time, and closed the distance between them an average of 78.59% of the time. Overall, infants were mostly responsible for the maintenance of proximity as evidenced in Figure 25b which plots the percentage approaches made by infants minus the percentage departures made by them. In terms of this index, positive values indicate the major role played by infants in the maintenance of proximity within the specified proximity distance which, in this case, is 1 metre (Nicolson 1982).

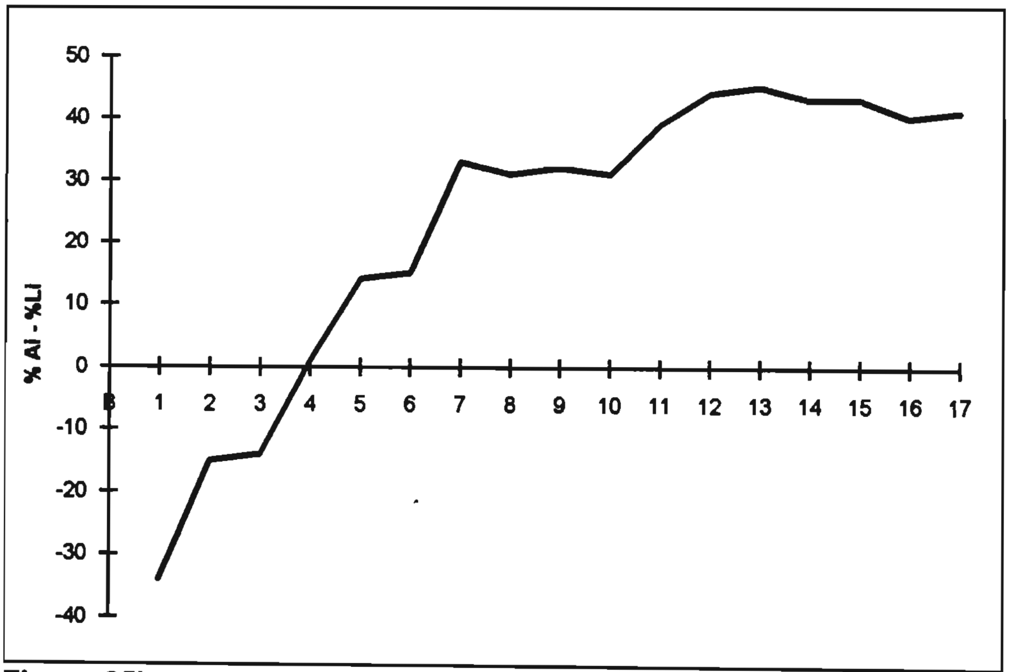

Figure 25b: Index for infant responsibility for maintenance of proximity between mother-infant dyads. Data presented are the percentage approaches (%Ai) to mothers minus percentage departures (%Li) from mothers made by infants during each monthly age (data from Figure 25a).

During the first three months of life, mothers were primarily responsible for maintaining proximity with their infants as is indicated by the negative values on the index over that time. It should be noted, however, that during the first 2 months particularly, very few mother-infant separations beyond 1 metre were observed. During month-4 the index became positive, showing that at that age, infants became primarily responsible for maintaining proximity with their mothers. Over the period 4-7 months, infants became increasingly more responsible for proximity maintenance, and this levelled out to average approximately 45.6% from month-7 through to month-17.

These data are very similar to those of comparative studies. As with the infants in this study, those observed by Altmann (1980) were reported to initially increase the distance between the mother-infant pair, with mothers decreasing the distance. She reported that after their fourth month the situation was reversed with infants assuming more responsibility for maintaining proximity, which is the age at which this happened for the infants in the present study. The same pattern through the first 4 months was also reported by Nicolson (1982). Nicolson (1982) found that after their sixth month, the index for infant maintenance of proximity maintained a constant level around 36%. This is lower than that for the infants in the present study (45.6% - see above). It is possible that the higher level for the infants in this study may be accounted for by the extended suckling by infants where infant time at the nipple accounted for the largest proportion of mother-infant contact as infants got older (Figure 21, Chapter 4). What is suggested by this is that infants, as shown in the previous chapter, remained nutritionally dependent on mothers, and so returned periodically to mothers during the day to suckle. Thus these return feeding visits, over and above normal contact, resting, and grooming proximity will probably account for the relatively high percentages of infant approaches.

If, as has been shown above, infants are spending increasing amounts of time away from their mothers, the question then arises as to what they are doing when apart. It will be shown in the sections which follow that as infants begin to move independently, they begin to interact with other members of the social group in contexts that differ from, and that are often separate from the interactions involving their mothers.

5.3 DEVELOPMENTAL CHANGES IN INFANT ACTIVITY

The life of a young, dependent infant can be described as being relatively carefree in the sense that it is not as tightly constrained in the allocation of time to various maintenance activities in the same sense that adult and independent immature animals are. Marsh (1992) pointed to this when she noted that the requirements of a still dependent and suckling infant are likely to be very different from those of a weaned and independent juvenile, and further different from those of an adult animal. Nonetheless, she notes that infants are, just as older animals are, constrained in their range of activity by limits such as the number of active hours in a day. In the sections which follow, I examine in some detail the development of various infant social and maintenance activities. I am concerned, in particular, with infant play and grooming interactions given that these are the two primary social categories of activity. That is, activity where one or more other individual(s) are necessary for interaction to take place. Thus, in discussing the development of play and grooming, I will attempt, as far as possible to describe the expanding social contacts infants make.

The data in each activity section are preceded by a review of the literature concerned with each particular activity. Once the data for each behavioural category have been presented, I will consider each in relation to the others in an attempt to present an holistic and intregrated perspective of infant behavioural development. Following from data presented in the previous chapter describing the infant transition from ventral to dorsal carrying, and given further that an infant needs to be independently mobile in order to engage in most of the activity categories that will be described, I will begin the section with a presentation of the time course and development of locomotion by infants in this study.

5.3.1 MOVING BY INFANTS IN THE PRESENT STUDY

Moving by infants tended to be recorded more as a default behavioural category than as an exclusive category in itself. Thus, if at the time of the point sample, an infant was locomoting during play, or was moving in search of food or moving while exploring for food, then the behaviour was scored as such, rather than as movement. In other words, movement was recorded only when an animal was moving in a context that was not obviously connected with, or an integral part of a different category of activity. Nicolson's (1982) locomotion category included movement while the subjects were foraging, walking, running, and climbing (see title: Figure 14), while Marsh's (1992) definition appears close to the one used in this study where she excluded from the move category any locomotion involved in exploration for food, as well as that used in social and environment exploration. Thus the data from the other studies can be broadly compared to the data for this study. Data on infant movement, at each monthly age, for the infants in this study and those in the Nicolson (1982) and Marsh (1992) are plotted in Figure 26.

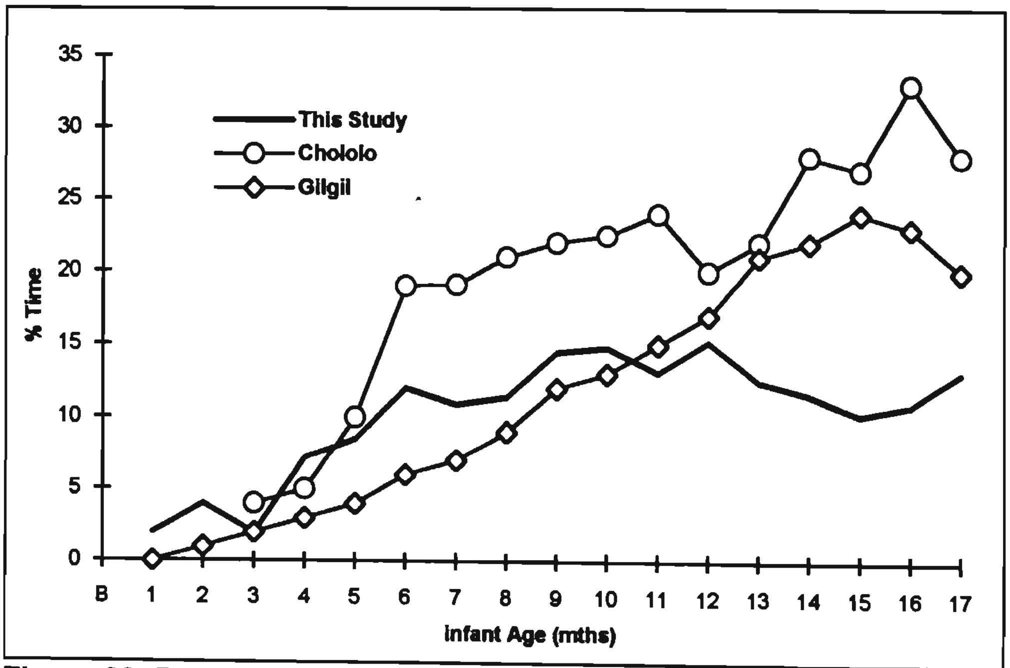

Figure 26: Percentage time infants spent moving. Mean for all infants. Also plotted is the mean percentage time that infants at Chololo spent moving (from Marsh 1992) as well as time spent locomoting by the Gilgil infants (from Nicolson 1982).

The average time over the first 17 months that infants spent moving (9.47%) is very close to the average time over a year that both adult females (non-mothers) and juvenile animals spent moving (10.01% and 9.15% respectively), but is lower than the average time that Marsh's (1992) infants spent moving through ages 3-17 months (20.31%). It is also slightly lower than the average 13.44% Nicolson's (1982) infants spent locomoting through to their 18th month. The relatively large difference in the average amount of time spent moving by the Chololo and the Drakensberg infants may appear less discrepant if it is noted that during their 17th month (which is when the last data were collected for the oldest infant in this study), the infants from both studies were moving as much on average as were adult animals in the respective studies (Drakensberg: adult females = 10.01%, infants = 9.47%: Chololo: adult females = ~30%, infants = ~28% month-17: from Marsh 1992, Figure 6.3 p.94b).

The development of independent locomotion by infants, as would be expected, facilitates infant environmental and social exploration and hence, further increased interaction with members of the social group (outside of those contacts that took place within the context of the mother-infant dyad). Given this, a positive relationship would be anticipated between infant movement and those behaviours that presumably require independent locomotion if they are to be engaged in (feeding, play). At the same time, independent movement by an infant would obviously be negatively related to mother-infant interactions such as contact and carrying (Table 12). For a social activity such as grooming, there would be no predicted relationship between the two (grooming and movement) given that infant mobility alone is not a necessary requirement for a grooming interaction in which an infant is involved, to take place. The absence of any significant relationship between the two was the case in this study (r = .3014, p > 0.1).

	Feed	Play	Contact	Carrying
Move	.5269 (p<0.05)	.8577	-.7408	-.9018

Table 12: Correlation coefficients for relationships between infant independent locomotion ('move') and independent feeding, playing, mother-infant contact, and maternal carrying of infants (ventral and dorsal combined). All significant at p<0.01 unless otherwise indicated.

The relationship between dependent transport and independent movement is plotted in Figure 27. The rapid decline in carrying time over the first 6 months is primarily accounted for by the decline in the amount of time that infants were carried in the ventral position (Figure 22a Chapter 4). It has already been shown that the appearance of the transition to dorsal riding for infants in this study is comparable in age to the appearance of dorsal riding for infants in other studies. The transition from dorsal riding to independent movement occurs relatively slowly. At each age, with the exception of the 17th month, infants were observed to move by both means.

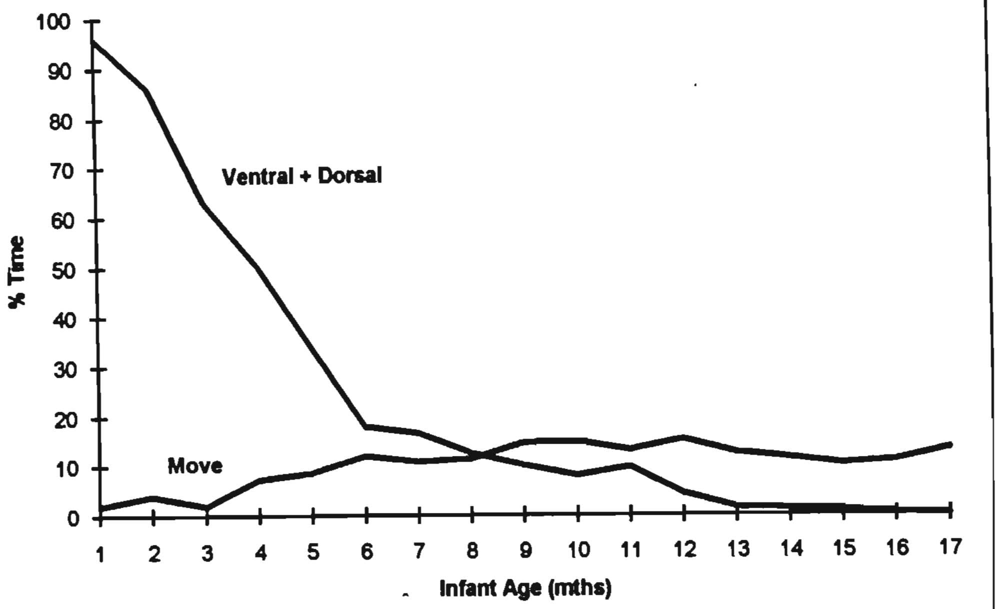

Figure 27: Mean precentage time per month that infants spent independently moving and in dependent transport (ventral and dorsal carrying combined).

However, while infants may have both walked and been carried dorsally in each month, the proportion of movement taken up by each mode of transport was different (Figure 28). As the amount of time being carried ventrally decreased, infants switched initially to riding in a dorsal position, as well as to moving independently. With increasing age, independent movement represented an increasing proportion of all infant movement, while dorsal riding represented a decreasing proportion. By their eighth month of age, infants were spending approximately the same amount of time riding as they were moving by themselves. At ages older than eight months, independent movement became the preferred mode of transport as measured by the comparison between the amounts of time spent moving and being carried.

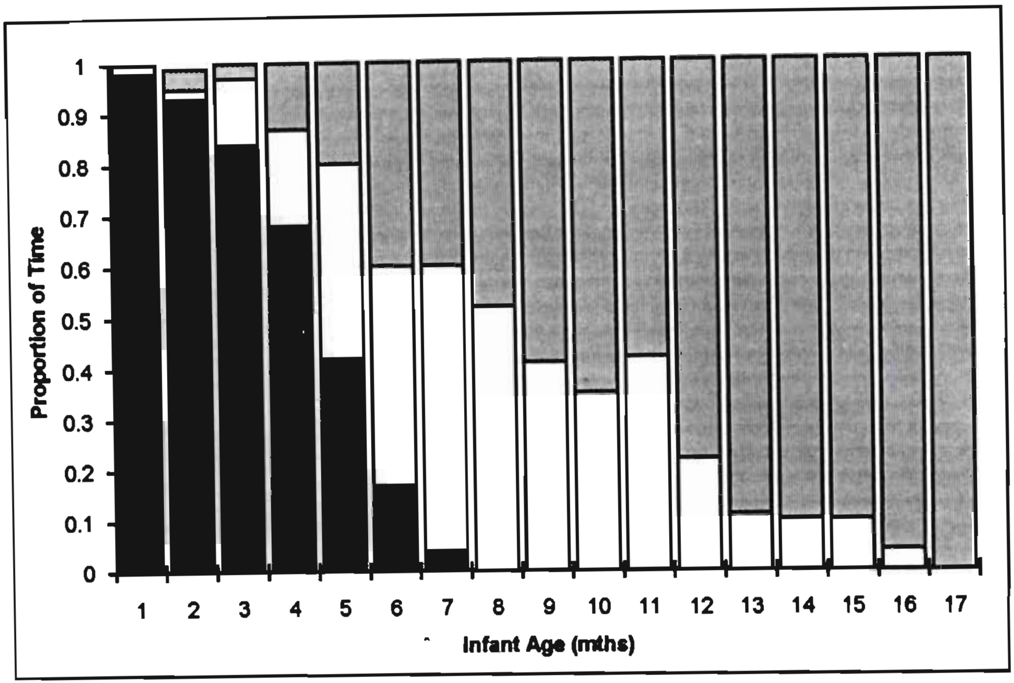

Figure 28: Proportion of infant movement by different modes of transport. Horizontal lined section: ventral carrying; Blank section: dorsal carrying; Dotted section: Independent movement.

5.3.2 PLAY

Play is a behaviour common to most mammalian species and some birds (Walters 1987). It is also a focus of research which has generated considerable debate. Foremost in these debates have been the hypothesized benefits, if any, derived for animals that engage in the activity. While particular benefits have been hypothesized, which will be described below, the largely unquestioned consensus is that play is costly and therefore, given the persistence of the behaviour through evolutionary time, it must in some way be beneficial (Martin 1982; Fagen 1993; But see Martin and Caro 1985).

According to Walters (1987), play usually occurs in three forms, these being (i) object play where an individual manipulates an object in a repetitive manner, (ii) solitary (locomotor) play, and (iii) social play which involves two or more individuals and is the distinguishing form of primate play. In its physical form, social play consists mainly of chasing and wrestling which is usually accompanied by a "play face" (Walters 1987). Among the primates, elaborate social and solitary play is characteristic of all species (Fagen 1993). He has estimates that between 1% and 10% of a free-ranging immature primate's time is consumed by play, and that this percentage will be higher for captive animals. For baboon infants, estimates of the amount of time, per day, dedicated to play have ranged from 3% (*P. ursinus*: Cheney 1978; *P. anubis*: Rose 1977) to 20%[1] (*P. anubis*: Nash 1978).

In most primate species studied, play begins during infancy, becomes frequent during the juvenile period, and then declines steadily during adolescence (Walters 1987; Fagen 1993). Fagen (1980) has argued that this bimodal distribution of play, where the amount of time spent in play declines for a short period during ontogeny and then increases again, may reflect "ancestral adaptations". Thus he hypothesizes that during the weaning period when mothers reject infants, both the frequency and the intensity of play decreases and that, subsequent to the end of the rejection period, it increases again to original levels. His argument is supported by data from chimpanzees (*Pan troglodytes,* Clark 1977), olive baboons (*P. anubis,* Nash 1978), and chacma baboons (*P. ursinus,* Cheney 1978). The ontogenetic decrease in play has also been

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[1] Nicolson (1982) has suggested that the 20% figure for Nash's study may have been due to her use of one-zero sampling procedures which has been argued to over-estimate the occurence of a given behaviour (Altmann 1974).

explained at the proximate level. Caine (1986) has argued that it is due to inter-male competition and heightened aggressiveness that play among males declines. Similarly Levy (1979, cited in Fagen 1993) reported that, with increasing age, old juvenile male rhesus monkeys (*Macaca mulatta*) begin to assert their developing rank and thus begin to monoploize opportunities to perform in particular roles and to make particular moves. As a result of this, it is claimed, these males find it difficult to attract play partners and thus play encounters are difficult to maintain. Simultaneously, play opportunities are further interfered with by sexual maturation and rank reversals. Pusey (1990) found that among common chimpanzees (*Pan troglodytes*) both sexes tended to become more aggressive in play as they reached adolescence. She observed that adolescents appeared more frequently to ignore invitations to play and, if they did play, to do so only briefly.

It was stated above that play has generally been considered to be an expensive activity. More specifically, these costs have been associated with (i) an energy cost resulting from increased metabolism during play where the differences in caloric intake required for immatures who play, as opposed to those who do not, are estimated to be 5% - 10% above resting metabolic requirements (Martin 1982), (ii) a time cost which results from play interfering with time allocation to other, mutually exclusive beneficial activities, (iii) a survivorship cost resulting from an increased risk of predation and injury, or from separation from the parent (Fagen 1981; Clarke and Glander 1984; Goodall 1986; Hausfater 1976). However, in a recent review of the functions of play and its role in behavioural development, Martin and Caro (1985) have questioned this widely held assumption that play is costly. In terms of the cost-benefit line of argument they consider, the costs associated with play are argued to be not as considerable as has generally been believed and are in fact reported to be "... relatively minor biological costs ..." (p.78). They claim that there is no convincing evidence to demonstrate that the absolute time and energy costs of play are substantial and, further, that there is some evidence to show the opposite. In terms of a survivorship cost, they observe that while anecdotal evidence is available, there have been few, if any, systematic attempts to define, estimate, or measure the cost such that ".... its possible magnitude and biological significance remain unknown" (p.81).

In terms of the benefits to play, it follows from this line of argument that there must be some benefit or function to play given the persistence of the activity in time. Numerous benefits have been proposed. Supporting the broad conclusion that play somehow facilitates social and physical development, play has been argued to be beneficial in the development of physical training and motor skills (Fagen 1993), the establishment of dominance relationships (Walters 1987), the learning of social, reproductive, maternal, and communicative skills which lead to social bonding (Muller-Schwarze *et al* 1982; Walters 1987; Fagen 1993), and other possible general cognitive effects such as the development of interpretative ability (Fagen 1993). Poirier *et al* (1978) point to the primary importance of play in the maintenance of peer integration and the socialization process. It has also been suggested that adaptive functions such as general neuromuscular and cardiovascular exercise, and sensory stimulation of the developing nervous system are serviced through play (Muller-Schwarze *et al* 1982) while Suomi (1982) postulates that active play facilitates cortical growth and differentiation. Additionally, and falling within the domain of the 'practice theories', it has been supposed that it is within the context of play that certain skills which might be too risky to rehearse in their normal context can be learned and practised. These include the skills used in fighting and predator avoidance (Smith 1978; Symons 1978, cited in Walters; Fagen 1981).

5.3.2.1 PLAY BY INFANTS IN THE PRESENT STUDY

Plotted in Figure 29 is the mean percentage time per month that infants in this study spent playing. Comparative data for the Gilgil and Chololo olive baboon infants are presented (from Nicolson 1982, Marsh 1992). It should be noted that where comparative studies concentrate on *social play*, the data presented for this study combine *solitary play, object play, and social play* and thus may over-estimate the amount of social play (for comparative purposes).

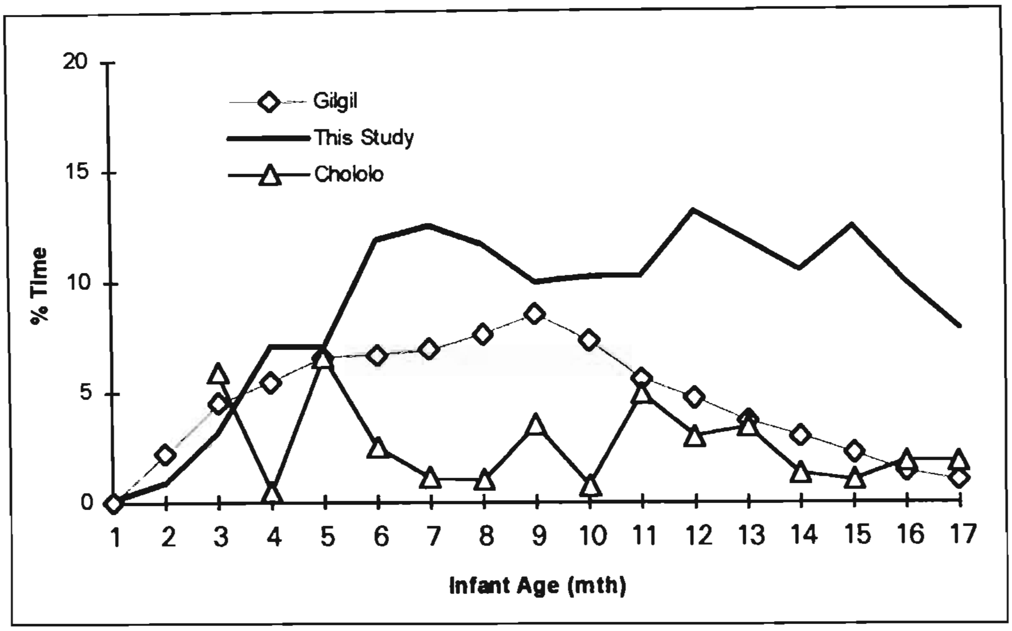

Figure 29: Proportion of observation time per month that infants spent playing (this study - thick line).Comparative data for Gilgil infant social play are also presented (marked line. Gilgil data: combined male and female social play taken from Nicolson 1982).

The amount of time infants in this study spent playing peaked during month-7 (12.48%), and then declined slightly through to month-9. A second and third peak are evident during months 12 and 15, although the latter one is based on data for only two infants. Note also that the seemingly significant changes in play during these months may appear to be larger than they in fact are partly due to the scaling on the y-axis. At the end of the 16th month, the two infants for which data are available were playing 8.48% of the time.

The peak in play during month-7 (12.48% - combined male and female play: Figure 29) is both later (in age) and higher than the peak in social exploration[2] (6.9% during month-5)

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[2] Marsh (1992) notes that while her behaviour category "social exploring" includes social play, it additionally incorporates exploratory social interactions longer than greetings. Thus, while her category encompasses a broader range of behaviours than other studies have within the category of play, Marsh (1992) claims that the data can still be broadly compared (p.90).

reported for the Chololo infants (Marsh 1992, Fig.6.4b), and is also higher, but earlier in age, than the peak in the average time male and female infants engaged in social play at Gilgil (4.25% during month-9, Nicolson 1982, Fig.23a). Nash (1978) reported that the amount of time her infants spent playing increased in frequency through to months 6-7 and then declined during months 8-10. Her increase in play frequency through to months 6-7 is similar to the pattern for the infants in this study.

5.3.2.2 SEX DIFFERENCES IN PLAY

Sex differences in the amount and type of baboon play have tended to be interpreted with reference to the functional purposes served by play. That is, differences in play by male and female baboons have been considered in terms of the different ways by which males and females assume and maintain dominance ranks as adults (Cheney 1978) where the fighting ability of males, as well as their ability to assess the fighting capabilities of other males, may be improved through play. Females, on the other hand, acquire rank similar to that of their mothers and thus play will not influence rank. This line of argument has been used to explain reported differences in the amount of play engaged in by immature male and female baboons (Nash 1978; Nicolson 1982). Additional male-female differences have been reported for playmate preference where infants preferentially play with peers of the same sex (Owens 1975; Cheney 1978; Nicolson 1982).

In Figure 30 is plotted the mean percentage time that male (N=3) and female (N=2) infants in this study spent playing. Due to the small sample size (for a gender split), particularly for the females, any interpretation should be treated with caution, and hence should be seen as only highlighting a possible trend.

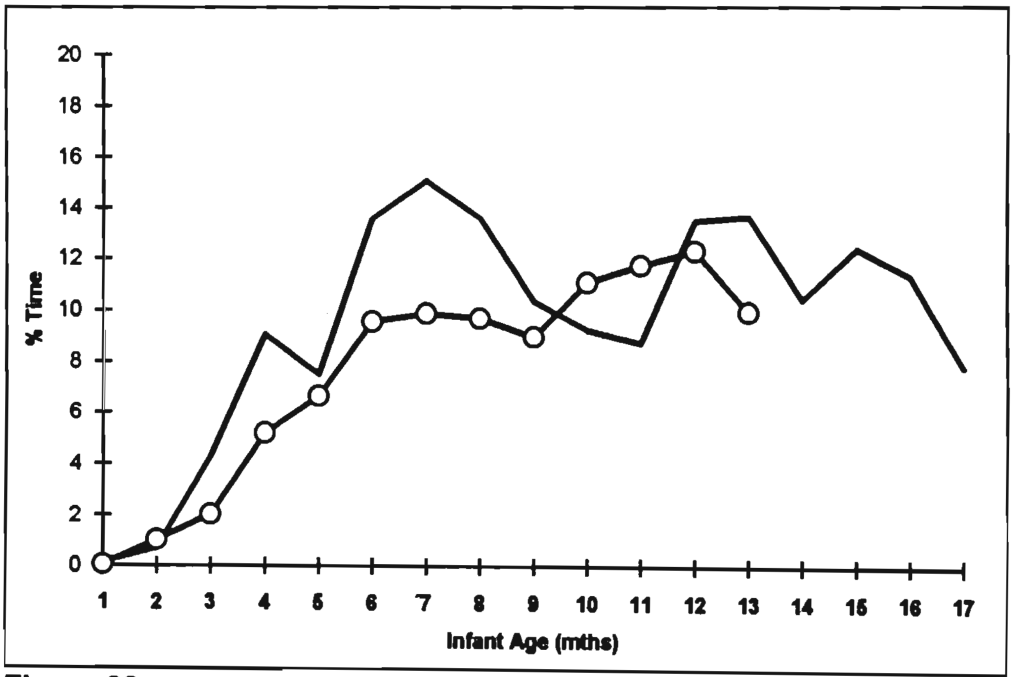

Figure 30: Percentage time male and female (marked line) infants spent in play. (Note: Female months 12 & 13 are data from 1 animal only, as is month-17 for males).

With the exception of the period after month-9 through month-12, at each other age block (1 - 4 months; 5 - 8 months) males spent more time playing than females (Average for 10 months:- males: $\bar{x}$ = 8.95%, SE = 1.27; females: $\bar{x}$ = 7.28%, SE = 1.12), although differences between the sexes were not significant (Mann-Whitney U Test, two-tailed, p = 0.5993). This lack of any significant sex difference in the amount of infant play is in line with suggestions that sex differences in baboon play will not become apparent until the second or third year of life (DeVore 1963; Ransom and Rowell 1972; Young and Bramblett 1977; all cited in Nicolson 1982), although Nash (1978) reported that during certain months females played less than males (p.754). Owens (1975), who looked at gender differences in the play of olive baboons, demonstrated that the play of male infants peaked twice; the first peak occurred around age 4.5 months and the second at about 14 months of age, and declined thereafter. This bi-modal peak in play is similarly apparent for the males in the present study (Figure 30), although the second peak at month-15 is based on data for two infants only. Owens (1975) found no identifiable peak in female play.

5.3.2.3 INDIVIDUAL VARIABILITY IN PLAY

There was individual variability between infants with regard to the amount of play engaged in, as well as the age at which playing time peaked (Figures 31a,b,c,d,e).

The amount of time infant G2 (Figure 31a) spent playing increased sharply after his second month, peaked during months 7-8 (14.9% and 15.3% respectively) and then declined through to month-10 (9.2%). A second small peak is evident in the amount of time this infant played during month-14 (12.3%).

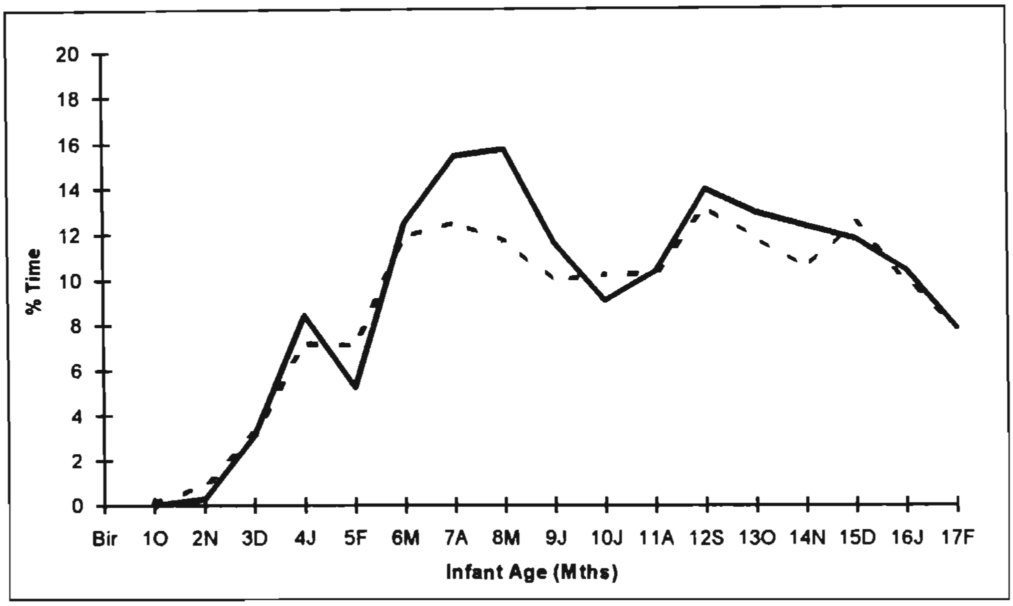

Figure 31a: Amount of time at each monthly age that infant G2 played (thick line). Also plotted is the mean amount of time all infants played (dashed line). Letters on the x-axis represent month of year corresponding to G2's age.

Figure 31b: Amount of time at each monthly age that infant F2 played (thick line). Also plotted is the mean amount of time all infants played (dashed line). Letters on the x-axis represent month of year corresponding to F2's age.

For infant F2 (Figure 31b), the amount of time he spent playing increased rapidly during the period 3-6 months, peaking during month-6 (16.7%). This peak during his 6th month coincided with the peak in the play of infant G2 (7-8 months, above). As with infant G2, a second peak is evident in the play of F2 during his 13th -15th months.

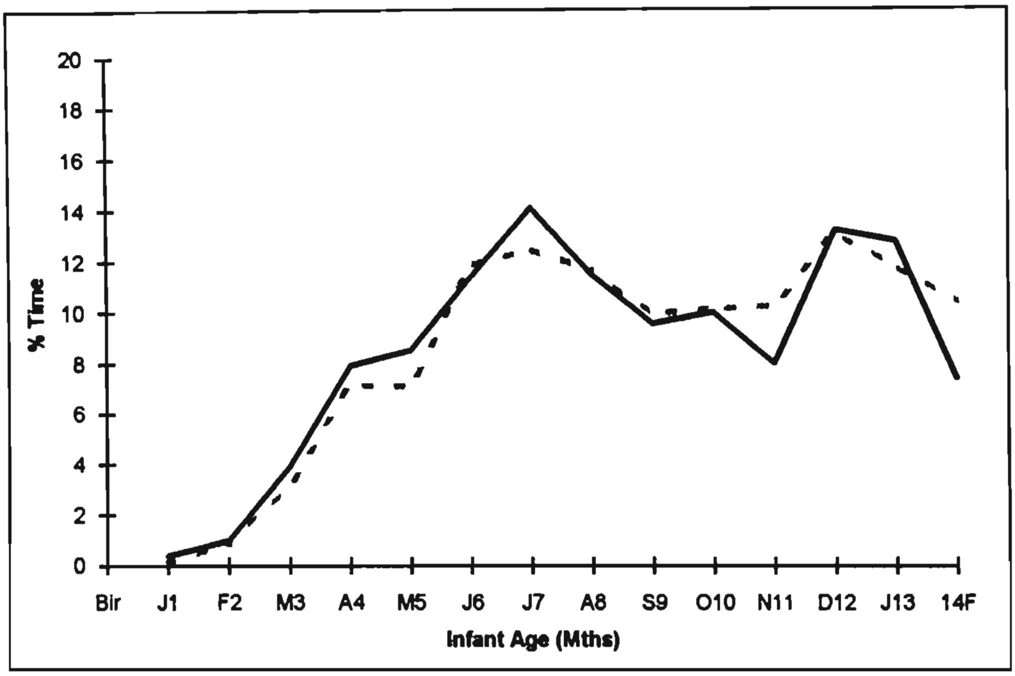

Figure 31c: Amount of time at each monthly age that infant J2 played (thick line). Also plotted is the mean amount of time all infants played (dashed line). Letters on the x-axis represent month of year corresponding to J2's age.

The amount of time infant J2 spent playing peaked during his 5th month (12.4%) and then again in his 7th month (13.6%). Unlike infants G2 and F2, no second peak is evident in the play of infant J2. After the peak during month-7, J2's play-time declined slowly to 7.4% at month-14 when the last data on him were collected.

The play profiles for the two later born female infants (C2 and R2) differ from those of the three male infants, most notably in that for the two females, the amount of time they engaged in play peaked at later ages than for the males.

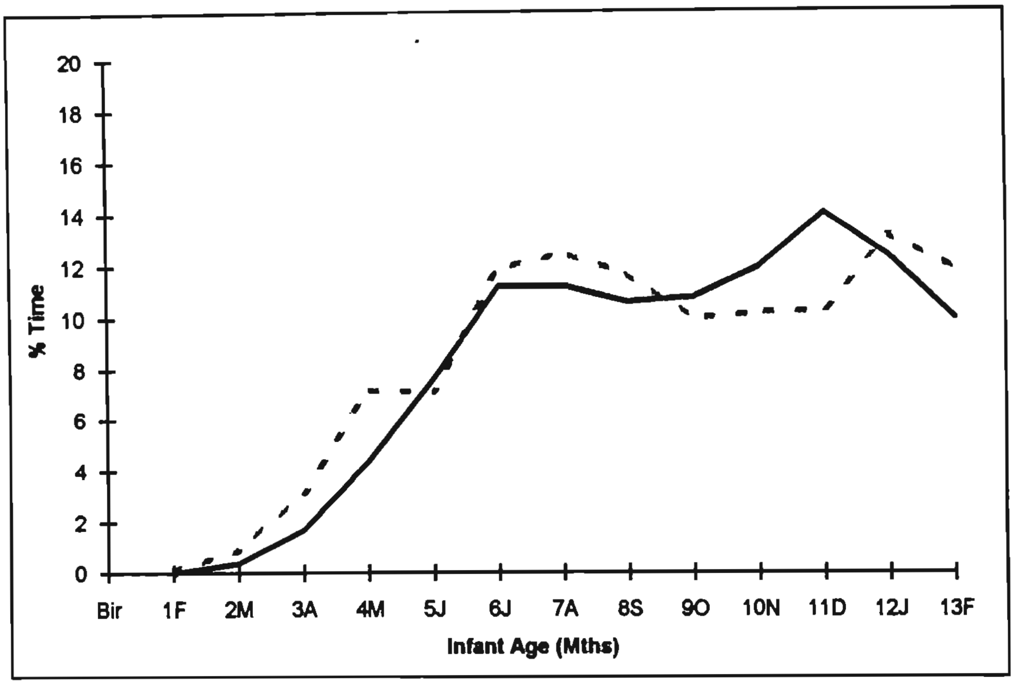

Figure 31d: Amount of time at each monthly age that infant C2 played (thick line). Also plotted is the mean amount of time all infants played (dashed line). Letters on the x-axis represent month of year corresponding to C2's age.

For C2 (Figure 31d) the peak occurred during her 11th month (14.3%), while for R2 (Figure 31e) play peaked during her 10th month (10.4%). Further, both females tended to spend less time playing than the mean for all five infants.

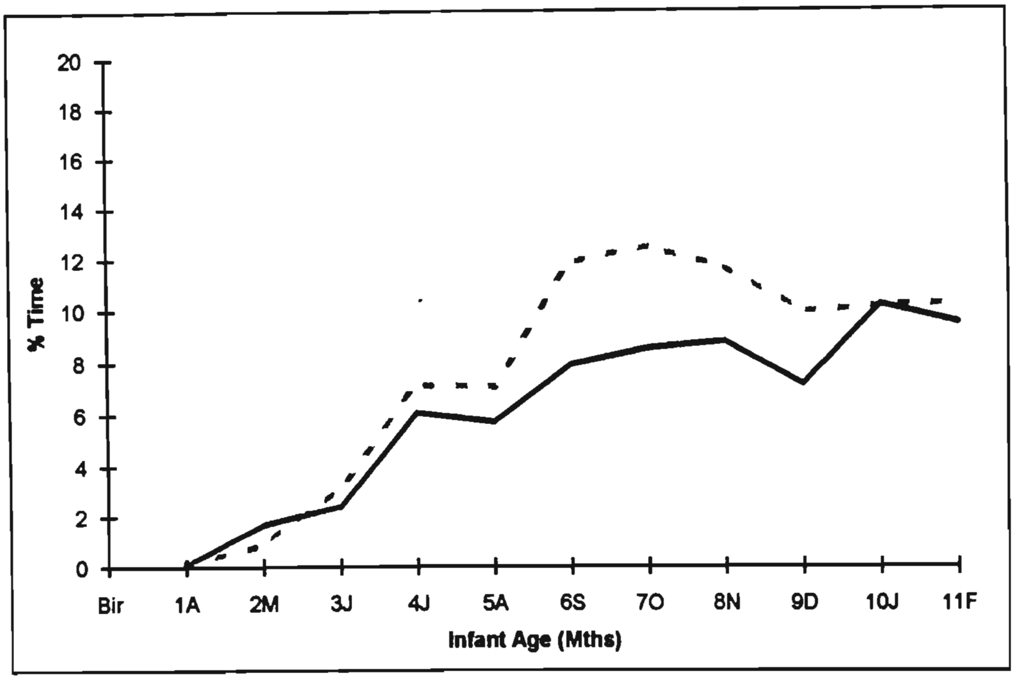

Figure 31e: Amount of time at each monthly age that infant R2 played (thick line). Also plotted is the mean amount of time all infants played (dashed line). Letters on the x-axis represent month of year corresponding to R2's age.

5.3.2.4 THE DISTRIBUTION OF PLAY PARTNERS

At this point attention is turned to identifying which animals infants preferentially engaged in social play with. By 'preferentially', it is not necessarily assumed that infants were actively seeking out certain individuals or a certain class of individuals; rather it may have been that due to demographic and/or activity budget constraints, only certain individuals were available for play with infants at specific times (sensu Cheney 1978). In order that it can be assessed which animals were *potentially* available for play with infants, analysis is confined to those months when all infants had been born and thus all troop members were present as potential playmates.

For the 5 infants in this sfudy, 694 episodes of social play were observed during the last 11 months of the study when all infants were present in the troop, and hence were potentially available for play. In each case, the identity/identities of the play partner(s) were noted. Plotted in Figure 32 is a comparison between the observed and expected play partners, by age-sex class, for any particular infant *assuming that there is no difference in the probability that any one infant will encounter individuals from each age class.* The expected values indicate which age-sex class the infant might be expected to be playing with were it to randomly encounter animals of a particular age-sex class as a proportion of the number of potentially available partners.

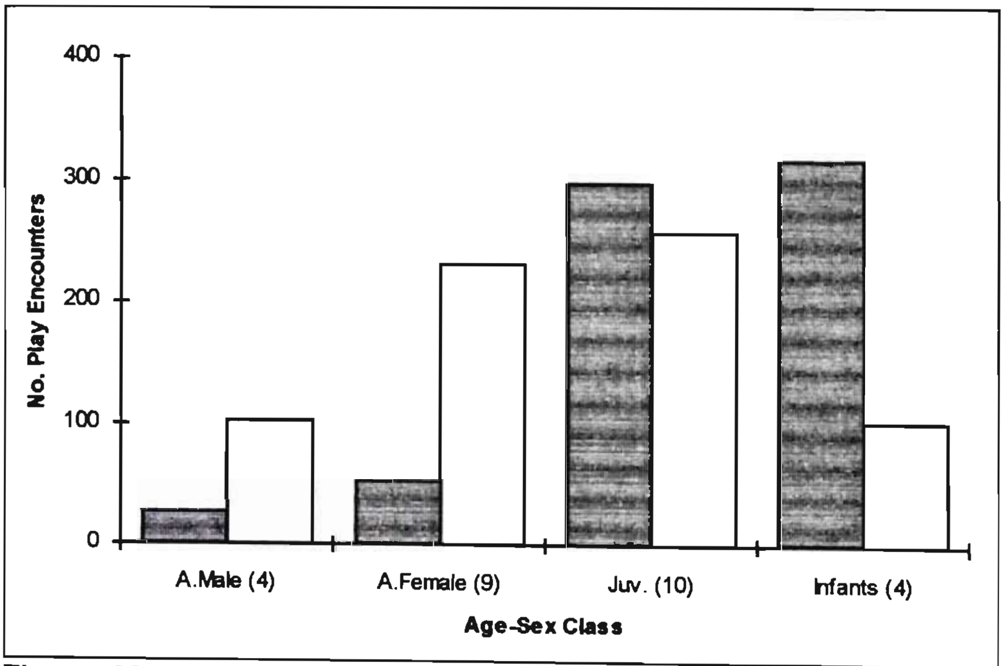

Figure 32 Observed (shaded blocks) and expected (clear) frequencies with which different age-sex classes were social play partners for infants. Number of animals in each age-sex class indicated in parentheses.

There were significant differences with regard to which age-sex classes an infant played with:- they played with adult males and adult females significantly less than would be expected given their respective representations in the troop, while both juvenile animals and other infants were played with significantly more than would be expected given their representation ($c^2_{\text{Adult Males}}$ = 54.33, 3df, $p < 0.001$; $c^2_{\text{Adult Females}}$ = 137.25, 3df, $p < 0.001$; $c^2_{\text{Juveniles}}$ = 6.29, 3df, $p < 0.1$; c^2_{Infants} = 443.014, 3df, $p < 0.001$). The results for the adult males and females are not unexpected given that those classes of animals were included in the analysis on the assumption that all troop members are potential playmates even though play is a behaviour confined almost exclusively to immature animals (Owens 1975; Walters 1987; Fagen 1993).

While the above analysis considers *potential* play partners, it then needs to be determined who infants preferentially played with if the analysis is confined to *probable* play partners. Presented in Figure 33 is the comparison between observed and expected probable playmates.

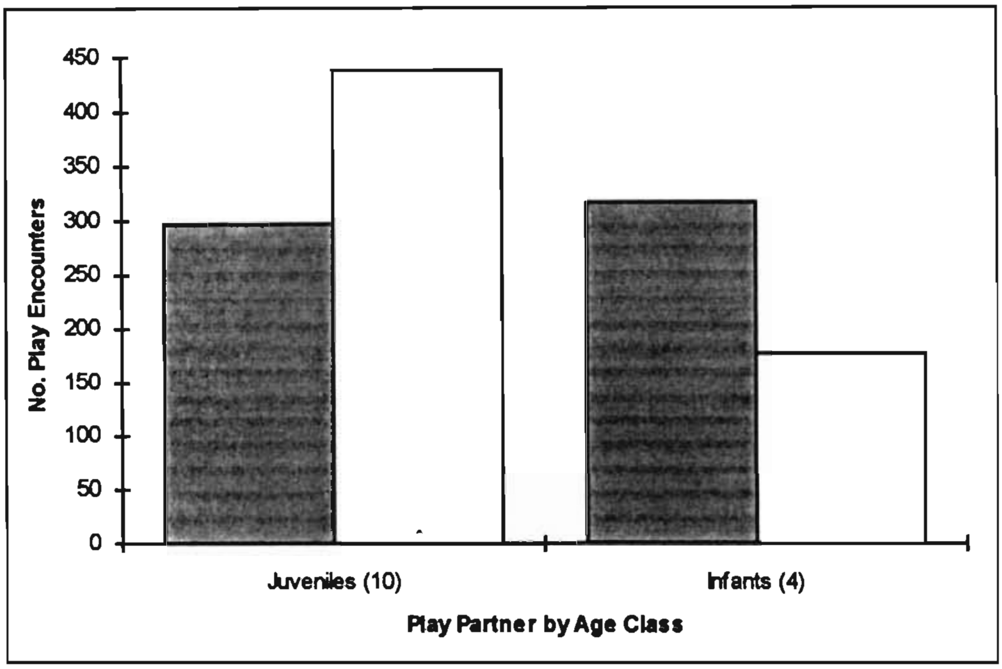

Figure 33: Observed (shaded blocks) and expected (clear) frequencies with which juveniles and other infants were social play partners of infants. Number of animals in each age class indicated in parentheses.

Given their proportional representation in the troop, juvenile animals were encountered as playmates significantly less than would be expected, while other infants were played with more often than would be expected ($c^2_{\mathbf{Juveniles}} = 45.4$, 1 df, $p < 0.001$; $c^2_{\mathbf{Infants}} = 109.2$, 1 df, $p < 0.001$). This observation that infants tended to play more with other infants has previously been reported for baboons elsewhere (Owens 1975; Cheney 1978; Nicolson 1982) as well as for other primate species (Rhesus monkeys:- Altmann 1962a, Southwick *et al* 1965; Bonnet monkeys:- Simonds 1965; Langurs:- Jay 1963; Squirrel monkeys:- Baldwin 1969; Chimpanzees:- Van Lawick-Goodall 1968). Considering the play partners of immature chacma baboons, Cheney (1978) has suggested that play among individuals of approximately the same age, weight, and social skill would appear to be less likely to break down than would play among animals of disparate ages. She further found that infant play appeared to be affected by the number and ages of potential play partners where the frequency of an individual's play was apparently determined by an interaction of the individual's age and those of his play partners.

For the infants in the present study, the possibility exists that other infants were played with more often than would be expected given their representation in the troop primarily because other animals, particularly juveniles, were not available for play given the time contraints on their activity budgets. In other words, juveniles, as independent foragers, may not have been available for play in light of the necessity for them to allocate a significant proportion of their time to foraging. It has previously been shown that the adult Drakensberg baboons dedicate, on average, approximately 67% of their available time to foraging. This figure is similar for juvenile animals. Over the last ten months of this study, juveniles spent approximately 64% of their time feeding, while the amount of time spent playing comprised only 7.61% of their daily activity budget.

In order to establish whether or not juvenile animals were available for play with infants, I compared the mean amount of time that both infants and juveniles were engaged in play (Figure 34). This comparison is confined to the last ten months of the study (May 1992 - February 1993) when all infants in the troop were available as play partners. During each month, infants spent more time playing than did juvenile animals, except during the last month of the study when both age classes played similar amounts of time. Over the ten month period, infants played significantly more than juvenile animals (infants: x = 10.31%, SE = 0.32; juveniles: x = 7.31, SE = 0.35; Mann Whitney U test, two-tailed, p = 0.0001).

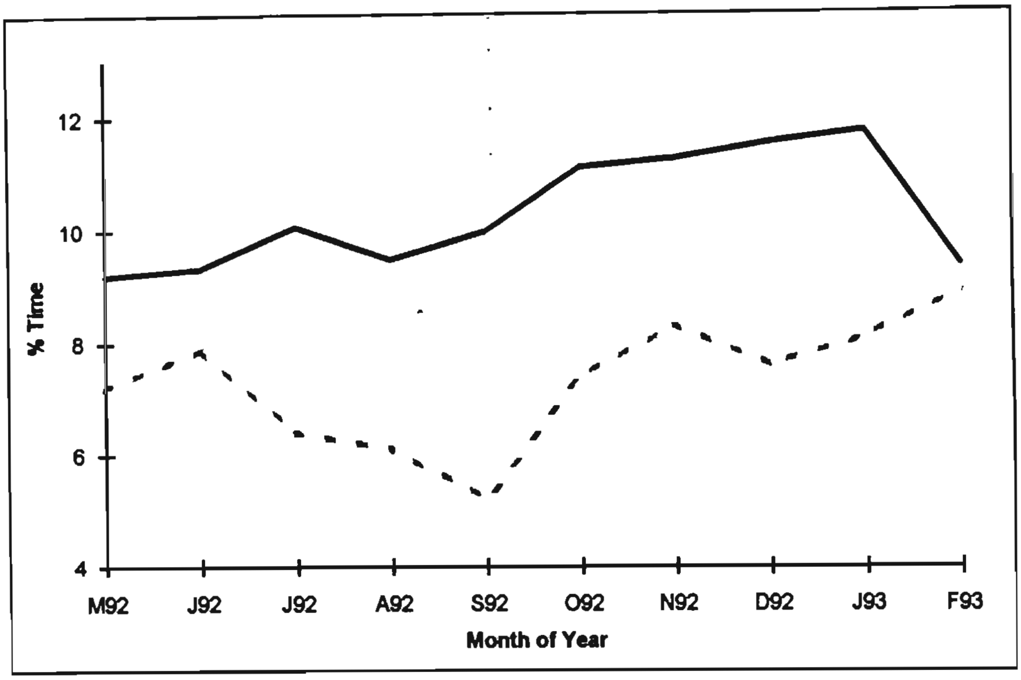

Figure 34: Mean amount of time that juveniles (broken line) and infants (solid line) were observed in play over the last 10 months of the study.

From Figure 34 it can be seen that the amount of time juvenile animals spent in play varied more on a month-by-month basis than did infant play time. Such monthly variability in juvenile play, and not in infant play, may be expected given that juveniles, as independent foragers, will be constrained in the amount of time they can allocate to different activities. That is, if feeding patterns vary with changing ecological conditions, so too will general activity budgets in order to compensate for increases (or decreases) in feeding time which is the major activity category. Infants, on the other hand, will presumably not be constrained in the same sense given that they are reliant on their mothers for most of their nutrition. The constraints on the amount of play an animal can engage in is presented in the following section.

5.3.2.5. PLAY AS AN INDICATOR OF ECOLOGICAL CONDITIONS

The amount of time, at different times of the year, that immature animals spend playing has been reported to be directly related to prevailing ecological conditons (Squirrel monkeys, *Saimiri scuireceus*:- Baldwin and Baldwin 1976; Olive baboons, *P. anubis*:- Oliver and Lee 1978; Vervet monkeys, *Cercopithecus aethiops*:- Lee 1983b 1983c 1984b, 1986; Gelada baboons, Theropithecus gelada:- Barrett *et al* 1992; Bighorn sheep, *Ovis canadensis*:- Berger 1980; White-tailed deer, *Odocoileus virginianus*:- Muller-Schwarze *et al* 1982). In each study, changes in the abundance or quality of food, either seasonal or experimentally induced, were associated with sharp reductions in the amount of play observed. The fact that immature animals play at original levels once food availability returns to normal, and do so with few, if any, detrimental side-effects, has been offered as evidence to support the view that play need not necessarily be an essential component of behavioural development.

For the animals in the present study, a significant relationship between play and ecological conditions was found for juveniles, but not for infants. For the juvenile animals, more time was spent feeding and less time playing as monthly rainfall declined with its concomitant decrease in the quality and quantity of food in the habitat. Rainfall and amount of time spent playing were positively correlated ($r = .6919$ $p < 0.05$), while feeding and play were negatively related to each other ($r = -.7161$ $p < 0.05$). This juvenile pattern of increased feeding time through the dry winter months as ecological conditions deteriorated has already been shown for adult female baboons in the study troop (Chapter 3). A positive relationship between rainfall and extent of play has previously been reported for other primate studies. Barrett *et al* (1992) found that rates of juvenile play among gelada baboons correlated positively with rainfall as a measure of the richness of the habitat, where play rates declined with deteriorating ecological conditions. Lee (1986) observed that immature vervet monkeys played less during the Amboseli dry season with its concomitant reduction in food availability (as measured by various indices). Oliver and Lee (1978) found that among both baboon and vervet juveniles, those living in ecologically poorer habitats played at lower rates than did juveniles living in wetter habitats.

For the infants in the present study, the relationships between play and rainfall, and play and feeding, are presented in Table 13. For the three male infants (G2, F2, R2), the amount of time spent playing was negatively related to monthly rainfall, but was significantly so for only one of these infants. For the two females (C2, R2), play was positively correlated with monthly rainfall, although significantly so for only one of the two. In terms of the relationship between play and feeding, for all five infants the relationship was positive, but only for three of them was it significantly so. However, if the first three months of almost complete infant nutritional dependence on their mothers are excluded from the correlations (Table 13, column 4), then the correlation for only one of the infants remains significant (R2) while for another two (G2 and J2) the direction of the relationship becomes negative.

Infant	Play/Rainfall	Play/Feed	Play/Feed - 2
G2	-.6150 (p<0.01)	.3273	-.0695
F2	-.3346	.4297 (p<0.1)	.1455
J2	-.3001	.4337	-.0137
C2	.1182	.6856 (p<0.01)	.4940
R2	.6353 (p<0.05)	.7112 (p<0.5)	.7449 (p<0.05)

Table 13: Correlation coefficient for individual infant play and monthly rainfall, and individual infant play and independent feeding. The fourth column (Play/Feed - 2) reports the correlation coefficient for feeding and play where the first 3 months of feeding data are excluded. ( ) denotes a significant relationship.

The lack of any consistent or predicted relationships is not entirely unexpected. A negative and significant relationship between feeding and play would only be expected if the animals were affected by seasonal variability in food supplies. That is, if they were no longer being suckled, and hence were not buffered against variability in food availability, and were having to allocate time to the harvesting of their own food (Barrett *et al* 1992). It has been shown that the infants in this study remained at least partially dependent on their mothers for nutrition and that, even by the end of the study, the amount of time they fed for themselves remained considerably below the levels at which juvenile and adult females foraged.

The point is that even though the baboons in this study inhabit an area which is highly seasonal in the temporal availability of food, and thus it may be expected that they would show fluctuations in the amount of time they can allocate to their various behaviours, infants did not appear to be doing this. The primary reason, it will be argued later in this chapter, is that their lack of nutritional independence did not constrain them in the same way that the activities of independent animals are. And hence the lack of any significant and predicted relationship between play, feeding, and environmental conditions.

5.3.3 GROOMING

Social grooming, according to Dunbar (1988), is characteristic of all primates. He notes, however, that the significance of grooming will be more pronounced among the more social species. While grooming undoubtedly serves some hygienic purpose (Hutchins and Barash 1976; Goosen 1981; Silk 1987; Marsh 1992), Nicolson (1982), Dunbar (1988) and Marsh (1992) have each pointed to the social function served by grooming. Nicolson (1982) noted that close social bonds and relationships among baboons of all ages are characterized by grooming, while Dunbar (1988) refers to the tendency for extensive grooming to occur between individuals following agonistic interactions, as well as to the fact that time spent grooming is often conserved in the face of pressures on time budgets (Sharman and Dunbar 1984; Lee 1984b; Dunbar and Dunbar 1988). Some of the more specific social functions supposedly served by grooming include the reduction of aggression and tension (Goosen 1981), avoiding unnecessary aggressive encounters before they occur (Goosen 1981), and servicing coalition partnerships and friendships where the ability to predict a potential ally's future behaviour may be enhanced through regular grooming contact (Dunbar 1988).

Grooming in relation to infants has usually been considered from a number of perspectives which include developmental changes in the amount of time that baboon infants engage in grooming (Nicolson 1982; Pereira 1984; Marsh 1992), male grooming of infants following infant use by males in agonistic encounters with other males (yellow baboons: Stein 1984; olive baboons: Packer 1980; gelada baboons: Kawai 1979), and the grooming partner preferences of infants (Nicolson 1982; Pereira 1984, cited in Marsh 1992; Pereira and Altmann 1985; Marsh 1992).

5.3.3.1 GROOMING BY INFANTS IN THE PRESENT STUDY

The mean amount of time, at each monthly age, that infants in this study engaged in grooming interactions with any other animal, regardless of whether the infant was grooming or being groomed, is plotted in Figure 35.

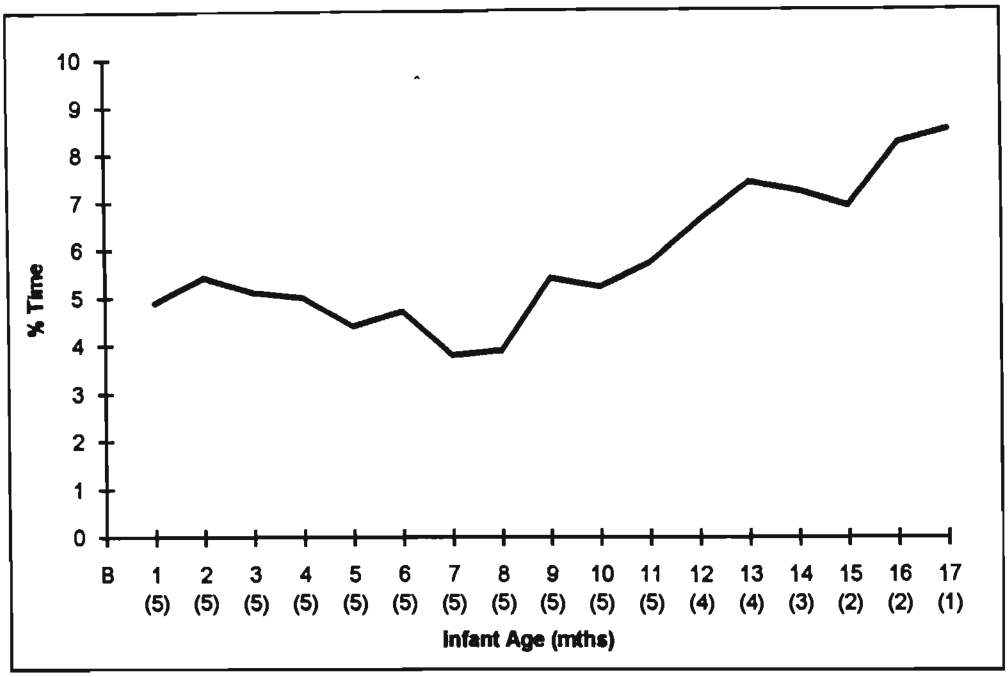

Figure 35: Mean percentage time, at each monthly age, that infants engaged in grooming interactions. The plotted values do not distinguish between whether infant was the groomer or the animal being groomed. Figures in parentheses (x-axis) indicate number of infants at each monthly age.

Over the 17 months, infants in this study were engaged in grooming interactions an average 5.28% of the time. The initial postpartum levels of grooming began to gradually decline through to month-8. At this age, participation in grooming increased again through to months 16-17 when the last data were collected. The infant grooming value of 8.2% during month-16 (N=2) remains below the average amount of time for a year that adult females (non-mothers) spent in social interaction (11.33%; Chapter 3), and this increased only slightly during the 17th month for infant G2 (8.5%). Compared to Nicolson's (1982) infants, the infants in the present study spent, on average, more time in grooming interactions than did those in her study (this study: 1-17 months - 5.28%; Gilgil: 1-18 months - 1.35%).

The relatively high postpartum levels with which infants in the present study were observed in grooming interactions is probably related to two aspects of infancy. In the first place, young infants are held in the ventral position by their mothers for most of the time over the first two or three months postpartum. While in this position, mothers often groom infants as they suckle and while mothers are resting (Nash 1978; Altmann 1980; Nicolson 1982; Marsh 1992; pers obs.). The second aspect of infancy which will contribute to initial high levels of grooming interactions relates to infants as 'objects' which elicit heightened interest and attention from other group members, particularly females, who attempt to touch, hold, and groom the new infant. Both of these phenomena will probably also account, in part, for the reduced participation of infants in grooming interactions during months 4-6. During that period, infants are not only spending increasing amounts of time out of the ventral position, but their attractiveness to other group members decreases as they lose their natal colouring (*P. anubis*: Ransom and Rowell 1972; Nicolson 1982; *P. cynocephalus*: Rasmussen 1979; Altmann *et al* 1977). The distinctive black natal colouring has been proposed as a proximate cue for interest shown in infants by other group members (DeVore 1963; Altmann 1980).

If infant participation in grooming interactions is partitioned between whether infants are acting as groomer or are being groomed (Figure 36), it becomes clear that infants did not participate as groomers until relatively late in their infancy.

Thus, over the period 1-10 months, infants were almost never seen to reciprocate in grooming interactions. From their eleventh month onwards, however, there occurred an increase in the amount of time that they acted as groomers.

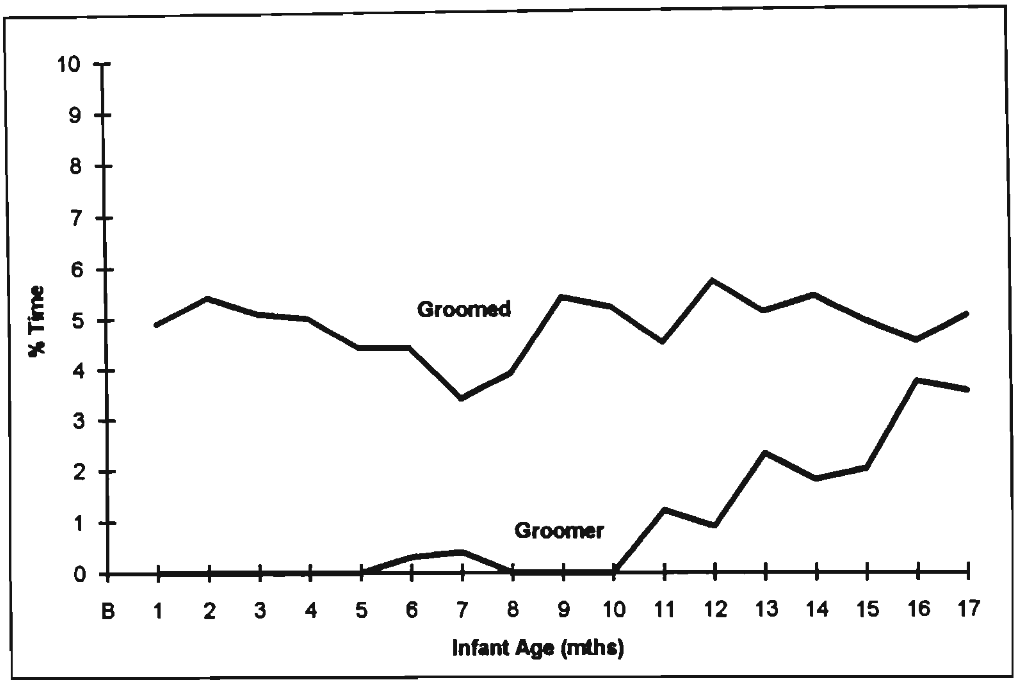

Figure 36: Comparison of infant participation in grooming interactions as either "groomer" or "groomed".

The late development of grooming reciprocity by baboon infants has previously been shown by Nash (1978) and Marsh (1992). Marsh (1992) reported that it was only during their ninth month that her infants become groomers. However, the pattern of being groomed reported for this study differs to that of Marsh. She showed a rapid decline in being groomed to 0% during months 6-8, which then increased again to approximately 2% for later ages. For the infants in this study, time spent being groomed did decline through to month-7, but did so fairly gradually, and then increased again to average 5% over the period 9-17 months. In explaining the pattern of the data relating to being groomed, Marsh proposed that the rapid decline for her infants was related to infant weaning whereby, as with infant contact and time at the nipple, time spent being groomed by mothers decreased. She supposed that around 9-10 months old infants resume grooming but on a changed basis which is indicative of their changed relationship with their mothers. Also, this increase in grooming time, she claimed, is related to two additional factors. The first is that by this age, infants are moving increasingly on their own, and hence will be picking up larger amounts of ectoparasites and dirt than they would have when they were in contact and being carried by mothers. Secondly, it would be expected that infants would engage in more grooming interactions as they mature given that with their increased mobility, they begin to encounter, and interact with, more members of the social group.

The expanding social world of infants as they get older is highlighted if attention is given to the distribution of infant grooming partners. Plotted in Figure 37 are the probabilities, at each infant age, with which different age classes were infant grooming partners. It is clear from Figure 37 that there was a greater probability that mothers were infant grooming partners than there was for other adult females and juveniles.

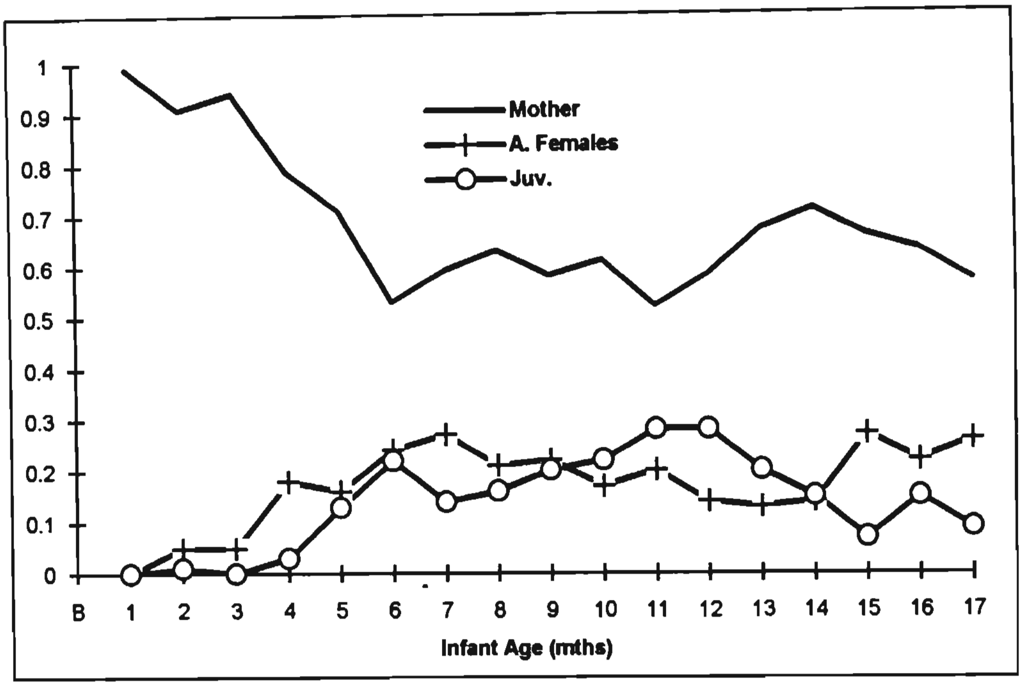

Figure 37: Probability, at each monthly age, that infants were engaged in grooming interactions with (a) their mothers, (b) adult females other than mother, and (c) juveniles.

For their first 3 months of life, infants were involved in grooming interactions almost exclusively with mothers. The probability of mothers being grooming partners decreased during the period 3-6 months, and then remained relatively constant through to month-17. During the period 6-17 months, approximately 61% of all infant grooming interactions involved mothers. However, with increasing age, infants began to encounter individuals other than their mothers during these interactions. During the period 3-6 months, there was a decreased probability that infants would be groomed by their mothers, and an increase in the probabilities that other adult females or juveniles would be grooming partners. From infant age month-6 through to month-17, the probability that an infant would be grooming with its mother remained relatively constant; - over this period, approximately 61% of infant grooming time involved mothers. The probability that other adult females would be infant grooming partners increased during months 3-4, and then remained relatively constant through to month-14, at which time there was an increase in the probability. Juvenile animals showed a marked increase in the probability of their being infant grooming partners over the infant age 4-5 months, increasing again over the 11th and 12th months, and then declined again during and after month-15.

Nicolson (1982) found that in the first year of life her infants were groomed by their mothers more than the combined total of all other grooming partners, with approximately 70% of an infant's grooming time through the first 56 weeks involving mothers, which is the same as the average of 69.8% for the first year of life for the infants in this study.

5.3.4 RESTING BY INFANTS IN THE PRESENT STUDY

The amount of time that infants in the present study spent resting is plotted in Figure 38. Resting was recorded when a subject was not otherwise engaged in any obvious activity. That is, if an animal was stationary (sitting, lying), and not participating in grooming, suckling, or investigating and eating food items, then the animal was recorded as resting. However, if the animal was obviously watching or paying attention to another animal(s), then resting was not recorded. Essentially, resting was a 'default' behavioural category which was utilized when no other behaviour could be appropriately categorized.

Nicolson (1982) characterized resting[3] as "recline, with torso in contact with the ground", while for Marsh (1992) resting referred specifically to "... sleeping and resting with eyes shut" (p.91). Pereira's (1984) 'default' definition (for juvenile animals) which applied when a subject was engaged in behaviour which he had not otherwise defined is relatively close to the definition used here. Data for month-1 are not presented given the high levels with which infants were observed in ventral contact (and hence were subsumed under either 'ventral' or 'at nipple' categories).

Figure 38: Percentage time per month that infants spent resting. Mean for all infants.

The average time through months 2-17 that infants spent resting was 7.22%, which is lower than the average (for a year)

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[3] Although Nicolson provides this definition of rest, she notes in the text that "... Most of the time infants were inactive they were on their mothers' backs, and the category Rest is therefore almost synonymous with riding" (p.142).

for both juveniles (10.5%) and adult females (non-mothers: 12.37%; Chapter 3). It is also considerably less than the average resting time through to month-18 for Nicolson's (1982) Gilgil infants (18.78%, from Table 36a), but higher than the average for Marsh's (1992) Chololo infants (2.12%; average 3-17 months; Figure 6.3), although data from other studies may not be directly comparable due to the definitional discrepancies between studies that were referred to above.

Resting is not really an activity in which one would expect some sense of development. There is no skill inherent in the activity (or, more appropriately, the lack of activity), and so no developmental trends will be apparent, with the exception perhaps of changes in the amount of time animals rest as their activity budgets come under pressure. Although the data are not available for this study, it would be interesting to know which individuals infants preferentially rest in proximity to, and whether such preferences in association will reflect any developmental trends.

5.4 BEHAVIOURAL CHANGES IN DEVELOPMENT

This chapter, as well as sections of the previous one, have described particular aspects of infant behavioural development of the Drakensberg baboons, but have done so individually. The point is that the different behaviours described do not develop in isolation to one another. Changes in the activity budget of an infant reflect, in a sense, the changing priorities of that individual.

It has been noted that while infancy has generally been considered to be a care-free time of life, infants are still constrained to some degree in 'what and when' they can do particular things. Some of the factors that constrain them in this way include maternal routines, group movement, and time constraints on the activities of other members of the group (Nicolson 1982; Marsh 1992). At the same time, infants are constrained by their own needs and activities. As Marsh (1992) noted, ".... when more time is spent in one activity, less time is (or must be) spent in another" (p.109).

Plotted in Figure 40 (end of the text in this chapter) is the basic activity schedule through 1-17 months for the infants in this study (Note that the data for month-17 are based on the activity budget for only one infant). It is clear from the graph that, with increasing age, changes in the allocation of time to different infant activities occurs. Thus, for example, it has been shown that the relationship between infant reliance on their mothers for transport (i.e. ventral and dorsal carrying) is negatively, and significantly, related to the amount of time that infants move independently. Logically this makes sense, as do similar relationships between other associated behavioural categories.

In terms of infant development toward the adult 'model' of allocation of time to the various behaviours which comprise the daily activity budget, the first (and probably the most obvious) point to note is the slow development of independent feeding by the infants in this study. Figure 39 illustrates this point.

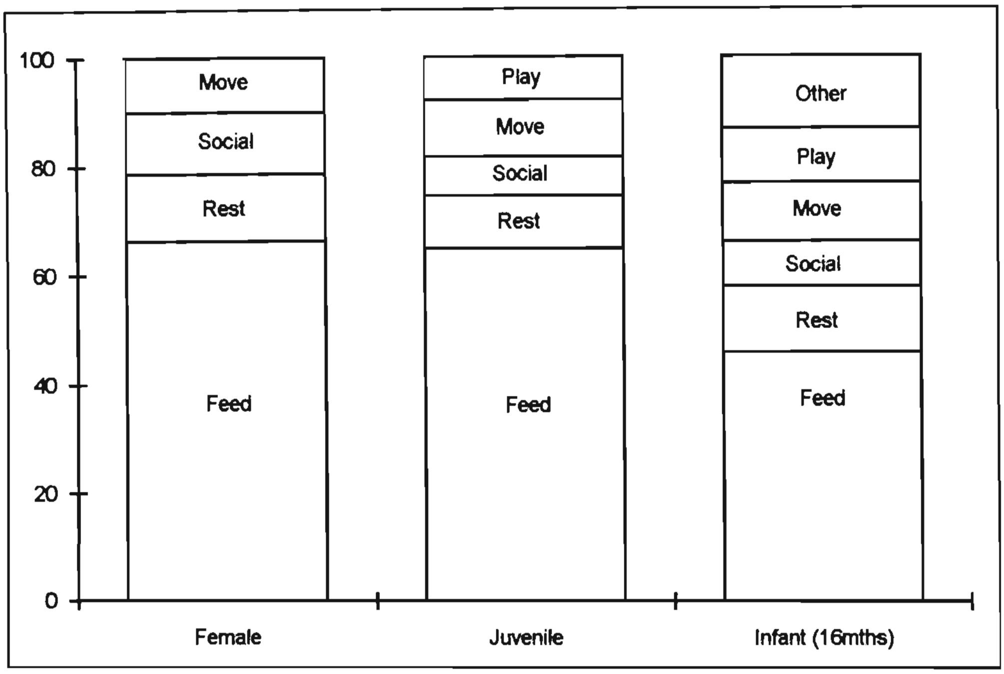

Figure 39: Comparison between age classes of time spent in activities which comprise the adult activity budget[4]. Time spent playing is included for juveniles and infants (month-16, N=2). Data for females (non-mothers) as reported in Chapter 3; data for juveniles averaged from scan samples covering an 11-month period (April 1992 - February 1993). Note that the "Other" category for infants includes continued suckling and dependent transport (see Figure 40 at the end of this chapter).

Even as late as 16 and 17 months the Drakensberg infants studied here are feeding at levels considerably below those of adult females[5] and juveniles in the same troop. It was shown in Chapter 4 that these levels of infant feeding are also below

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[4] The activity categories presented in Figure 39 are those which are traditionally viewed as comprising the adult activity budget. For the infants and juveniles, the standard categories also include play behaviour.

[5] Note that the feeding reported for females is that for females in the troop who did not have a currently dependent offspring. Mothers were not used in the comparison given that they feed at levels above normal, and hence will not be representative of the adult 'model'.

those for comparative studies. By their 15th month, Nicolson's (1982) infants were spending 53% of the time feeding, and Marsh's (1992) were feeding 52% by their 19th month. While these amounts of time spent feeding may not be too dissimilar across the studies, the point is that at the specified ages, the infants in the comparative studies were feeding *at adult levels.* Thus the activity budgets of infants in those studies could be said to already approximate the adult model *at the same age* at which the infants in the present study were still demonstrating some dependence.

In terms of the definitions of the activity categories used in this study (see Chapter 2: Methods section), the standard behaviour categories were mutually exclusive. Extending this, if the subjects in the study were constrained in some manner in the allocation of time to their various maintenance activities, then each of the activities should have been negatively related to feeding time (given the centrality of feeding in the construction of activity budgets). The probable exception to this would be moving, where animals may have to move further as they spend more time feeding. Thus, for example, it was shown for adult females in Chapter 3 that resting and social time were negatively correlated with feeding time, and that moving was positively but not significantly correlated with feeding time. The same pattern is true for juvenile animals in the Drakensberg. Juvenile feeding time was negatively correlated with resting, grooming, and play, and was positively related to moving (see additional notes at the end of this chapter for correlation coefficients for juvenile activity).

For the infants in this study, however, all the behaviours which make up the bulk of the infant activity budget (standard activity categories) were positively correlated with feeding time (Table 14).

	Rest	Groom	Move	Play
Feed	.8103	.9048	.5269	.4710

Table 14: Correlation coefficients for relationship between infant feeding and: resting, grooming, moving, and play. Correlations significant at $p<0.01$, except:- (T) = $p<0.05$ and (TT) = $p<0.1$.

That most of the behaviours were positively correlated with feeding does not imply any causality in the sense that increases in feeding were causing increases in the associated behaviours (or vice versa). Rather, of interest is the fact that increases in feeding behaviour, which is the primary behaviour category, were not associated with decreases in any of the other infant behaviours. This is most probably due to the fact that the 'upper limits' on the allocation of time to particular behaviours had not been reached. In other words, at month-16 the infants in the present study were not feeding at the same levels as independently feeding immatures and adults, and so the amount of time available for participation in other activities was, for the infants, not contingent on feeding time demands. This finding stands in partial contrast to the data from Nicolson (1982) which demostrate that infant resting and 'other' behaviour (which included play) are negatively related to feeding time, while moving and social are positively correlated (correlations based on data from Nicolson 1982, Table 36a). A similar pattern to Nicolson's data is suggested by that of Marsh (1992), but no definate parallels can be drawn[6] due to a lack of information.

The general picture which emerges for the Drakensberg infants is that infancy probably *is* a care-free and unconstrained time of life, and that this period of infancy is extended beyond the normal length of infancy in other populations. It is, however, noted that infants may be constrained in a less direct sense in terms of a need to get to their mothers to suckle and also in the sense that they will need access to other animals for social interactions. Nonetheless, whether infancy for these baboons is, in fact, relatively demand-free and limitless in its scope is something for further research to uncover. While the implications of the present study for future research will be discussed in Chapter 7, some of these can be raised at this point. In particular, closer attention will need to be given to the *dynamics* of the relationships (social, spatial, temporal) that infants have with other members of the troop, and this should be conducted at a level of analysis which goes beyond a mere description of who and when, and at what age infants, associate with particular individuals, or with individuals from different age-sex classes. The impetus for such an analysis is to be found in the description of infant development presented here. That is to say, we *know* from previous work conducted on

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[6] Marsh provides Pearson correlation coefficients for only those correlations which have values greater than 0.7 and where at least 50% of the variance (R^2) is explained. Thus any correlation less than 0.7 was not presented.

the Drakensberg baboons (see references in Chapter 2) that food items are, at the same time, cryptic and hence difficult to find, hyper-dispersed, and difficult to obtain. We now know from this study that infants demonstrate slow development toward attaining an independent diet. What we don't know are the nature of the tasks infants must become competent in, in order to be functionally independent. Integral to this issue must be the role in learning and the attainment of competence that is played by particular relationships and associations infants have with other animals.

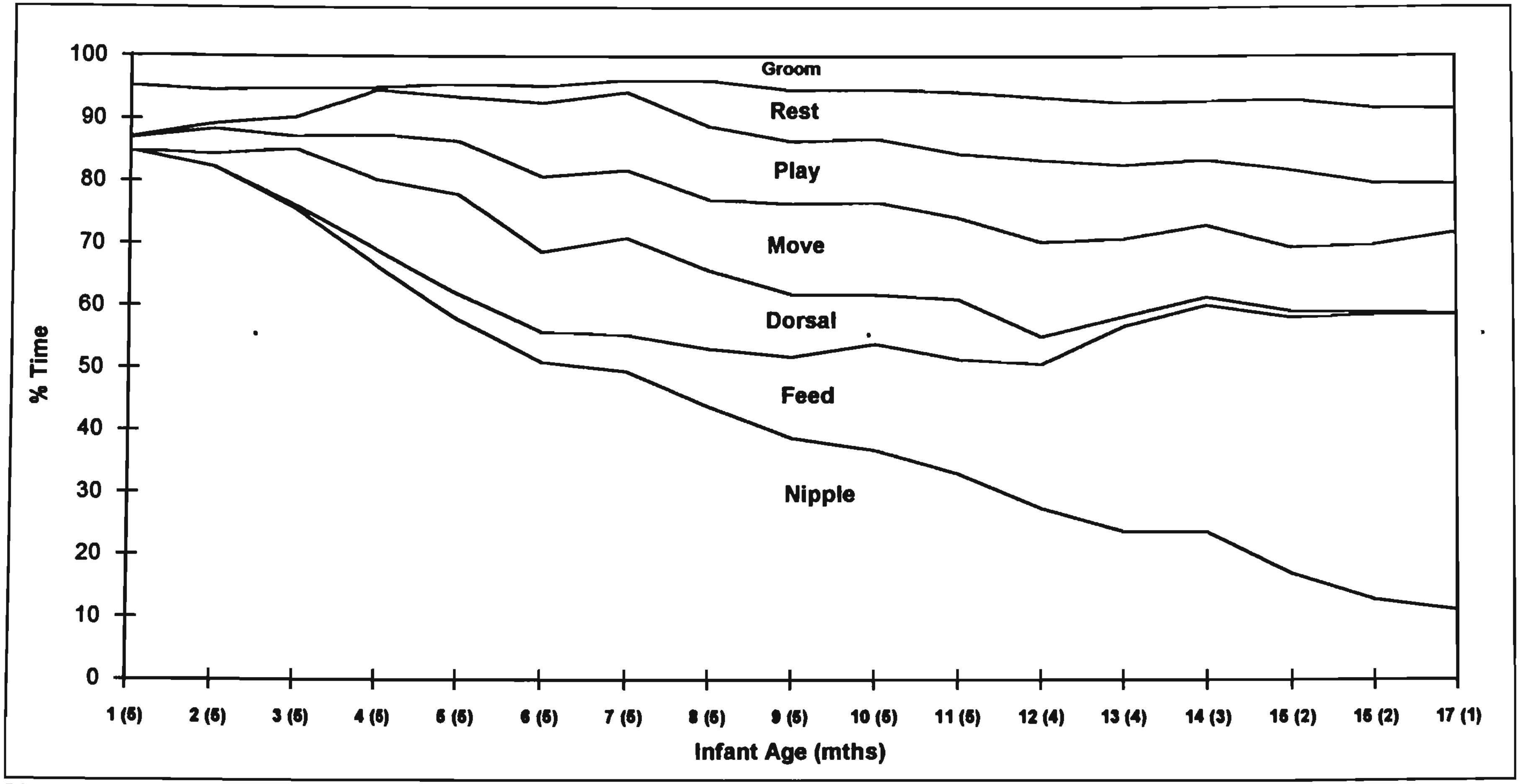

Figure 40: Activity budgets of infants for the period 1-17 months. Figures in parentheses (x-axis) indicate how many infants were sampled at each age.

ADDITIONAL NOTES

CORRELATION COEFFICIENTS: JUVENILE ACTIVITY

	Move	Rest	Social	Play	
Feed	.5862 *	-.7203 **	-.8175 ***	-.7863 ***	
Move		-.6560 **	-.2222 (NS)	-.7398 **	
Rest			.2962 (NS)	.4768 (NS)	
Social				.4792 (NS)	

*** ($p<0.01$)
** ($p<0.05$)
* ($p<0.1$)

CHAPTER 6

ADULT MALE - INFANT RELATIONSHIPS

6.1 INTRODUCTION

While the task of parental care in primates is usually the responsibility of, and is generally associated with females, the role of males is not necessarily insignificant (Dunbar 1988). Three broad ways in which males can assist in the rearing of offspring have been described. They might assist females directly in the transport and care of offspring. Secondly, they might contribute indirectly through active protection of the female and her offspring against both predators and conspecifics and, thirdly, assistance may be provided through the defense of a territory which might provide access for the female and her offspring to resources (Dunbar 1988). Among savanna baboons, the post-mating component of reproduction for males has been described as including the protection of infants against predators and conspecifics, influencing offspring rank, improving offspring access to resources at the expense of other group members, or improving the well-being of other care-givers such as the offspring's mother (Noē and Sluijter 1990).

In this chapter I report on interactions between males and infants that were observed during the course of this study. From the outset, it should be noted that very few, if any at all, speculations will be forthcoming regarding the functional purpose these interactions might have for the development of infant competence. The behaviours which underlie the categories of care which males provide, and which were outlined above, were so infrequent in their occurence that the magnitude of the benefit infants (or mothers) would derive is minimal. However, the point is acknowledged that, for example, any instance where a single act by a male prevents the death of an infant will derive enormous benefit for the infant and for it's mothers lifetime reproductive success. Thus, the infrequent behaviours that are referred to include those such as the transportation of infants (in situations distinct from male-male agonistic encounters: see below), overt protection of infants from predators and conspecifics, male grooming of infants, and the protection of infants from social interference. Nonetheless, it remains highly probable that males *do* contribute to infant development in more subtle and indirect ways. These would include, for example, interactions such as male tolerance of the presence of infants during feeding bouts[1]. The detailed data required to assess in what way these male-infant interactions might benefit the infant are, however, not available for analysis in the present study.

So, if these kind of detailed data are not available to assess the impact males may have on infant development, the question arises as to what *will* be presented in a male-infant chapter in

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[1] Data relating to male-infant contact/proximity in different behavioural contexts, including male feeding and resting, will be presented in this chapter. However, these data provide only a gross indication of the context within which male-infant interactions took place, and do not assess the kind of processes which might arise during such interaction, and which may facilitate infant independence in the manner being referred to here.

a presentation which has, until this point, been concerned with infant development? Indeed, the question might be asked why even include such a chapter which claims to offer no insight on developmental processes? In the first place, the data required for a detailed examination of the role contributed by adult males to infant development are not available due to conceptual and methodological short-comings encountered during the course of data collection. Specifically, the nature of the study and the techniques of data collection did not make allowance for the categories of interactions which, with hindsight, *should* have been collected.

Before answering the question posed as to what *will* be presented in this chapter, an answer will be put forward as to why the chapter is indeed included, given its stated 'irrelevance' to infant developmental processes. Stated as simply as possible, it became clear too late in the study[2] that the presence of infants influenced, to a certain degree, the behaviour of particular males and did so in differing contexts. The presence of an infant is, to a different extent and in a different manner, akin to the effect that they have on mothers which was considered in Chapter 3. In other words, while it was shown that infants *do* affect the functioning of mothers in the ecological arena, they *can* influence the way in which males function socially with other animals, particularly other males. Bearing this in mind, what *will* be presented in this chapter is

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[2] By "too late in the study", what I refer to was the inability to refine data collection techniques in order to quantify male-infant interactions which had already taken place, and whose impact became obvious only once the study was nearing completion.

the albeit incomplete data set which will be used to try and understand the observed extent of male interaction with infants. In doing so, an attempt is made to apply the data to predictions contained in the literature which purport to explain why males might interact with infants. From the data which are available, but which are not conclusive given their explanatory limitations, the extent of observed individual male interaction with infants, it will be shown, is discrepant with predictions that males might assist females in the care of offspring to the degree that such care will contribute in some way to the enhancement of male reproductive success. It will be argued that, in terms of theoretical predictions, the available data do not conform with expectations.

I begin by reviewing how male-infant relationships have been interpreted in the literature. Following this I present data on male mating behaviour within the study troop in order to attempt to predict paternity and the consequences this might have for male-infant relationships. Once the probability of paternity has been established, I will present data on the extent and context of adult male interaction with infants. These interactions will be interpreted in terms of their possible functional significance for males.

6.2 THE FUNCTIONAL SIGNIFICANCE OF ADULT MALE-INFANT RELATIONSHIPS

While male-infant interactions have been widely reported as a feature of all primate species, the extent thereof is variable.

Additionally, the theoretical significance of these relationships remains inconclusive (Taub and Redican 1984). According to Whitten (1987), male-infant interactions (including male care of infants) were, when initially observed and reported, an expected and unremarkable phenomenon. This was in line with the preeminence at the time of group selection theory which held that individuals (i.e. males) were acting for the good of the group. It was only with the resurgent interest in individual selection that this class of relationship became a focus of thorough discussion and enquiry. Where kin selection theory proposed that individuals should, when costs and benefits are held constant, invest preferentially in close relatives (Hamilton 1964), sexual selection theory was premised on males attempting to maximise reproductive output and hence minimizing parental investment in any one offspring (Trivers 1972). Given the observed variability in the type and extent of male-infant relationships, both interspecifically as well as intraspecifically, these interactions became a means of testing the predictions of kin- and sexual selection theories.

6.2.1 CATEGORIES OF MALE CARE OF INFANTS

Hamilton (1984) identifies a number of categories of care or male-infant interactions that males might engage in with infants. Central to paternal care-giving is complementarity of paternal behaviours with maternal caregiving (Hamilton 1984). That is, where the costs of paternal behaviour(s) are low and the benefits potentially large, males might accrue proportionately more benefit by substituting maternal care with their care such that the costs of maternal care are reduced, and thereby the future reproductive effort of the mother and the care of the infant is enhanced (Hamilton 1984). Thus males may contribute to infant care through the provision of infant transport; infant use in counter-carrying against other usually higher-ranking males; the protection of infants against social interference; food sharing; status allocation; grooming; and protection from predation. Each of these is considered briefly.

6.2.1.1 THE PROVISION OF INFANT TRANSPORT

Hamilton (1984) has suggested that while mothers generally carry infants in the immediate post-partum period, young ('preadult') males (as well as preadult females) might carry an infant if it is orphaned. The benefit of this to the infant is primarily found in terms of the infant's energy requirements, while the benefits to the carrier are probably found in terms of inclusive fitness[3] (Hamilton 1984). For adult males, Hamilton (1984) proposes that it is only worthwhile for a male to reduce maternal carrying to the extent that the male may father further offspring by the female, or where male carrying enhances a female's ability to care for a current offspring that is the progeny of the carrying male.

6.2.1.2 COUNTER-CARRYING OF INFANTS AGAINST OTHER MALES

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[3] Hamilton (1984) suggests that the carrying of orphaned infants may represent a 'fitness-enhancing' behaviour in that young chacma baboons will probably have limited alternative means of expressing such behaviour.

Counter-carrying is distinguished from providing infants with transport in that counter-carrying is usually temporary and occurs predominantly during male confrontations with other males who are usually of higher-rank than the carrying male. Two hypotheses have been proposed to explain the phenomenon of infant counter-carrying. The first, the *use* or *exploitation hypothesis*, asserts that males use or exploit infants in order to alter the outcome of an agonistic interaction with a higher-ranking male (Packer 1980; Stein 1981, 1984; cited in Smuts 1985). A male who uses an infant in this way may be able to challenge a higher-ranking male (Collins 1981, 1985; Stein 1981; cited in Smuts 1985), or may be able to resist aggression from a higher-ranking male (Stein 1981).

The second hypothesis proposes that males carry their own infants, usually against recently immigrated males, in order to protect the infants against possible infanticidal tendencies of the newly arrived male (Busse and Hamilton 1981; Busse 1984; cited in Smuts 1985). This *protection hypothesis* suggests a degree of genetic relatedness between the male and the infant.

6.2.1.3 PROTECTION OF INFANTS AGAINST SOCIAL INTERFERENCE

Intense interest in young infants by individuals other than the mother is a phenomenon widely reported for the primates, and is true for baboons (Altmann 1980). While usually viewed as being relatively harmless, Hamilton (1984) suggests that, particularly for low-ranking females, this interest may have negative consequences in that the time spent 'fending off' this interest may cut into feeding time during the phase of maternal care when the energetic demands on females are considerable. In this regard, male associates of mothers may displace interested animals either overtly or indirectly simply through their spatial proximity to mothers.

6.2.1.4 FOOD SHARING AMONG ADULT MALES AND INFANTS

Food sharing is not a characteristic feature of primates in general, and is certainly not prevalent among baboons in particular. However, while engaged in feeding, male baboons are often tolerant of the presence of infants and young juveniles. Through this tolerance it is possible for these immature animals to gain access to food sources, such as discarded, ignored, or overlooked food scraps which they may not ordinarily enjoy (see 'Discussion' p.82, Altmann 1983).

6.2.1.5 ASSISTANCE IN THE ALLOCATION OF STATUS

In terms of the allocation of status, young female baboons take relatively the same status in the troop as their mothers, while young males acquire rank through agonistic encounters as they mature. Hamilton (1984) suggests that being supported by an adult male will be of benefit to male infants in their conflicts with other individuals.

6.2.1.6 ADULT MALE GROOMING OF INFANTS

Hamilton (1984) notes that male grooming of infants, particularly for probable progeny, is often extended and intensive following male use of infants in counter-carrying situations. While the value of ectoparasite removal in this situations may be low, the reinforcement of the male-infant bond will probably be beneficial to both parties.

At a more general level of male care of infants, Smuts (1985) has supposed that if females and their offspring benefit from male care of offspring, and if females mate with males who have demonstrated their 'willingness' to care for, and invest in offspring, then a male who forms and maintains friendships with females will probably enhance his potential reproductive success. In defining this friendship, Smuts (1985) used the frequency of grooming and spatial proximity as a measure of affinity between males and females.

Indirectly, males may provide support for progeny through behaviour which benefits the troop as a whole. Such behaviours include, amongst others, predator defense, participation in inter-troop encounters, and participation in the coordination of group movement.

6.3 PATERNAL CARE: THE MALE PERSPECTIVE

Among baboons, who live in multi-male/multi-female groups, the focus and extent of male care of infants is directed primarily toward probable progeny or to those situations where male support of infants (or their mothers) may enhance a particular male's probability of mating access to females (Hamilton 1984; Smuts 1985). That is to say, males who are probable fathers may assist, at low cost to themselves, a female in the provision of certain categories of care for the infant, or may assist an unrelated infant in the hope of improving his 'status' insofar as future mating opportunities with the mother are concerned.

The high degree of complementarity of male care with that of female care has been referred to above. Hamilton (1984) has pointed out that, for the range of male-infant interactions outlined above, the cost to the male is minimal while the potential benefits, in terms of improved opportunities in access to females, is great. He notes that where complementarity is low, maternal caregiving will be primary.

Before presenting the data on the relationships individual males held with infants, it is necessary to first consider the reproductive relationships between males and females in the troop, and the consequences these might have for male-infant relationships. These data will show a rank related pattern of reproductive access to females.

6.3.1 MALE REPRODUCTION: PATTERNS OF CONSORT

For the purposes of the analyses which follow, data are confined to a 12 month period covering June 1991 - May 1992. All female swellings were monitored to the day of detumescence as were the identities of observed consort pairs (sensu Hausfater 1975). Male rank was determined by scoring displacements in non-sexual contexts. No changes in the male dominance rank occurred during the year from which these data are extracted.

During the 12 months covered by the period reported here, 5 of the 9 females in the troop were sexually receptive, for which 22 complete cycles were recorded. Four adult males were present in the troop throughout the year. Data have been sorted in terms of the total number of days males were observed in consort (N=123), as well as the stage of the female cycle on which these days fell. Consort days are a valid measure of reproductive success in the Drakensberg given that all observed copulations involved consort partners and all consortships lasted the whole day (*pers. obs.*). Opportunistic copulations with a female in consort with another male were never observed.

6.3.2 MALE RANK AND ACCESS TO FEMALES: NUMBER OF CONSORT DAYS

Access to swollen females, as measured by the number of consort days, and hence the probability of fathering offspring were positively correlated with male rank ($r = .9381$ $p < 0.01$).

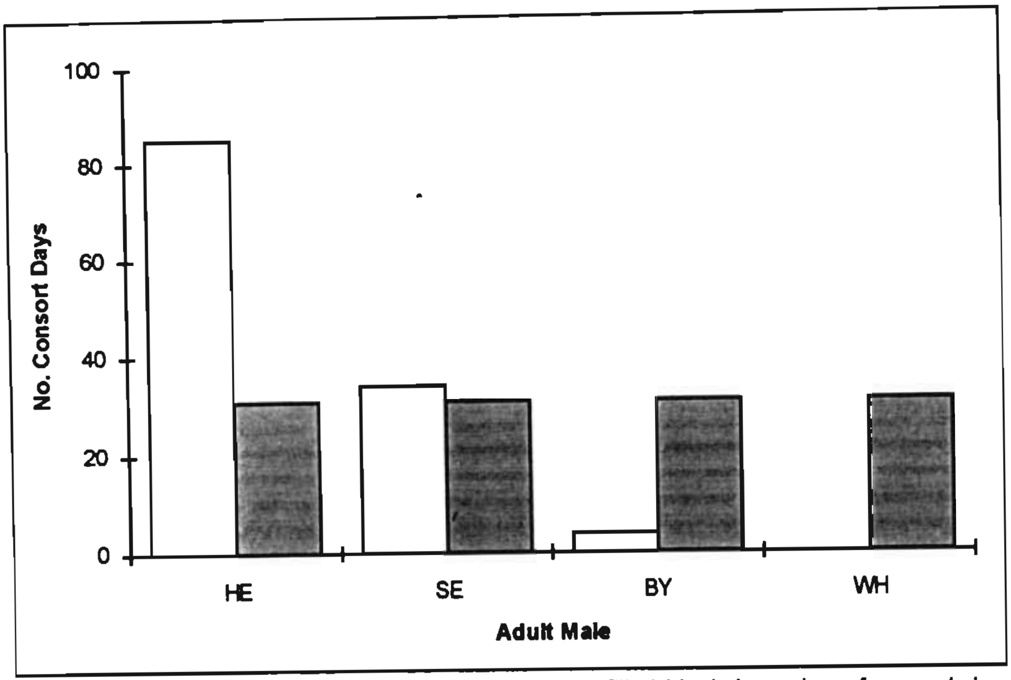

Figure 41: Observed (clear blocks) and expected (filled blocks) number of consort days adult males were engaged in. Expected values assume each male has equal access to cycling females. Males are ordered in terms of decreasing rank from left to right (i.e. HE = highest rank, WH = lowest rank).

The alpha male (HE) was involved in 69.1% (N=85) of all observed consortship days, the beta male (SE) in 27.6% (N=34), the gamma male (BY) in 3.25% (N=4), while the delta male (WH) was never observed to hold a consortship. These differences between the number of male consort days are significant (c^2 = 150.073, 3 d.f., p<0.01 Figure 41).

6.3.3 DISTRIBUTION OF MALE CONSORT DAYS OVER THE FEMALE CYCLE

Not only did the highest ranking male have more access to swollen females in terms of number of consort days, but he further tended to engage in these consortships during particular days of the female cycle (Figure 42).

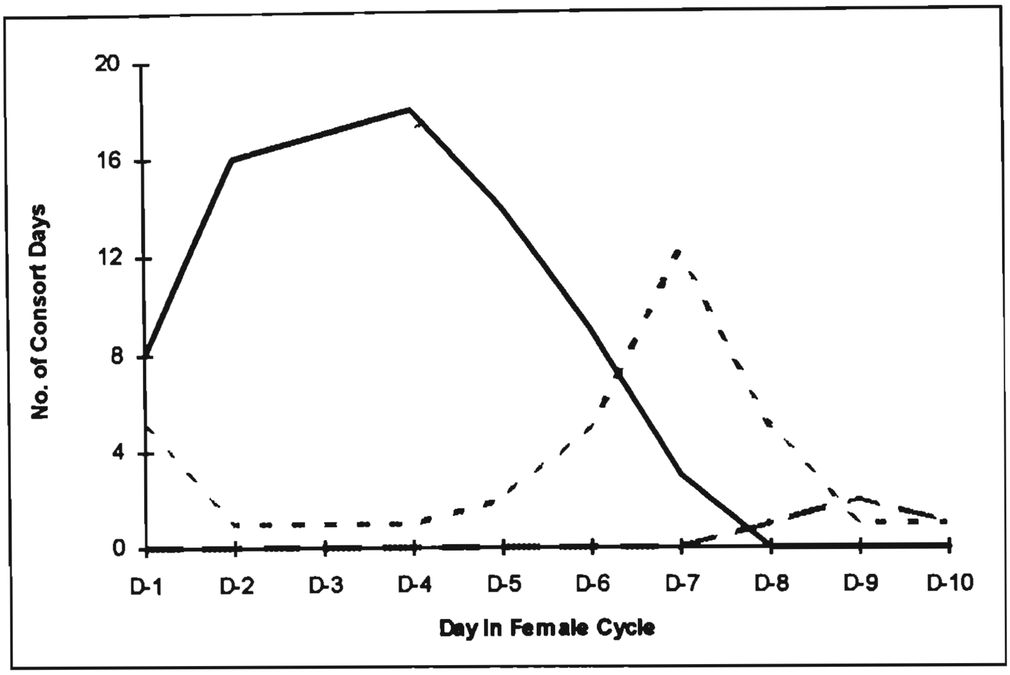

Figure 42: Comparison between the number of consort days, per male, and the day of female cycle that these consort days took place on. Solid line: alpha male (HE); Dotted line: beta male (SE); Long-dashed line: gamma male (BY). Data for the delta male (WH) are not plotted given that he was never observed to hold a consort (see text above).

The distribution of male consort days has implications in terms of male reproductive success. Although almost all conceptions are likely to take place between day -7 and day +1 of the baboon female cycle, the greatest chance of conception falls between day -3 and day 0 (Bercovitch 1986). For the males in this study, rank appeared to determine not only the number of consortships held, but also the timing of these during the female cycle. For the alpha male (HE), all of his observed consort days fell within the period of likely conception and, of those days, 48% (N=41/85) occured during the days of probable conception. For the beta male (SE), 80% of all observed consorts took place during the days of likely conception, but only 21% (N=7/34) of those occured during days of probable conception. None of the observed consortship days that the gamma male (BY) was engaged in occured during either the probable or the likely days of conception. A comparison of male consort days over the female cycle is presented in Figure 43.

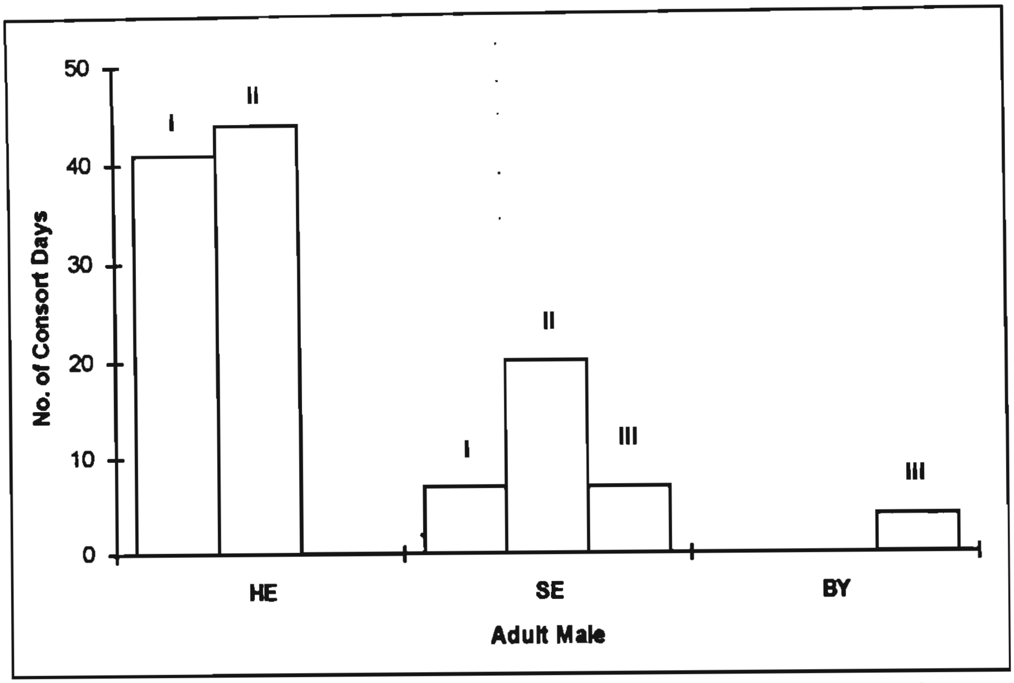

Figure 43: Comparison of the number and distribution over the female cycle of consort days engaged in by individual males during (i) female cycle day D-3 to D-1, (ii) female cycle D-7 to D-4, and (iii) female cycle D-10 to D-8. The delta male (WH) is not represented due to his failure to engage in consortships.

Of the 22 cycles upon which these data are based, the alpha male participated as a consort 21 times, while the beta male was engaged 20 times. The gamma male only participated in 3 cycles. The one cycle that the alpha male did not participate in occerred during a month when the timing of the cycle was precisely synchronous for 2 females and thus the alpha and beta males each consorted a female over those days.

An important point to note is that mating opportunities did not accrue to the beta male only during those times when the cycles of two or more females were synchronous. Rather, his access to females appears to have hinged on whether or not the alpha male was engaged in consort at that time, hence the distribution of male consort days over the female cycle (Figure 42). This confirms the point made by Altmann (1962b) and Packer (1979) that, where dominance is the only factor governing access to females, the alpha male would have priority and the beta male's access would hinge on the probability of two females cycling simultaneously. Given the low probability of female cycles tending to overlap[4], the beta male in this study tended to consort most often during days when females were less likely to ovulate.

Evidence on the relationship between male rank and reproductive success from other studies is inconclusive. Among a free-range group of long-tailed macaques (*Macaca fascicularis*), adult male rank was positively correlated with reproductive success in terms of priority of access to females at times when they were thought most likely to ovulate (de Ruiter *et al* 1992). That study reported that alpha males fathered most offspring while the remaining fertilizations were attributed to the beta male. For vervet monkeys (*Cercopithecus aethiops*) studied over seven years in Amboseli Park, Kenya,

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[4] The probability that, in a troop with 9 females, the cycles of 2 females will tend toward complete overlap is 0.04 (estimated from Dunbar 1988 Fig.7.9 pg. 142). However, for the Drakensberg baboons this value will probably be lower given that Dunbar's calculation assumes a 2-year interbirth-interval which is shorter than the estimated interval for the Drakensberg females (Chapter 3).

neither male dominance rank nor tenure in the troop was correlated with copulatory success (Cheney *et al* 1988). Among baboons the relationship between rank and reproductive success is disputed (Altmann 1984). Altmann *et al* (1994) report for a group of Amboseli savanna baboons that behavioural and genetic data both confirm male dominance-based priority of reproductive access, and that genetic paternity determination was predicted by mating data. Packer (1979b) found that, for his population of olive baboons, male dominance rank was significantly correlated with consort activity in general as well as with consortships during fertile female cycles. He also found that alpha males tended to engage in consortships with females more on days of probable conception than on any other days during the female cycle. This tendency for higher ranking males to dominate access to females during particular days of the cycle was also observed by Cheney and Seyfarth (1977) for chacma baboons. Similarly Hausfater (1975) reported that the copulations of higher ranking males in Alto's troop in Amboseli tended to be concentrated around the optimal day for mating (D-3). However, Bercovitch (1986, 1987b), Manzolillo (1982, cited in Smuts 1985) and Smuts (1985) found no such tendency or relationship for their olive baboon troops at Gilgil. Bercovitch (1987b) argues that no correlation between male rank and access to females on days of probable conception would be expected given the consistent finding from baboon field studies that it is over those days that the greatest amount of male reproductive activity occurs (De Vore 1965; Hausfater 1975; Rasmussen 1980; Collins 1981; *all cited in* Bercovitch 1987b).

Accordingly, given that male interest in females and hence consorting is at its highest on days of probable conception, the ability of any particular male to monopolize access to a female over that time is presumed to be reduced (Bercovitch 1987b). One of the proposed means whereby lower- to middle-ranking males might reduce monopolization by higher-ranking males is through the formation of coalitions (Bercovitch 1988, 1989) which is reported to be a widespread phenomenon among savanna baboon males (De Vore 1965; Saayman 1971; Hausfater 1975; Packer 1977; Popp 1978; Rasmussen 1980; Collins 1981; Ransom 1981; Sapolsky 1983; Smuts 1985; Noë 1986a,b; all cited in Bercovitch 1988). However, none of the male-male behaviours described by Bercovitch (1988) which he suggests are definitive criteria for coalition formation in sexual contexts was observed during male-female consortships over the period reported here, and it is doubtful whether the Drakensberg baboons, both male and female, form coalitions in any context (pers. obs.), although recent suggestive evidence indicates that females might, at times, form temporary coalitions against males (A.R. Weingrill, pers. comm.).

From the above data it becomes clear that all possible mating opportunities in the study troop were accounted for by the alpha male and, to a lesser extent, the beta male. The data indicate that, for at least three of the infants in the present study (J2, C2, R2) and probably for a fourth (F2), the highest ranking male (HE) was probable father in that he dominated consort days during the respective fertile cycles. The fifth infant (G2) was conceived before the study began, and thus no data from which to infer paternity are available.

Thus, in terms of predictions which suggest that the extent of male care-giving might be positively related to the degree of kinship between male and infant (Hamilton 1964, 1984; Wilson 1975; Kurland 1977; Estrada 1977; all cited in Stein and Stacey 1981), then it might be expected that the majority of male-infant interactions observed in this study should involve at least the alpha or beta males, or both. On the other hand, this relationship between extent of interaction and degree of kinship might not be as direct. Smuts (1985) has argued that paternity, in itself, is not necessarily a sufficient condition for the existence of an affiliative relationship between a male and an infant. She showed that, for the Gilgil olive baboons, an affiliative relationship between an infant and its probable father is likely to result only if the male had a prior friendship with the infant's mother. The importance, for male-infant interactions, of this prior relationship between the mother and the male has been demonstrated for captive rhesus monkeys (Berenstain *et al* 1981).

The data to test both the kinship prediction and the Smuts (1985) qualification are presented below. During the course of data collection I noted all occasions when infants were either in contact or within 1-metre of an adult male, and whether or not the infant's mother was also in proximity (< 1metre) to the male. I also noted the context within which adult male-infant interactions took place (see ADDITIONAL NOTES at the end of this chapter for definitions on categories of behaviour included in each context).

6.4. ADULT MALE-INFANT INTERACTIONS: PARTICIPANTS AND CONTEXTS OF INTERACTION

There were individual differences between males in terms of both the extent of male interaction with infants as well as the contexts within which interaction took place. These differences are considered below.

6.4.1 MALE VARIABILITY IN INTERACTION WITH INFANTS

The total number of adult male-infant interactions, per male, is presented in Figure 44.

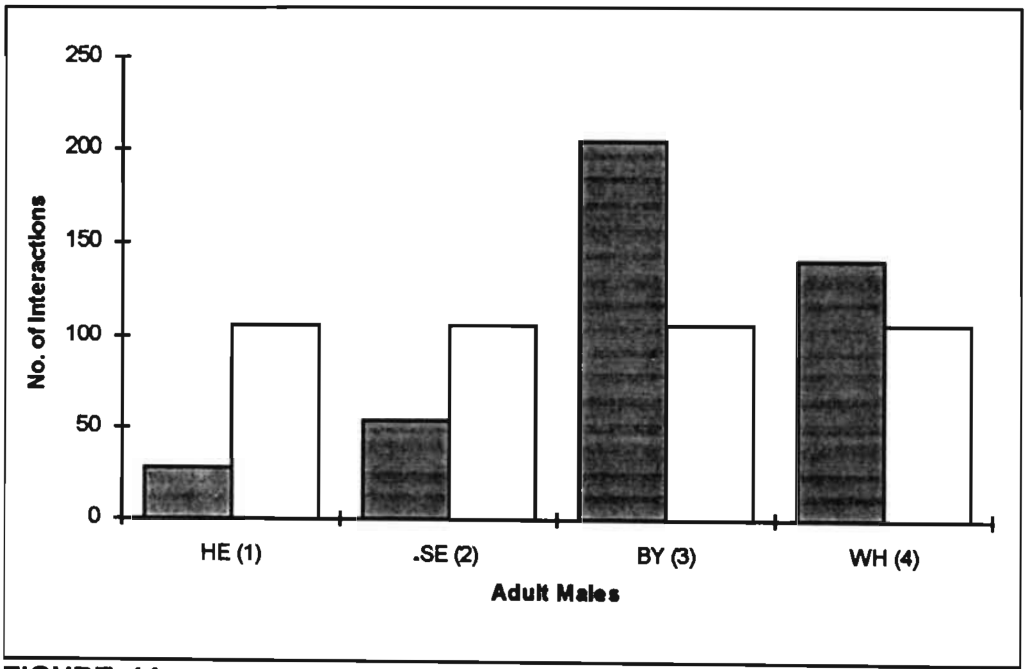

FIGURE 44: Total number of observed interactions, per male, with infants. Expected number of interactions (clear blocks) assume that there are no differences between males in the extent of their interactions with infants. Male rank indicated in parentheses.

Significant differences exist in terms of the total number of interactions that the various adult males engaged in with infants, regardless of the context of such interaction (c^2 = 183.54, 3 d.f., $p < 0.01$). The two lower ranking males (BY and WH) interacted with infants significantly more than the two higher ranking males (HE and SE).

For these data, the first point to be noted is that, contrary to the prediction that the extent of adult male-infant interaction will be positively related to the degree of kinship (references in Stein and Stacey 1981), the alpha male in this study, who was probable father to three or four of the five infants, interacted with infants the least of the four males, while the gamma male interacted most. Thus, the gamma male, and to a lesser extent the delta male, appear to have been forming bonds, through interaction, with infants who were probably not their own. Within the context of male - female friendships, Smuts (1985) supposed three possible benefits to males under these circumstances. In the first place, a male's friendship with an infant and its mother might, in certain ways, increase the mother's ability to care for an infant sired by the male which will increase the male's reproductive success. Secondly, through a relatively long-term relationship with a female, a male might enhance his future prospects of mating with a female once a currently dependent offspring has become independent, even if this offspring is not the male's. Finally, a relationship with a female might increase his opportunity to use her infant during agonistic interactions with other males.

For the gamma and delta males in this study, only the latter two benefits will apply given that the first will accrue only to the father of an infant.

In the section which follows I present data on the contexts within which males interacted with infants.

6.4.2 CONTEXTS OF ADULT MALE-INFANT INTERACTION

As may be expected from the differences in the total number of male-infant interactions, differences between males are evident in terms of the contexts within which they interacted with infants (Figure 45).

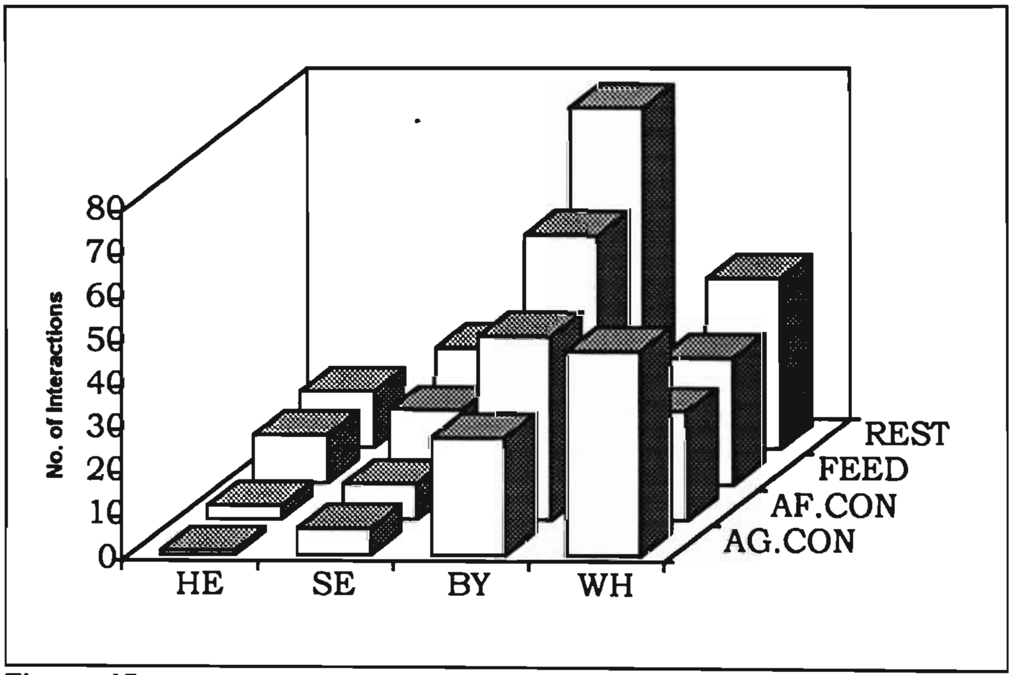

Figure 45: Number of male interactions with infants, by context of interaction. AF.CON = Affiliative Contact; AG.CON = Agonistic Contact. Males are ordered from left to right by decreasing rank (HE = 1; WH = 4).

The alpha male (HE) interacted more with infants while he was feeding and resting than he did in affiliative or agonistic contexts. These differences are significant ($c^2 = 27.62$, 3 d.f., $p < 0.01$). The same differences are evident for the beta male ($c^2 = 14.00$, 3.d.f., $p < 0.01$). Given the four contexts of interaction, the gamma male (BY) interacted with infants significantly more while he was resting and significantly less in agonistic contexts than he did in the other two contexts ($c^2 = 27.88$, 3 d.f., $p < 0.01$), while the delta male (WH) interacted with infants significantly more in agonistic contexts than in any other context ($c^2 = 8.46$, 3 d.f., $p < 0.05$). These specific differences in individual male interaction with infants will be considered in more detail later in this chapter.

Two aspects of male interaction with infants become apparent if the interaction across contexts is expressed as a proportion of the extent of male interaction (Figure 46).

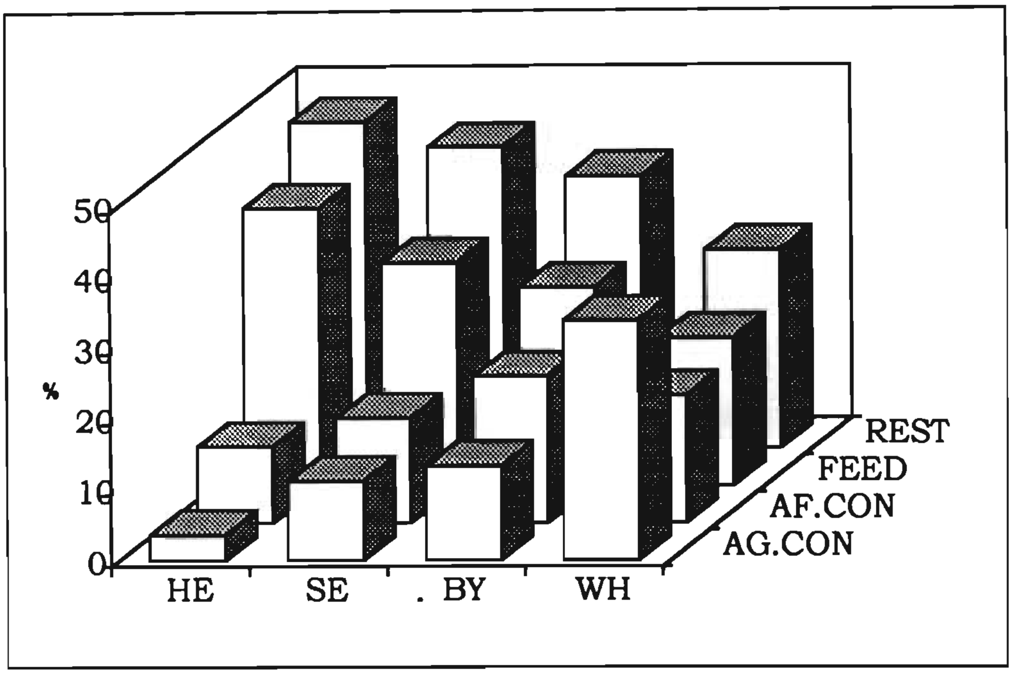

Figure 46: Proportion of each male's total interaction with infants by context of interaction. (AF.CON = Affiliative contact; AG.CON = Agonistic Contact. Males are ordered from left to right by decreasing rank - HE = 1; WH = 4).

Firstly, insofar as comparisons between the four males are concerned, a rank-related pattern becomes apparent in that with decreasing rank, males spent proportionately less of their interactions with infants in both resting and feeding contexts. That is, as a proportion of their total interactions with infants, the two lower-ranking males interacted less with infants while resting and feeding than did the two higher-ranking males. In contrast to this, the two lower-ranking males interacted with infants in agonistic contexts more than did the higher-ranking males.

An identical pattern of proportional interaction with infants is evident when males are considered individually, at least for three of the males (the alpha, beta, and gamma males). That is, proportionately more of their interactions with infants occurred while they were resting, and the least amount in agonistic contexts. For the delta male, the highest proportion of his interactions with infants were in agonistic contexts.

These differences between males are considered in terms of the possible purposes, for males, served by interactions with infants. I will apply the data to predictions which follow from hypotheses outlined above which purport to explain why males may interact with infants.

6.4.3 MALE PROTECTION OF INFANTS?

If males interact with infants in order to protect and care for their possible progeny, then it would have been expected that the alpha male would have interacted most with infants, particularly during agonistic encounters with other males. This was not the case in terms of both total number of interactions as well as across contexts of interaction. Both the alpha and beta males interacted with infants in agonistic contexts significantly less than would be expected given the distribution of their respective interactions with infants across the contexts.

However, if the hypothesis hinges on whether infants are under possible threat from recently immigrated males (the *progeny protection* hypothesis), then this finding for the higher-ranking males in this study is not unexpected. No males immigrated into the study troop during the course of this study, and no attempt at immigration was observed. Insofar as the progeny protection hypothesis applies to the two lower-ranking males, it has already been shown that neither the gamma nor delta male could have been father to 4 of the 5 infants in the study, and so their interactions with infants could not have served to protect or care for possible progeny.

6.4.4 MALE USE OF INFANTS AS AGONISTIC BUFFERS?

If lower-ranking males use infants as buffers against aggression from higher-ranking males, then it would be expected that the extent of adult male contact with, or proximity to, infants in agonistic contexts will be related to the rank of males. This was the case. The number of male-infant interactions in agonistic contexts was negatively related to rank ($r = -0.9732$, $p < 0.02$). The two lower-ranking males interacted with infants in agonistic contexts significantly more than did the two higher-ranking males.

Male use of infants in agonisitic contexts during the course of this study is not easily compared to that reported from other study sites, in that male use of infants has usually been linked to male immigration into troops and the use of infants against such males, or the use of infants by immigrating males. Reviewing data on why males use infants, Strum (1984) noted that males who use infants are primarily residents of the troop of long enough duration to have been in the troop at the time infants were conceived or at least when they were born, as opposed to short-term residents (i.e. recently immigrated males). It has already been reported here that for the present study, all males were present in the troop at the time of at least four of the five conceptions[5], and all were present during the births of the five infants. Tied to this is the fact that no attempt at immigration into the troop by an outside male was made during the course of the study. So, the male-infant interactions reported and discussed here relate to male-male interactions where both male participants were relatively long term residents of the troop.

Given that fully 91.3% of all male-infant interactions in an agonistic context involved the gamma and delta males, with the delta male accounting for 58% of those, it needs to be established in what way males were using infants.

To establish this, the data relating to male contact with infants during agonisitic events were partitioned between whether or not the male with the infant was a *direct partipant* in the event at the time of its inception. In other words, did the male's interaction with the infant occur before, during or immediately after he had been involved in an agonistic encounter with another male, or did his interaction with the infant occur before, during, or immediately after two or more other males in the group were involved in an encounter which the carrying male did not participate in immediately, but may have done so as/if the event escalated in intensity and number of participants. This partitioning for the gamma and delta males is presented in Figure 47.

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[5] The infant born first during this study was conceived before the study began, and thus it is not known which males were in the troop at that time.

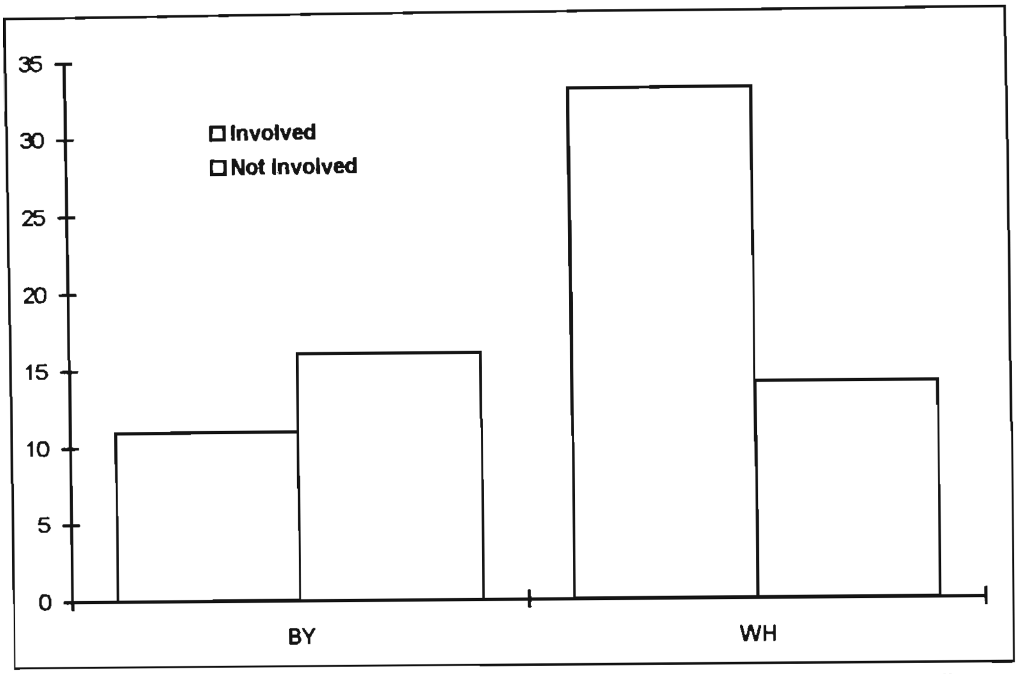

Figure 47: Comparison between whether or not the gamma and delta males were directly involved in agonistic events with other males when they were observed to be in contact with infants while agonistic events occured in the troop.

There was no significant difference, for the gamma male (BY), between the number of times he was directly involved in an agonistic event while having an infant in contact, and the number of times he was not initially directly involved ($\chi^2 = .93$, 1 d.f., $p>0.1$). The delta male (WH), however, was in contact with infants significantly more while he was a participant in agonistic events at their inception than he was when he was not directly involved ($\chi^2 = 7.68$, 1 d.f., $p<0.01$).

The point of these data is to show that the delta male tended to actively "over-use" infants in agonistic contexts, particularly those in which he was directly involved from the outset. What the data do not tell us in this regard, is whether his direct involvement in relatively more agonistic events than other males was related to his rank position in the troop. That is, was it because of his low rank that he needed to use infants more than did any of the three other males?

There is another aspect to this. For those instances where the two lower ranking males carried infants (or maintained proximity to them), but were not initially directly involved in the agonistic event, two possibilities emerge, although the data to assess each are not available. Nonetheless, if the carrying male *did not* get drawn into the aggression that began elsewhere, what is the liklihood that his proximity to an infant (if such proximity was the case when the aggression started) inhibited the escalation of the aggression to include the carrying male? Secondly, and further to this, when males carried infants during aggressive encounters in which the carrying male was not directly involved, were they attempting to protect infants, or were they indeed attempting to buffer themselves from escalated aggression?

Thus, while these data say very little about male use of infants as agonistic buffers, and even less on the role of infants in the interactions, what they do indicate is that there appears to be a very real use of infants by males in situations that are varied and complex. At best what emerges from these data relating to infant use by males during agonistic encounters is that closer attention needs to be taken of the kind of data that are to be recorded in follow-up studies. In particular, what will be required are specific details of the type and intensity of male agonistic encounters, as well as data which can be used to establish whether it is the male or the infant that is primarily responsible for the maintenance of spatial proximity in order that infants can be available to males for use in these contexts.

6.4.5 MALE USE OF INFANTS TO ENHANCE MATING OPPORTUNITIES?

If males are investing in the care of infants that are not necessarily their own in order to increase their opportunities for mating with mothers at a later time, then the following assumptions with regard to the lower-ranking males in this study can be made:

1. Given the distribution of consort behaviour, and hence the probability of paternity as reported above, then it would be expected that the gamma and delta males interacted with infants more than the alpha and beta males,
2. In terms of care-taking behaviours which benefit the infant, males should interact with infants more under affiliative, non-agonistic circumstances than in situations which might not benefit the infant.

Insofar as the first assumption is concerned, it has already been shown that in terms of the total number of interactions, the two lower ranking males interacted most with infants. Between them, they were involved in 80.9% (N = 347/429) of all observed adult male-infant interactions (BY = 48.3% [N = 207/429]; WH = 32.6% [N = 140/429]).

As far as the second assumption is concerned, it has been shown, albeit inconclusively, that the delta male tended to 'over-use' infants during agonistic, and hence potentially threatening, contexts. His interaction with infants across the three other contexts were not significantly different from chance expectations of interaction.

For the gamma male, it was shown that his use of infants in agonistic contexts was not characterized by an over-representation of his direct participation in such events. That is, he was as likely to not be directly involved as he was to be involved. In any case, this male's contact with infants in agonistic contexts was significantly under-represented as a proportion of the total extent of his contacts with infants across different contexts. A greater proportion (than for the delta male) of his contact with infants took place in neutral, or non-threatening contexts. Again, given the large number of his contacts with infants, relative to the other males, the possibility remains that the under-representation of his contact with infants in agonistic contacts was in some way a consequence of the fact that he was so often in contact with infants, and so may not have been drawn into aggression.

The logic of this argument is as follows: if males attempt to enhance their prospects for mating with females by establishing friendships with females and their infants, and if the two assumptions outlined above are met, then in the absence of confounding variables, a theoretically possible outcome will be increased potential opportunities for these males to mate with females to whom they have demonstrated their 'goodwill'.

On the basis of the male mating data presented earlier, the point remains that even if these males, particularly the gamma male, *were* attempting to pursue such a strategy, then their strategy was not producing the theoretically intended result. The data showed that neither the gamma nor the delta male were, in any real sense, functional breeders in the troop. There is a degree to which such a strategy is, for low-ranking male baboons in the Drakensberg, flawed from the start. Any male who waits for a female to return to oestrus in order to reap the rewards of caring for her offspring is going to wait for a long time. It was reported in Chapter 3 that the interbirth interval for the Drakensberg females is in the order of 38 months. Taking account of the six month gestation period, and an average of four infertile cycles before conception takes place (Altmann 1980), then, and in the absence of any rank changes, males in the Drakensberg who pursue a *"friendship now, mating later"* strategy will still have to wait for at least 28 months before, at best, the *possibility* of mating with a female arises. Assuming, that is, that the alpha and beta males have not dominated access to the female once she resumes cycling. Under circumstances such as these, where:-

- priority of mating access is dominance based,
- where the probability of female cycles tending toward overlap is very low,

- where males do not form coalitions to militate against the dominance of females by high-ranking males during female sexual swellings, and
- where male care of offspring does not appear to any significant degree to enhance a male's prospects of mating with a female at a later date,

then a low ranking male can pursue either of two additional options[6]. He can leave the current troop and attempt to gain higher rank in another troop, or he can attempt to induce females in his current troop to leave with him and so become alpha male in a uni-male troop. Both of these alternatives were attempted by the gamma male.

An incipient attempt at male-induced fission was observed during September - October 1992 when the gamma male left the troop in the company of two adult females (one of whom had an offspring) and two juvenile animals. While the circumstances and means whereby this separation was achieved, as well as the assumptions which underlie such a strategy, are the subject of work in preparation, the point is that this male was not successful in his attempt. After being separated from the main body of the troop for six days, the females were eventually herded back into the troop by the alpha male who met the sub-troop during the course of the FT's daily route.

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[6] It is of course possible that by the time this study ended, this strategy had simply not become operational given that the mothers in the study had not yet resumed cycling, and that a long-term study will shed light on the possibilities for success of such a strategy.

It was following this failed attempt at fission that the gamma male, who had also returned to the troop, began attempting to leave the FT and immigrate into neighbouring troops. Although he was absent from the FT on a number of occasions, for varied lengths of time, and was seen to be present in a neighbouring troop on at least two occasions, by the end of the present study he had not yet left the FT[7]. However, during the course of ongoing population monitoring following the completion of the field work for this study, it was found that both the gamma and delta males were no longer resident in the FT. Whether they successfully immigrated into another troop(s), or whether they died is not known.

6.5 MALE INTERACTION WITH INFANTS: CONCLUSIONS

The data that are available at this time, and which have been introduced here, do not support any firm conclusions concerning the functional purpose of male interactions with infants. At best they have indicated some kind of trend for the Drakensberg baboons which reveals male variability in both the extent and the contexts within which individual males interact with infant animals. The trend that is suggested appears to indicate that Drakensberg males do not, 'across the board', use infants in an "either-or" manner. What this means is that all males do not seem to use infants in the same way,

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[7] Identifying possible factors on which might turn a male's decision to immigrate into a particular troop is the subject of a study in progress in the Drakensberg (A.R. Weingrill).

for example, as buffers against aggression. Rather, it appears that different males use infants under different conditions and to different ends which are not entirely compatible with predicted infant usage as it has been discussed in the literature. This remains another area for further research. Part of these further investigations should focus closely on, for example, *what* exactly the infant does while it is in proximity to a male that is engaged in on-going activity (eg. feeding), and whether in such a situation, infants are deriving some measurable benefit from male tolerance of the presence of infants.

ADDITIONAL NOTES

CATEGORIES OF ADULT MALE-INFANT CONTACT:

Feeding: Infant either in contact or within 1-metre of a male while the male was feeding in either a seated or stationary position. This category of contact did not apply to the tendency of the Drakensberg baboons to "travel-feed" (see Chapter 2).

Resting: Infant either in contact or within 1-metre of a male while the male was seated or lying down, and not engaged in any other concurrent activity (e.g. grooming, feeding while stationary).

Affiliative Contact/Carrying: Infant is either carried by, or in contact with, a male (or within 1-metre of a male) without any agonisic event (specifically male-male aggressive interactions: see below) having taken place before, during, or immediately following the male-infant contact

Agonistic Contact/Carrying: Infant is either carried by, or in physical contact (usually ventral) with, a male (or within 1-metre of a male) immediately prior to, during, or following an agonistic event (particularly those between males). The contact/carrying male needn't have necessarily been part of any such agonistic interaction. Aggressive, or potentially aggressive interactions between males included:- (a) Male-

male fighting, chasing, (b) Overt threats by a male toward another male (eg. charging, yawning), (c) Male dominance displays (mounting another male, "walk-past") (d) spatial displacement of a male (from food, social partners).

CHAPTER 7

INFANCY, DEVELOPMENT, AND INDEPENDENCE: CONCLUDING REMARKS AND FUTURE DIRECTIONS

7.1 OVERVIEW

This study was initially conceived with the aim of explicating the kind of cognitive demands which confront the Drakensberg baboons, and how these are met by the animals during the course of ontogeny. It was intended that the focus would be not only on the infants and their interactions with features of their environment, but would also provide an extensive and detailed analysis of the relationships and interactions that infants have with other animals, and how these might contribute, if at all, to the development of sociocognitive competence. For reasons which will be considered below, the study did not manage to address and answer these specific aims. With hindsight, however, the aims were exactly what was, and still is, needed. Yet the intended study would probably not have been adequately accomplished without the findings of the present study becoming available. That is, it is clear that there are significant problems for Drakensberg baboon infants to overcome in the course of their development toward becoming competent and functional adults. Specifically, that there are factors which limit the expression of foraging independence. Whether these factors are of a cognitive or a physical nature, or a combination of both, has yet to be established.

In the remainder of this chapter, I will review the substantive findings reported in this dissertation. These will be considered in relation to the implications they have for future research. The shortcomings of the study, vis-á-vis the intended aims will also be discussed, specifically in terms of methodological and sampling limitations.

7.2 CURRENT FINDINGS AND THEIR IMPLICATIONS FOR INFANT DEVELOPMENT AND FEMALE REPRODUCTIVE SUCCESS

7.2.1 SUBSTANTIVE FINDINGS OF THIS STUDY

The first point of interest is the finding reported in Chapter 3 of an operational birth season for the Drakensberg baboons. As best I am aware, this finding represents the first reported account of a significant seasonal effect on the timing of female reproductive events among *Papio* baboons which are not seasonally breeding animals (Bercovitch and Harding 1994; see Chapter 3). In terms of female reproductive success, the implications of this seasonal effect are considerable and, at the same time, circular. They are considerable in the sense that the timing of birth initiates a process which results in comparatively low reproductive output at comparatively high cost. The implications are circular to the extent that the very consequences of birth timing eventually become a major factor in the timing of subsequent conceptions, and hence births. Thus, extended infant dependency which arises from birth timing is not conducive to a rapid turn-over in infant production. And this leads to another substantive finding of this study.

The timing of weaning, and hence the rate of infant development toward independence, has previously been linked to the availability of appropriate weaning foods. For the average Drakensberg infant born during the summer months, the age at which it would be expected to demonstrate emergent independence is the exact time of the year when this would be least likely to occur. The age at which an infant should start to feed significantly for itself coincides with the time of the year in the Drakensberg Mountains when easily obtainable, easily digestible, and easy to harvest weaning foods are not present in the habitat. As a consequence, and if there are no alternate food sources available, mothers necessarily had to remain the principal source of nutrition (Chapter 4). It has been suggested that this demonstrated lack of emergent independence had further implications for general behaviour integration and the imposition of constraints on behaviour typical of adult animals (Chapter 5).

The findings reported here should provide a framework within which an examination of the original aims of the study can proceed. A number of issues arise from the findings of his study which will probably have an important impact not only on a future examination of the development of cognitive competence in these animals, but also generally for lifetime reproductive success of individual animals.

7.2.2 IMPLICATIONS FOR FEMALE REPRODUCTIVE SUCCESS AND INFANT DEVELOPMENT

Aside from the direction that future research should take, most notably with regard to a qualitative description of infant developmental trajectories (see below), the results presented in this study raise intriguing questions regarding general demographic processes in this mountain baboon population. It is only through continued long-term study that answers will become available. Specific issues which need to be addressed are considered below.

In the first place, what is the fate of females who give birth outside of the optimal time of the year? By giving birth during the dry, winter months, do such mothers place additional stress on themselves, over and above the normal costs of motherhood? Are the survival prospects of these females, and hence their infants, reduced? Data collected after the completion of the present study suggest that such females *are* additionally stressed, and that infant survival prospects may indeed be reduced (pers. observation).

In terms of individual ontogeny, what is the fate of infants born out of phase of other infants? If they survive the stressful winter period, do such infants experience delayed social development given that there may not be any same or similar aged peers for exploration, play, and general interaction? Tied to this, questions are raised regarding the maternal restriction of movement and exploration of those infants which do not have a cohort of same aged peers. From personal observations, there are suggestions that mothers of infants who do not have a peer group might be more restrictive of offspring than are females who gave birth at approximately the same time as other females in the group. It also remains to be seen whether infants born outside of the optimal birth months demonstrate significant advances in the development of independent feeding. For example, an infant born in June or July will be at the correct (or expected) age for independent feeding when summer weaning food availability is at its peak (December - January).

Given the finding of extended infant nutritional dependency, two tentative issues need to be addressed. The first relates to delayed infant independence in terms of suckling versus independent foraging as alternate feeding strategies. On the one hand, do infants need to be dependent on their mothers in order that they have sufficient time to learn which are appropriate food items in an habitat which otherwise does not provide immediate clues to their recognition and seasonal availability? Or, on the other hand, is prolonged dependency an immediate consequence of an infant physical inability to manipulate the environment in the harvesting and extraction of the food? This latter hypothesis supposes two things. In the first place, infant knowledge as to what constitutes an appropriate diet develops and is 'in place' during the course of infancy (i.e. the first twelve months), and so awaits physical skill or ability to be put to use. The second assumption leads from the first and supposes that mothers may not, as is usually thought, be encouraging the development of infant independence through the weaning process. Such a perspective suggests that it is infants themselves who are determining the age at which they no longer need their mothers. Such a focus from the infant's point of view will require a re-evaluation of the respective roles of mother and infant in parent-offspring conflict as this relates to the development of infant independence.

7.3 FUTURE RESEARCH: IDENTIFYING LIMITATIONS ON DEVELOPMENT

While this dissertation has described the general behavioural development of a small cohort of Drakensberg baboon infants, what is further required is a detailed analysis of the development of feeding selectivity in these animals. As outlined above, such a focus will need to assess whether there are developmental constraints, at specific ages, which prevent these infants from becoming nutritionally independent sooner than they have been shown to be in this study.

One way of achieving this might be through the utilization of a Piagetian-based analysis (Brainerd 1978 for a critique of Piagetian stages in development; Doré and Dumas 1987) of the kind of feeding tasks and problems that confront individuals during ontogeny. This type of approach has been successfully used in a study of development in young orangutans (*Pongo pygmaeus*) (Bard 1987, 1990, 1992, 1993, in press) and appears, to some extent, to be guiding research concerned with describing the complex hand manipulations of mountain gorillas (*Gorilla G. beringei*) (Byrne, in press; Byrne and Byrne, in press). The point of using a Piagetian approach is to ascertain not only *what* the animals are capable of in terms of cognitive manipulations, but also what they *need* to be capable of. For the latter question, a description of the nature of the tasks that inhere in the harvesting and processing of food items is required. Simultaneously, and perhaps integral to such a description, will be the need to qualitatively describe the developing animals physical interactions with features of the environment. For example, the onset of physical actions such as locomotion and prehension, and the interaction of both, will have consequences for the extent of infant interaction and manipulation of environmental features (cf: Antinucci 1990). In Piagetian terms, developmental rates, or physical maturation, will probably impact upon the speed of cognitive constructions which develop through assimilative-accommodative interaction with the environment. In the words of Antinucci (1990), "Faster developmental rates mean that the subject will experience fewer (of these) events and will generate fewer (of these) action schemata at each developmental stage ..... The correlate of this longer or shorter duration of the subject's interaction might well be a greater or smaller variety and richness of the constructions at each stage" (pg. 169). Given the comparatively slow developmental trajectories that have been demonstrated for the Drakensberg infants, combined with the cryptic nature of the cues which mark the presence of food items (Whiten et al 1987; Chapter 3), it remains a possibility that extended dependency allows for extensive interaction with, and manipulation of, food items in order that cognitive constructions are developed.

While the potential contribution offered by Piagetian theory is large, the theory and methodology offer little insight on the social component to knowledge acquisition. Piaget's theory is, after all, a-social in its treatment of cognitive development. Something additional is required. It was argued in Chapter 1 that learning proceeds most efficiently when it is socially mediated or based. Given this, the focus of study should go beyond an elaboration of *what* is required by way of cognitive structure, to an examination of the social influences and means whereby competence is acquired. In this regard, theories of human cognitive development which are rooted in the social domain, and which rely on the role played by older, more experienced individuals, might be influential (Vygotsky 1978; Greenfield 1984; Rogoff 1984; Rogoff and Gardner 1984). The opportunity and potential for learning that is guided or facilitated by adults becomes apparent from the data presented in Chapter 6. It was argued that infants and adult males interact in relatively complex and sophisticated ways. Although these interactions were not considered from the perspective of the infant, the repercussions of such interaction must be considerable for the infant. They are drawn into, and appear to be playing a significant role in, a complex web of social relationships. In so doing, infants are exposed to subtleties of social interaction, at least, which they may not otherwise be witness to. These adult-male interactions are but one class of interaction which might, in some way, facilitate the development of competence. At the same time, it should not be forgotten that with the exception of other infants, all other animals in a social group will be older, presumably more experienced, potential 'tutors'. Accordingly, the nature of *all* social interactions infants engage in with other animals should be of interest in a study such as the one argued for here.

If the outline for future research presented above is a logical and necessary continuation of the study reported in this dissertation, and if this outline is what the present study had initially hoped to achieve (see Section 7.1 above), then it is worthwhile to consider some of the reasons why the present study failed to achieve what it set out to do. This is discussed below.

7.3 LIMITATIONS ON THE FINDINGS IN THIS STUDY

The primary factor which will have limited the findings of this study as originally conceived is related to methodology in general, and the extensive use of scan sampling techniques in particular.

7.3.1 SCAN SAMPLING TECHNIQUES

One of the study's stated aims was to examine the impact that infant relationships with other group members had on ontogeny and the development of competence. These kind of questions, where detailed descriptions of relationships and interactions are required, were impossible to attain through the use of scan sampling procedures. Altmann (1974) has explicitly stated that instantaneous or scan sampling is "... a sample of states, not events" (pg.258). Thus the often continuous or sequential nature of infant interactions with other group members would not have been recorded in any useful way using scan sampling. The limitations of this sampling technique become most obvious in Chapter 6 of this presentation where infant relationships with adult male animals were considered. From the data that were presented it became apparent that infant relationships with males appeared to have served some important function(s), at least for the males. To confirm this, as well as the role that males might play in infant development, a sampling method other than a "broad brush" technique such as scan sampling will be required. The need for a sampling methodology, such as intensive focal sampling (Altmann 1974), which will record more complex and subtle behaviours in a continuous manner is clear. This is especially true given that this study argued for a move beyond a description of development toward a truly developmental analysis of change (Chapter 1).

7.3.2 DEFINITIONS OF CATEGORIES OF BEHAVIOUR

A further problem which emerged during the course of data presentation and analysis related to definitional discrepancies in categories of behaviour which were recorded during data collection. For example, where comparative studies explicitly focussed on social play, this study did not distinguish between solitary play, object play, or social play (section 5.3.2.1: Chapter 5). All three types of play were recorded under the single "play" category. The consequence of this was that the results of this study may have over-estimated the extent of social play which is the category of play against which the data for the present study were compared with previous studies (Figure 29). There is a further problem insofar as the categorisation of different kinds of play is concerned, and this refers specifically to the category of object play. It makes sense that as young animals mature, object play will become more elaborated and probably more experimental as familiarity with the object(s) increases, and gross play-manipulations of objects become more refined. The decline of play with maturity might, therefore, represent less a decline in play activity as it might a transformation of an undifferentiated behaviour into skilled and coordinated action(s) against objects in the environment.

The point is that it is probable that the infant behaviour categories that were used were too broad for detailed description and analysis. Thus the five major activity categories would have been preferentially recorded over a behavioural category that was considered less important. Illustrating this point, an activity such as "environmental exploration", which may be similar to "play" in appearance, would have been subsumed under the "play" category given that "play" ranked higher as one of the major behaviour categories. Similarly, the distinction between infant independent movement and solitary locomotor play was not made explicit enough to allow for consistent categorisation, both across individuals and over time. The consequence of using such broad categories of behaviour was an inability to identify and describe subtle behaviours, such as infant exploration and hand manipulation of food items. A more informed analysis will require that the categories be further refined such that individual actions and behavioural sequences, which together will constitute a broader behaviour, can be identified and quantified.

7.5 CONCLUDING REMARKS

Additional to the more specific findings which have been reviewed above, this study has highlighted issues relating to the development and integration of behaviour for this cohort of Drakensberg baboon infants, and which might characterize primate development more generally. Among these is the indication that, certainly for the infants in this study, physical development places the infant 'out of step' with the demands of the environment. Following from this, if they are unable to manipulate the environment in a competent way, what then are the implications and consequences for the development of species-typical behaviour? While delayed nutritional independence is the immediate and specific consequence, the described pattern of broader behavioural integration sheds light on the mutually dependent nature of specific behaviours. It is only with the recognition of the complex nature of this interdependence that development will be adequately understood. Although not completed, this study marks the beginning of a focus on nonhuman primate infant development which views developmental trajectories as more than a series of parallel, but not necessarily related, individual domains of competence.

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