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**DEVELOPMENT OF  
FORAGING IN WILD  
CHIMPANZEES**

**Dissertation submitted to the University of St Andrews for  
the Degree of Doctor of Philosophy**

**Clea Assersohn**

**March, 2000**



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# DEDICATION

I dedicate this thesis to the memory of

**Laura Wilcox**

&

**Amoorti Tinka John**

Two friends whose courage

I will never know.

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# ABSTRACT

Recent work on social learning in primates has primarily been approached from a perspective that focuses on demonstrating human-like learning abilities rather than the efficacy of social learning within natural and ecologically relevant conditions. This thesis takes a functional approach and investigates the development of foraging behaviour in wild chimpanzees. Data were collected over 12 months on mother, infant and juvenile chimpanzees in Budongo Forest, Uganda.

Feeding behaviour was studied comparatively, relating infants' foraging with the more competent patterns of juveniles and mothers. Infants started to feed independently in the second half of their first year but only on soft-shelled, easily processed foods. The infant's diet was similar to the mother's by the end of the fourth year in terms of the breadth of food items consumed but at this age infants were still less proficient at processing foods. Infants had particular difficulty processing some embedded foods and these were the final items to be incorporated into the diet. Young infants under the age of 2.5 years selectively spent time near their mother when she was feeding, visually attended at higher levels to their mother's feeding behaviour, and synchronised playful manipulations of food items and later their own independent feeding attempts when their mother was feeding. However, none of these effects were more evident when their mothers were feeding on difficult food items.

The sharing of food between mother and infant emerged as a more important opportunity for social learning. Infants initiated these interactions by soliciting food from their mothers. Difficult foods were shared at higher rates than easy foods and most frequently in the infant's first and second year. The higher sharing rate of difficult foods was due to infants focusing their solicitations on these items that they found difficult to procure or process. These results suggest that infants are refined not only in their attempts to acquire food from their mothers but perhaps also information about feeding habits.

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# CHAPTER 1:

## INTRODUCTION

Ars longa, vita brevis  
(The life so short,  
the craft so long to learn)

*Hippocrates*

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Infancy is viewed as a particularly consequential stage in life because surviving it is so difficult: this is the life-stage with the highest rates of mortality (mammals: Clutton-Brock *et al.*, 1982; primates: Altmann, 1980). It also represents a 'sensitive period' in an animal's development (Bateson, 1979) and as such, it is a singularly significant developmental phase for two reasons. First, some events are essential if normal growth and maturation is to continue. Behaviours are built into the repertoire sequentially on the basis of abilities in earlier phases and progress will only occur if previous stages are accomplished (Parker, 1990). Second, the effects of specific experiences are more cogent during the period of infancy than if they occurred at any other time. Consequently, it is in these early years of life that it is important for an animal to acquire information, with infants remarkably receptive to learning and able to acquire particular skills more easily at this stage of development than at later ones.

The fact that universally throughout the animal kingdom, slow rates of development are linked to large body size (Pagel & Harvey, 1993), has led to the formulation of mathematical models seeking to explain why delays in reproduction have evolved and why some animals spend such a large proportion of their life as immatures. Young are particularly vulnerable to starvation and predation dangers, and some authors view immaturity as a period of risk aversion (Janson & van Schaik, 1993). Theoretical models find that despite the cost of spending longer in a pre-reproductive state than is physiologically required, juveniles grow at sub-maximal rates to minimise the risk of mortality per unit time (Janson & van Schaik, 1993). Pagel and Harvey (1993) argue that large animals experience lower mortality rates as adults and, if this supposition is correct, their model demonstrates a longer period of immaturity automatically results from large body size. Moreover, they suggest that the maturational delays beyond, and not attributable, to these body size effects probably reflect the time required for a young animal to gain the behavioural skills required for its survival and future reproduction (Pagel & Harvey, 1993). This suggests that ultimately the period of immaturity is fixed by the degree of complexity in the adult behaviour of the species. This is supported by evidence that brain size is highly correlated to the relative age at maturity once the effects of body size are removed across primate sub-orders, suggesting that longer periods of physical development are closely related to learning skills (Harvey *et al.*, 1987).

Amongst mammals, primates have the longest periods of immaturity. Infants must learn not only how to locate, identify and process food, but also how to avoid predators, conspecific aggression and accidental injury; further, as juveniles, they will need to acquire and refine other social and reproductive skills if they are to survive and successfully reproduce as adults (Pereira & Fairbanks, 1993). Primate

mothers must continue to support their infants through an extended period of dependency, acting as a continuing source of nutrition, security, transport, and warmth to their infants. The challenge of obtaining sufficient food to sustain themselves whilst also providing enough food for their offspring is an onerous one and is thought to be the biggest burden in terms of a mother's survival and reproduction (Altmann, 1980). Trivers (1974) provided a theoretical framework for the process of weaning<sup>1</sup>, arguing that the timing and amount of maternal investment should vary according to the cost/benefit ratio of a mother's reproductive fitness. Lactation is particularly costly to the mother. Not only is the energetic cost of conversion of fat reserves into milk involved (Buss & Reed, 1971), but also the reproductive cost of delayed return to fertility (McNeilly, 1979). Inter-birth intervals are determined by the length of time that an infant suckles (monkeys: Simpson *et al.*, 1981; apes: Nadler *et al.*, 1981) and shorter inter-birth intervals will result if mothers complete weaning as soon as possible (baboons: Nicholson & Demment, 1982; vervets: Lee, 1984, 1987). Since mothers are equally related to all their offspring but offspring are less closely related to each other (see Hamilton, 1964), with time, as her infant matures, a mother will need to start investing resources in future, potential offspring. The time when a mother should begin to

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<sup>1</sup> Weaning is a rather nebulous term because it does not occur at specific junction in time, but rather over a protracted period of time; it can be difficult to accurately determine when it is complete (Lee, *et al.*, 1991). Although commonly there is a sharp decline in suckling rates, representing the transition from maternal dependence to increasing nutritional independence, this may not coincide with complete cessation of suckling nor the final termination of lactation. Infants that are not predominantly reliant on their mothers for nutrition may continue to suckle at low rates in different contexts. Accordingly, studies usually use inter-birth interval data to determine the age of full or final weaning (e.g. Fragaszy & Bard, 1997).

withdraw her investment is determined by the point where the increasing fitness costs of supporting her current young exceeds the benefits gained by starting to invest in future offspring. Clearly at this point withdrawing care is optimal for a mother but not for her offspring and, hence, there will be a fundamental conflict between mothers and their offspring over the timing of weaning and the length of maternal investment ('parent-offspring conflict': Trivers, 1974).

Studies have employed Trivers' theoretical model to examine the passage to nutritional independence from an evolutionary perspective. They have done this by investigating the level of proximate mother-offspring conflict, analysing the costs, infant survival and lifetime reproductive consequences of the different forms of maternal care. For example, investigations into conflict over access to the nipple have measured the frequency of maternal rejections and infant contacts and concentrated on how different ecological conditions affect the timing and duration of weaning (Altmann, 1980; Altmann, *et al.*, 1978; Hauser & Fairbanks, 1988; Van de Rijt-Plooij & Plooij, 1987). Thus, although the form and process of weaning is ultimately governed and set within the limits of life history variables, it also fluctuates according to ecological parameters. Work has demonstrated that mothers in better quality habitats wean their infants quicker, have shorter inter-birth intervals and overall have higher reproductive rates (Cheney *et al.*, 1988; Lee, 1986; Lee, 1987). However, in completing this they experience higher levels of weaning conflict with their infant (Hauser & Fairbanks, 1988; Nicholson & Demment, 1982). Vocalisations that infants employ to elicit care from their mother have also been investigated. These calls in particular are used to gain access to the nipple and to obtain transport, so they may be a more sensitive measure of infant demands in

comparison to the more traditional assessments of proximate conflict (Hauser, 1994).

The great apes share life history features of prolonged infancy and juvenility, long life spans and large brain size (Martin, 1990). The distribution of their food and their ranging patterns differ, regulating their mating systems and ultimately their social organisation (Wrangham, 1987). In comparison to gorillas, chimpanzees grow slower, they reproduce later, produce less offspring, live longer lives (Nishida *et al.*, 1990; Tutin, 1994) and experience higher rates of pre-weaning mortality (Goodall, 1986; Nishida *et al.*, 1990; Watts, 1989), perhaps because chimpanzees do not benefit from paternal investment (Tutin, 1994). Chimpanzees are also relatively larger brained than gorillas (Martin, 1990). In the case of mountain gorillas and chimpanzees this is in accordance with the general principle that frugivores have larger brains than foliovores (Clutton-Brock & Harvey, 1980). It has been argued that a frugivorous diet, and subsequent developments of sophisticated skills in spatial mental mapping, have been the major selective pressures in the evolution of primate intelligence (Milton, 1981, 1988). Fruits are unevenly distributed in time and space and consequently frugivores have larger home ranges than foliovores (Clutton-Brock & Harvey, 1980). The need to remember the location and abundance of a widely dispersed and patchily distributed food resource that is somewhat predictable but does not follow simple annual patterns and is only briefly available, may have favoured the development of advances in the information processing and memory skills of frugivores. Hence, an increasing complexity in their abilities in mental mapping and spatial reasoning might be expected, perhaps explaining the larger brain sizes of frugivores (Clutton-Brock & Harvey, 1980; Milton, 1981; Milton, 1988). There are, however, several other evolutionary

pressures relating to diet that may have favoured the evolution of large brains and intelligence (Byrne, 1995). Individuals need to be experienced and proficient not only at identifying and locating appropriate food sources, but also in some cases foods may be embedded within an inedible outer casing, requiring specialist or complicated skills to remove the nutritious part (Gibson, 1986; Parker & Gibson, 1977, 1979). The advanced dexterity or manipulative ability required to procure and process these technically difficult foods may pose considerable cognitive demands (Byrne & Byrne, 1993; Byrne, 1998), and these difficulties are likely to be compounded by the complexities of mediating arboreal travel (Russon, 1998).

Wild chimpanzees are well-known for their use and manufacture of a wide variety of tools and scientists' selective interest in tool use as a method of food acquisition has been natural because of the relevance of tool use to human evolution (McGrew, 1992). Chimpanzees use objects in many different circumstances to solve a very disparate set of problems. For example, chimpanzees in Tai Forest, Ivory Coast crack open hard *Panda* and *Coula* nuts by selecting a rock, root or branch to act as an anvil and carefully placing the nut on this anvil. They then position the nut in the correct orientation so that when they strike the nut with a stone or wooden club it breaks open (Boesch & Boesch, 1981, 1983). Chimpanzees at Gombe fish for *Macrotermes* termites and for *Camponotus* ants at Mahale. They insert a grass stem, strip of bark or section of a vine into a termite mound or ant hill, and insects attach themselves to the probe. Resistance on the tool increases slightly, providing a tactile assessment of the correct moment to gently remove the probe, and the chimpanzee is then able to consume the insects still attached to the tool (Goodall, 1964; Nishida, 1973). Stems are also dipped into swarming columns of *Dorylus* driver ants which swarm up the stem and are removed and eaten with a swift stroke

of the chimpanzee's cupped hand (McGrew, 1974). Probes of different sorts are also inserted into bees' nests to access honey and into bones and skulls to extract marrow (Boesch & Boesch, 1990), and sticks are used as protectors in stepping over thorny branches (Alp, 1997). Leaves are used in various forms of personal hygiene to wipe blood, semen or faeces from the body; they are also chewed and then used as a sponge to collect water (Goodall, 1964). The range of chimpanzee tool use indicates its inherent flexibility and complexity but this is also demonstrated by the ability to substitute tools, consecutively use two or more tools to solve one problem, and to adapt normal techniques when novel situations demand it (Boesch, 1995; Boesch & Boesch, 1990; McGrew, 1992; Sakura & Matsuzawa, 1991; Sugiyama, 1995). A number of lines of evidence suggest that chimpanzees use of tools requires insight. For example, they select only those materials that are ideal for the task (Boesch & Boesch, 1983), suggesting that chimpanzees' understanding of the problem involves a discrimination of the physical and functional properties of the tool. They also modify tools to improve these physical properties. For example, in fashioning an effective termite fishing probe the chimpanzee must select a flexible thin grass stem that is pliable enough to accommodate the twists and inconsistencies of the ant or termite tunnel. They then bite off its end to reduce it to a suitable length and remove the leaves along its length to modify its shape so it can be inserted sufficiently far down into the tunnel. These modifications are very rarely made after the first use of the tool (in only 7% of cases) suggesting this is not a case of trial-and-error learning (Boesch & Boesch, 1990). More likely is that chimpanzees are mentally representing the goal they are attempting to reach before they start to modify the tool. Thus, this requires a mental capacity to form not only the primary perception of a stem as a stem, but at the same time a 'metarepresentation' of a stem as a termite fishing probe (Whiten & Byrne, 1991).

When hammers for nut cracking are excluded from calculations (due to the nature of the tool little modification is actually possible), Tai chimpanzees modify tools three or more times in 76% of tool using observations (Boesch & Boesch, in press). Tools are sometimes selected at a remote site in advance of their use and transported to another location in order to exploit the food, providing evidence of sophisticated mental mapping skills (Boesch & Boesch, 1984a). Evidence also suggests that chimpanzees are perhaps capable of using tools to make tools ('metatools'). Before starting to crack nuts on an anvil three different chimpanzees at Bossou, Guinea were observed to place a small stone under the anvil, to level and stabilise it (Matsuzawa, 1991). For these reasons tool use by wild chimpanzees is commonly regarded as "intelligent" and evidence for advanced cognitive skills. It seems no coincidence that the majority of tool use is concerned with food acquisition, with food providing an immediate, and highly desirable, reward. Indeed, authors have argued that "intelligent" tool use and development of advanced cognitive abilities originated in the procurement of high-quality embedded foods which were intermittently available and spurred advances in innovative foraging techniques when other food was generally scarce (Gibson, 1986; Parker & Gibson, 1977, 1979).

The acquisition of these increasingly complex foraging skills is intimately linked to the prolonged ontogeny of chimpanzees. Skill development and subsequent independent foraging would require a longer period of time which would limit the mother's reproductive potential (Trivers, 1974). There would be obvious benefits in the ability to learn foraging skills rapidly through some form of social learning from the mother as this would accelerate the infant's progress to nutritional independence (Parker, 1996). Compared to learning basic foraging skills, the length of apprenticeship is even longer for tool use. Chimpanzees living at Gombe take 4-5

years to become competent termite fishers (Teleki, 1974), 6-7 years to become accomplished ant fishers (McGrew, 1977) and chimpanzees in the Tai forest take 6-7 years to learn to crack nuts (Boesch & Boesch, 1983) only becoming fully accomplished during adolescence (Boesch & Boesch, in press). Hence, it has been suggested that the long apprenticeship associated with extractive foraging and tool use may be dependent on the capacity for cogent social learning. The enhanced cognitive abilities of self-awareness, true imitation and teaching by demonstration may have emerged concomitantly (Parker, 1996). Although social learning may be particularly adaptive in the case of learning complicated technical skills (Byrne & Russon, 1998), it is only one example of the many behavioural domains in which learning from social partners may be useful to 'exploit the expertise of others' (Russon, 1997). Chimpanzees at Budongo do not use tools in any form to acquire food (personal observation; also see Whiten *et al.*, 1999), and for this reason this thesis will focus on the fundamentals of early foraging behaviour.

The term social (or observational) learning encompasses a full range of processes where learning and behavioural acquisition is contingent on, or at least influenced by, the observation or interaction with another group member (Box, 1984; Galef, 1988). This distinguishes social learning from individual (or asocial) learning which does not involve any social observation or interaction and is educed solely from the animal's experiences with its physical environment (Box, 1984; Heyes, 1994). A variety of learning processes, all occurring within social contexts, can lead to the same outcome of homogeneity of behaviour (e.g. of feeding habits) amongst animals living in the same social group (Galef, 1988; Whiten & Ham, 1992). There has been considerable controversy and discussion about the cognitive mechanisms (by which information is transmitted) that underlie social learning (Galef, 1988; Galef, 1990;

Heyes, 1994; Whiten & Ham, 1992). The debate has centred on testing for evidence of imitation, which is considered to be the most cognitively complex type of social learning (Whiten & Ham, 1992). Generally it is considered that imitative learning involves a naïve individual copying a new behaviour that it has observed a more experienced individual perform, if:

- the naïve individual has no inherent propensity towards the new behaviour, and observing the model perform the behaviour was necessary but sufficient alone
- the behaviour is copied first time without the need for subsequent practise
- the form of the behaviour is copied alone, not the goal or overall objective of the behaviour.

Imitation is regarded as cognitively advanced because it involves the imitator translating the visually perceived information of the movements of another directly into its own matching motor actions (Heyes, 1993; Whiten & Ham, 1992). It may involve the naïve individual projecting to the experienced individual's mental state to comprehend their intention and perspective of their actions (Tomasello *et al.*, 1993). It is argued imitation is a remarkably rapid and accurate process by which to acquire skills, much more efficient than the trial-and-error process of individual learning. In addition, imitation is regarded as the only mechanism that will ensure that information is transmitted faithfully and without errors across generations, and together these two features lead authors to regard imitation as the foundation of culture (Tomasello *et al.*, 1993). However, there is a convincing case that imitation cannot support culture because it does not ensure the faithful retention of

information during the period between behaviours being acquired and their later re-transmission, which may be up to a generation later (Heyes, 1993).

The traditional and well-established notion that primates, and great apes in particular, were exemplary in their imitative abilities began to be doubted earlier this decade with the suggestion that not only do monkeys not 'ape' but that apes rarely 'ape' (Visalberghi & Fragaszy, 1990; Tomasello, 1996). Most notably, in many reported cases imitation had been falsely inferred when in fact a cognitively less advanced process, referred to as stimulus enhancement, could have been operating. In this case the influence of a social partner directs an observer to the salience of an object or another feature of the environment, thereby improving the course of this individual's trial-and-error learning. These different mechanisms of social learning have been exhaustively defined (Heyes, 1994; Whiten & Ham, 1992).

Controlled experiments were devised to distinguish matching behaviours arising by imitation from those arising from other 'simpler' social learning processes, such as stimulus enhancement and emulation (for a description of 'do-as-I-do' methods and two-action test see Whiten & Custance, 1996). Initial work suggested that chimpanzees fail to imitate another individual who was raking food into reach (Nagell *et al.*, 1993; Tomasello *et al.*, 1987). They were only being able to 'emulate' the demonstrator, by using the tool in the same way regardless of the demonstration they saw, therefore understanding the goal of the task and reproducing the end results that they had observed. When investigators then removed the possibility of emulation, orang-utans were not able to imitate whereas 3-4 year old human children could (Call & Tomasello, 1995), but later

experimenters demonstrated that chimpanzees living in enriched captive conditions can and do imitate (Whiten *et al.*, 1996). However, further controversy surrounded this last set of experiments, critics maintaining that emulation had not been ruled out (Tomasello, 1996) and imitation could not be inferred because the behavioural actions were not novel to the observers (Byrne & Tomasello, 1995). Even in the laboratory, imitation has turned out to be exceedingly difficult to prove.

Although these experimental approaches provide the necessary controls to identify imitation, they are inevitably undertaken in artificial circumstances. Experimenters have endeavoured to set their subjects appropriate and relevant tasks, which are suited to the subject's age and are not too complicated (e.g. artificial fruits, used by Whiten *et al.* 1996). However, this is inevitably the experimenter's assessment and may not reflect the true perceptive needs of the subjects. Further, although the subject may be motivated to complete the task because of food rewards, it may not be motivated to copy the model, particularly in the case of those experiments that have used human models. Clearly, in setting a task where an animal is required to share the perspective of another individual cross-species comparisons of such tasks will only be equitable if the animal is required to share the perspective of the same species. There is good evidence that differences in the identity and quality of the model are important and in the case of using human models for chimpanzee subjects it can actually reverse results. Sumita *et al.* (1985) used a human demonstrator to show a naïve juvenile female chimpanzee in a zoo how to crack nuts but the demonstration failed to evoke even much interest in the chimpanzee over 30 sessions of one hour each. Yet, when an adult female chimpanzee was substituted as the demonstrator the same naïve juvenile tried and successfully cracked nuts on the very first session. However, even when a

conspecific model is used, the relationship of the observing animal to the model has to be considered because outside of the situation of vertical transmission between mother-infant dyads, certain relationships are likely to be more salient than others in terms of the potential for social learning. Field evidence has demonstrated that traditional behaviours spread between individuals in predictable terms, on the basis of the social relationships of the knowledgeable individual, for example the stone play tradition of Japanese macaques spread along kin and peer playmate lines (Huffman, 1984; Huffman & Quiatt, 1986). Differences in social organisation across species are known to be important in the transmission of information because particular individuals pay attention only to particular models (Cambefort, 1981). With limited numbers of potential subjects experimenters may not always have available the animals that would make the most effective or influential models.

An additional problem is that the different ontogenies of experimental subjects have a strong influence on these studies (Call & Tomasello, 1996). The differences in environmental complexity are clear between chimpanzees growing up under the normal wild condition, a captive setting, being trained or regularly instructed in a laboratory, or being raised in a human home. Chimpanzees reared by their mothers have produced negative results for imitative learning in comparison to human-reared chimpanzees and human children who imitated much more frequently (Tomasello *et al.*, 1993). It was therefore argued that the socio-cognitive skills of chimpanzees are enhanced beyond their normal abilities when they are raised by humans through a process of 'enculturation', with chimpanzees developing a human-like skill in their imitative learning abilities (Tomasello *et al.*, 1993; Tomasello, 1996). It is also possible that the process of enculturation simply increases the motivational character of the chimpanzee, such that individuals are predisposed to copy the species that has

raised them or that they have had most contact with (de Waal, 1998). There is little disagreement that the socially and physically impoverished captive environment is likely to reduce cognitive abilities and that the process of enculturation develops them (Tomasello, 1996; Whiten, 1993). However, it is a matter of some debate whether the enculturation process enhances the cognitive abilities of chimpanzees beyond normal species-typical capabilities (Tomasello, 1996), or whether it more accurately represents the cognitive abilities of wild chimpanzees who live in socially and ecologically complex and, consequently, cognitively more challenging natural environments (Boesch, 1996a,b; Whiten, 1993).

The development of species-typical behavioural patterns and skills during infancy that promote survival and eventual successful reproduction is an adaptive process that has evolved as a result of individuals interacting with their social and physical environment. Accordingly, in addition to studying this process experimentally under controlled conditions, it is also important to study it in the animal's natural setting where the selective forces that shape the process operate. However, in natural environments, the major problem is that the previous experience of subjects is rarely fully known so a behavioural pattern can rarely be proved to be novel. Even when a new behaviour is acquired it is not usually possible to attribute it to something specific an individual has observed because any modification in behaviour or increment in performance may have been the result of individual trial-and-error learning. However, there are some exceptions, where unusual circumstances implicate imitation as the most likely candidate amongst the possible learning processes. One example is when a completely novel and innovative behaviour is introduced into a social group. Hauser (1988) was able to carefully document one such case, the spread of an innovative feeding technique in a group of

wild vervet monkeys during a drought. The behaviour had not been observed before and diffused very rapidly throughout the group, at speeds too swift to indicate individual learning, suggesting the monkeys may have been learning by imitation. Another unusual circumstance is when the behaviour acquired is arbitrary. This was the case with rehabilitated orang-utans that were re-introduced into the forest and had acquired a number of behaviours that were very different to any orang-utan-typical behaviour (Russon & Galdikas, 1993, 1995). These behaviours were normally associated with human activity in the camp, for example: brushing teeth, bailing out canoes, washing dishes and clothes in the river, sweeping and weeding paths, hanging up hammocks. It seemed improbable that orang-utans had learnt these behaviours individually, rather it was more likely that they had imitated their human care-takers. Finally, another case where individual learning appeared improbable was because the behaviour was a complex string of sub-actions. Byrne & Byrne (1991, 1993) detailed the complicated manual techniques that wild mountain gorillas use to remove plant defences in the preparation of food for ingestion. The manual skill elements (details of digit manipulations and laterality) of these techniques were idiosyncratic, varying greatly between individuals, yet the overall technique (the structure in which these elements were organised) were standardised across the gorillas (Byrne & Byrne, 1991, 1993). It seemed implausible that these complicated sequences of actions making up these overall techniques could have been learned individually, leading the authors to conclude that gorillas imitate the overall structure of the behavioural sequence but without the details, termed 'program-level imitation' (Byrne, 1994, 1998).

The most impressive evidence of the potential scope of learning species-typical behaviour from social partners in chimpanzees is demonstrated by the large number

of population-specific patterns of behaviour that cannot be attributed to ecological or genetic differences, suggesting 'chimpanzee cultures' may exist (Boesch, 1996a; McGrew, 1992; Whiten *et al.*, 1999). Amongst the many examples there are some where a reasonable functional explanation for the difference is not evident. For example, different ant dipping techniques to obtain driver ants, *Dorylus nigricans*, are used by Tai and Gombe chimpanzees, which are unique to these sites (Boesch & Boesch, 1990; Goodall, 1986). No ecological factor could be found to prevent the use of either of them at both sites yet the Gombe technique is four times more effective than the one at Tai (Gombe: 760 ants per min, Tai: 180 ants per min; Boesch & Boesch, 1990). Hence, Tai chimpanzees use an inferior, less well-adapted technique. If they were learning by trial-and-error they would be expected to develop the best ecological solution, a more efficient technique to collect ants similar to the one at Gombe. However, the argument remains that such homogeneity of behaviour could also result from individual learning processes constrained within the ecological limitations of the environment in which the task is learnt (Tomasello, 1994, 1996). Perhaps there is something specific at Tai (as yet undiscovered) that prevents chimpanzees using the Gombe technique. Since it may not be possible to recognise all ecological determinants, let alone exclude them completely (Tomasello *et al.*, 1993), and there are many opportunities to individually interact and learn by trial-and-error over long periods of development - such an argument, theoretically, cannot be disproved. Thus, except in the unusual circumstances previously described it will be difficult to prove that social learning actually has any effect on an infant's progress and development of foraging behaviour, let alone prove its exact contribution. For example, the first time an infant is observed to encounter a food item, it cannot be proved that the food item was completely novel to the infant and consequently it will be impossible to control for the infant's previous experience

with this food item. Learning processes are unlikely to occur singly; we might expect that socially-mediated influences work concurrently with individual learning through play and exploration over long periods of development. Further, if social learning is involved, then the processes occurring are likely to be varied. The field of social learning appears to be in a predicament equivalent to Morton's fork: experiments cannot prove the functionality of social learning, but ecologically and functionally relevant conditions cannot provide the necessary controls. The two approaches are reciprocal yet not fully supportive.

Authors are starting to suggest new approaches that move away from the focus on cognitive processes (Box, 1994; Coussi-Korbel & Fragaszy, 1995; King, 1994). Box (1994) noted "the heavy emphasis on 'cognition' in studies of primate social learning has tended to create a conceptual straight-jacket that has diverted attention away from other realistic avenues of exploration". King (1994) also takes a functional approach, instead of considering the processes and mechanisms of transmission, and emphasises the importance of examining the relative roles of mothers and infants in the acquisition of skills and knowledge. Coussi-Korbel & Fragaszy (1995) believe that that by predetermining that novelty is required for definitive evidence of imitation, success on these experimental tasks will be intrinsically unlikely. They suggest that the field of social learning has become distracted by these paradigms that seek to identify the operation or incidence of different social learning processes in the acquisition of skills or information and correspondingly ignore the importance of the contingencies of ecologically relevant social learning.

This thesis addresses these issues. It takes a functional perspective, examining the foraging behaviour of young chimpanzees throughout development. It aims to assess opportunities and potential efficacy of social learning within the natural and ecologically relevant context of foraging.

The following chapter provides details on the study site and study population, a complete description of the methods common to the entire study, including the use equipment, data collection procedures employed and definitions of behaviours. Chapters 3 - 6 are the data chapters. These start with an introductory review of the pertinent literature and theory, present all analyses and results, and discuss these findings within the context of the other available data. Chapters 3 - 6 consider different elements of a young chimpanzee's life that are important in identifying the opportunities and likelihood for social learning within the dynamic context of its development. Chapter 3 describes the social and general behavioural development of a young chimpanzee infant. This provides an overview and description of the infant's behavioural development and investigates the changing relationship with the mother, presenting data on spatial relations and two positive forms of social interaction: grooming and play. Chapter 4 examines the overall pattern of feeding as it emerges throughout development. This involves comparing infant feeding choices, procurement actions, processing and intake rates with those of juveniles and their mothers. In Chapter 5 the specific social context of early foraging experiences is investigated in relation to maternal feeding behaviour and the extent of behavioural co-ordination. This involves investigating indices of proximity whilst foraging, attention to the mother and the degree of feeding synchrony with the mother. Chapter 6 is the substantive part of the thesis, focusing on mother-infant food sharing not only as an alternate maternal investment strategy but also as an

opportunity for infants to learn about foods. Finally, Chapter 7 is a synthesis of my findings. Here I discuss the potential efficacy of social learning within the context of the development of foraging behaviour and suggest new directions for future work.

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# CHAPTER 2:

## STUDY SITE, STUDY POPULATION & GENERAL METHODS

The world is too much with us  
late and soon, getting and spending  
we lay waste our powers.  
Little we see in nature that is ours.

*Wordsworth*

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### **2.1 Introduction**

Chimpanzees live in multi-male, multi-female social groups of up to 105 individuals (Nishida & Hiraiwa-Hasegawa, 1987): ‘communities’ (Goodall, 1973) or ‘unit groups’ (Nishida, 1968). Individuals within a community share a common range and associate in small temporary subgroups, or parties, which are continually changing in their size and individual membership. Chimpanzee society is characterised by this particularly flexible and fluid (‘fission-fusion’) social system (Goodall, 1986). Males form the nucleus of the community. They co-operate with each other to defend the range by vocal advertising and border patrols (Goodall,

1986; Nishida, 1968) and will remain in the same community their entire lives (Nishida, 1979). Most females will join a new community at least once, usually leaving permanently in late adolescence to reproduce outside their natal range (Nishida, 1979; Pusey, 1980).

A central feature of chimpanzee society is the intrinsic difference in the sociability of male and female chimpanzees. Males are principally gregarious (Goodall *et al.*, 1979; Nishida, 1979). Adult males have the greatest tendency to congregate with others and, with the exception of oestrus females, favour the company of other males (Nishida, 1979; Wrangham *et al.*, 1992). These patterns of spatial association and strong affiliative relations (males forming alliances and frequently grooming each other) suggest that certain male-male bonds are strong (Goodall, 1986; Nishida, 1968), although dominance relationships are complex (Hayaki *et al.*, 1989). The formation of alliances appears to be critical to a male's social status and reproductive strategy (Goodall, 1986; Hasegawa & Hiraiwa-Hasegawa, 1983; Nishida, 1979); males clearly benefit by co-operating to prevent alien males gaining access to community females (Wrangham, 1979). In contrast to males, females with offspring tend to avoid each other<sup>2</sup>: they are generally solitary, spending 50-80% (Halperin, 1979) or 65% (Wrangham & Smuts, 1980) of their time alone at Gombe, and up to 70% of their time alone at Kibale, in distinguishable but

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<sup>2</sup> Chimpanzees living in Bossou, Guinea have an unusual pattern of social organisation. Females living in this community are sociable, mothers travel together and frequently groom each other (Sugiyama & Koman, 1979; Sugiyama, 1988). However, since the habitat is highly disturbed and the forest geographically isolated, female emmigration/immigration is rare and females seem to be closely related. No other community of chimpanzees has been found to have such close female relationships and this pattern of female social organisation is the exception to the rule.

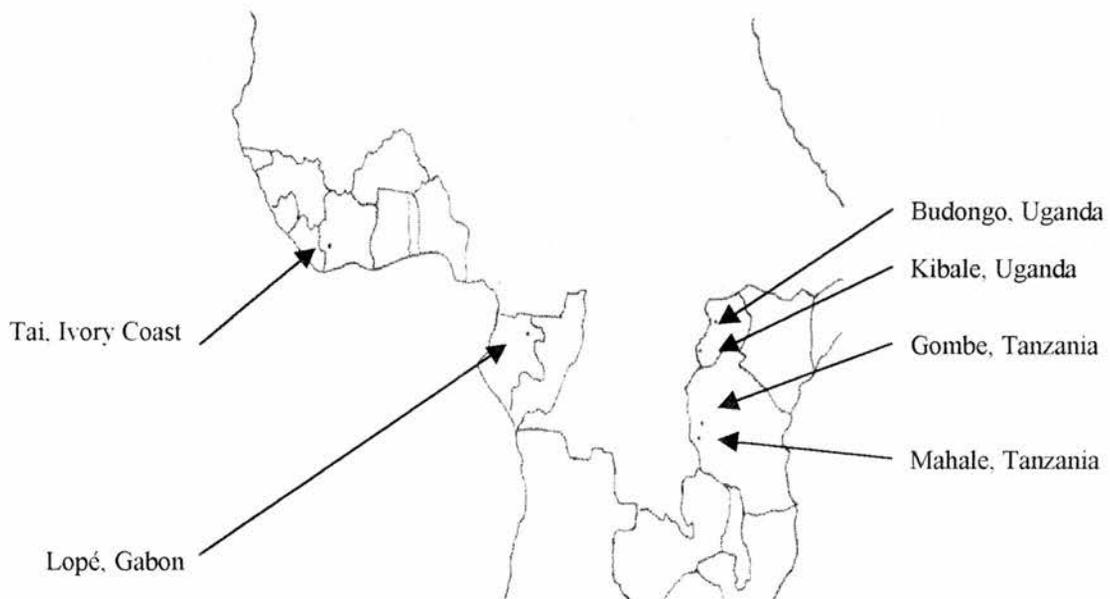
considerably overlapping core areas (Wrangham *et al.*, 1992). Females are also more affiliative towards males than they are to other females: non-kin female-female grooming and interaction is particularly rare (Goodall, 1986; Wrangham *et al.*, 1992). Some females appear 'peripheral' to the community: their core areas can change so that they spend a week or more within the range of a neighbouring community (Wrangham *et al.*, 1996). These females may only be seen frequently during periods of high fruit productivity. Periods of sexual receptivity transform a female's ranging and association pattern; during this time she will associate within larger parties and more frequently travel with males (Wrangham & Smuts, 1980).

Ecological factors, such as food patch size and dispersion, primarily determine male feeding and travelling party size but this is not the case for females (Chapman, *et al.*, 1995). There is evidence to suggest that females have lower feeding efficiency if they spend long periods within large parties (Wrangham & Smuts, 1980) and this may explain why females travel individually and forage alone even when prevailing ecological conditions would support larger subgroups (Chapman *et al.*, 1995). It is assumed that travelling will be energetically more costly for females than for males because of the weight and encumbrance a mother endures when carrying an infant (Wrangham *et al.*, 1996). Since females without infants are as gregarious as males (Wrangham *et al.*, 1992), it has been argued that mothers spend time travelling and foraging alone in order to reduce feeding costs and competition (Nishida, 1979; Wrangham *et al.*, 1992).

## 2.2 Study Site

Budongo Forest Reserve is the largest lowland tropical rainforest in Uganda, covering some 793km<sup>2</sup> (Struthsaker, 1987). It is situated on the edge of the western rift valley in the northern end of a series of forests in the west of Uganda, lying between latitudes 1° 35' and 1° 55' North, and longitudes 31° 18' and 31° 42' East (see Figure 2.1).

**Figure 2.1:** Map of Africa showing Budongo and the other major chimpanzee field sites

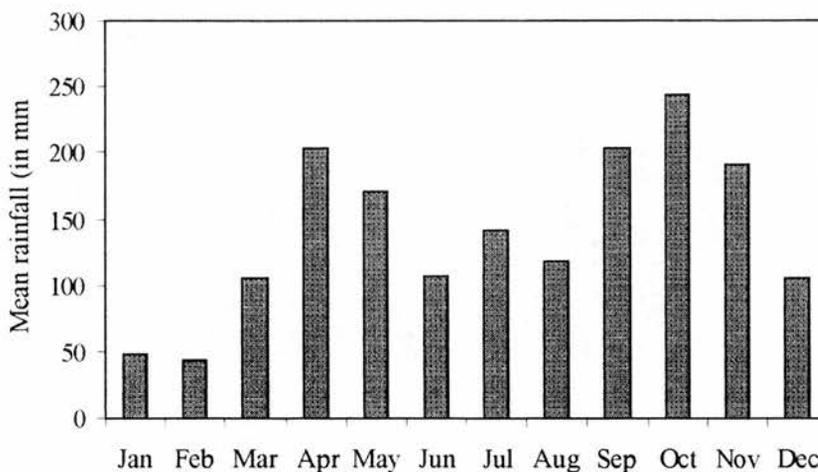


Fifty-three percent of Budongo is continuous forest cover (for descriptions of the vegetation types see Eggeling, 1947; Langdale-Brown *et al.*, 1964; Synott, 1985). Almost all areas of the forest have been selectively logged for timber at least once. Howard (1991) estimated that more than 75% of the forest had been influenced by timber extraction. As a result of this selective logging there exists an uneven

distribution of different vegetation communities and forest habitats within Budongo (Plumptre, 1996). Increasing human activities continue to jeopardise the integrity of the forest. Despite efforts by the Forestry Department, the old more valuable mahogany trees continue to be removed by illegal 'pit sawing' (trees are cut up where they are felled by digging a pit around the trunk).

Budongo Forest has an altitudinal range of 700-1270m above sea level. It lies on undulating terrain, with a series of valleys and ridges running south-east to north-west and an overall gentle NNW slope towards the rift escarpment valley. Two small rivers drain the forest: the Sonso and the Wasisoke. Both these rivers empty westward and eventually flow into Lake Albert. Other smaller streams run eastward to Lake Kyoga. Rainfall is plentiful, between 1150 and 1500mm annually, with a double peak in rainfall April through to May and September through to December. Rainfall tends to be more common in the afternoons and evenings during these rainy periods (see Figure 2.2).

**Figure 2.2:** Mean rainfall (in mm) '93-'97 Sonso fieldstation, Budongo (BFP data)



Budongo typically has a dry season of about three months duration from mid-December to mid-March there is also 'minor dry season' of about a month towards the middle of the year but this is highly variable in its timing and its effects are not as apparent. Mean annual temperature varies between minimums of 17-20°C and maximums of 28-29°C; temperatures are appreciably higher during the dry season from December through to March.

Budongo is widely regarded as the most commercially valuable timber forests remaining in Uganda (Howard, 1991). It is also of considerable importance in terms of the conservation of Uganda's flora and fauna bio-diversity and botanically speaking it may be one of the best studied forests in East Africa (Synott, 1985). The floristic composition of Budongo is particularly diverse. The reserve has some 37% (465) of all Uganda's known tree and shrub species and its value lies not only in the large number of species it contains but also because many of these are rare, restricted range species (Howard *et al.*, 1996). Budongo has five species of diurnal primates: the chimpanzee (*Pan troglodytes schweinfurthii*), black and white colobus (*Colobus guereza occidentalis*), blue monkey (*Cercopithecus mitis stuhlmannii*), red-tail monkey (*Cercopithecus ascanius schmidtii*) and olive baboon (*Papio cynocephalus anubis*). Potential predators of chimpanzees include lions and leopards (Boesch, 1991a; Hiraiwa-Hasegawa *et al.*, 1986; Tsukahara, 1993). Although lion (*Panthera leo*) are regularly seen in the north of the reserve and doubtless leopard (*Panthera pardus*) also occur in these parts, they do not appear to be a current threat to the study community, as there were no physical signs that they had entered within the range of the Sonso chimpanzees.

## 2.3 Study Population

The subjects of this study were individuals of the eastern sub-species of common chimpanzee (*Pan troglodytes schweinfurthii*). This is the same chimpanzee sub-species as at other study sites in Uganda (Kibale Forest National Park) and in Tanzania (Gombe and Mahale National Parks). At present it is estimated that there are between 675 and 2046 chimpanzees within Budongo Forest Reserve, this number depending on the census method employed (Plumptre, 1996). This may make the Budongo Forest chimpanzee population the largest one in Uganda, but only when a full census of chimpanzees within Uganda is completed (currently underway by A. Plumptre, D. Cox and colleagues) can such a claim be verified. Currently, the main threat to chimpanzee populations in Uganda is snare injury. Snares are not set for chimpanzees, rather they are set for diuker, bush-buck or guinea-fowl; most injuries to chimpanzees are incurred by them 'accidentally' becoming caught in these wire snares. Nearly a quarter of the Sonso community has snare wounds, at Kibale this figure is much larger (E. Stokes, personal communication). Debby Cox at Uganda Wildlife Education Centre (based in Entebbe) has initiated a snare removal programme with the Jane Goodall Institute (JGI) funding.

Early chimpanzee studies at Budongo were undertaken in the 1960's (Albrecht, 1976; Reynolds & Reynolds, 1965; Sugiyama, 1968), but these were interrupted by the later political instability and civil war. Studies began again with the creation of The Budongo Forest Project (from here on, BFP), started in 1990 by Professor Vernon Reynolds at Oxford University. With initial funding from JGI and National

Geographic Society, habituation of the Sonso community of chimpanzees began, eventually allowing individual recognition of community and the start of behavioural observations. Funding was continued by the Overseas Development Agency (ODA), allowing long term studies on the effects of selective logging on forest ecology to be undertaken by Professor Vernon Reynolds and the BFP Co-Directors, Dr. Andrew Plumptre and Christopher Bakuneeta between 1992 and 1997 (e.g. see Bakuneeta *et al.*, 1995; Plumptre, 1996). BFP has created a trail system, which is a grid of north-south and east-west running trails that intersect every 100m so that forest blocks are approximately 100m by 100m in area. The trail system allows researchers easy navigation in the forest.

The study subjects were members of the Sonso community of chimpanzees, which numbered 51 individually recognisable individuals for the duration of the study period, between August, 1997 and August, 1998. This community has never been artificially provisioned. Definitions of developmental stages are given in Table 2.1 and the number of community members within each of these age-sex classes is summarised in Table 2.2. Table 2.3 provides a detailed breakdown of all named individuals, their identity codes and known kin. In November 1997 a female infant, RS, was born. By this time an adult male, CH, had been missing for some months. When he did not later return to the community he was presumed dead.

**Table 2.1:** Definitions of developmental classes (taken from BFP records)

Age Class	Definition
Infant: stage 1	Always carried by the mother, not yet weaned from mother's milk. Infants under the age of 2.5 years.
Infant: stage 2	Not always carried by mother, feeding on foods other than mother's milk but not yet fully weaned. Infants older than 2.5 years. Infancy terminated by the birth of the next sibling.
Juvenile: stage 1	Still close association between the mother and offspring, but juvenile feeds and moves completely independently and makes own night nest.
Juvenile: stage 2	Increasing independence from the mother. May or may not always be in the same sub-group as the mother. In the case of males there is a closer association with adult males. When feeding in the same sub- group they are often far apart from the mother.
Sub-adult female	Beginning of full sexual swellings, may be irregular. Does not elicit much interest from adult males when in oestrous. No offspring.
Sub-adult male	Development of testes. Beginning to challenge females for dominance.
Adult female	Has offspring, regular swelling cycles
Adult male	Testicular development complete. Face fully black. Now dominates all females and challenges other males for position in hierarchy.
Old adult male/female	Baldness developing around the head and lower back. Greying of hair.

**Table 2.2:** Age-sex classes of the Sonso community of chimpanzees

Age Class	Number of individuals (by sex)	
	Female	Male
Infant: Stage 1	4	2
Infant: Stage 2	1	3
Juvenile: Stage 1	3	3
Juvenile: Stage 2	2	1
Sub-adult	5	5
Adult	12	10
Totals	27	24

This study focused on 9 infants, 4 juveniles, and 10 mothers within the community. With the exception of HT and HW, this represented all mothers and infants within the community (see Table 2.3). HT and her male infant, HW, were excluded because HT was very rarely seen and insufficiently habituated. It also amounted to four of the six juveniles at developmental stage one (see Table 2.3). Data were originally collected on all six juveniles. However, the amount of data collected for two juveniles, GR and SH, were considered insufficient for analysis as the number of focals on these two subjects totalled less than half those on the other juvenile subjects.

With the exception of RS, who was born during my study and observed on her first day of life, accurate ages of the other Sonso infants were unknown. Infant ages in BFP records were estimates made by the field assistant who had first encountered the new infant, based on its size and behavioural dependency. In order to age infants more precisely I examined the party composition record notebooks of the senior field assistants (Z.T. Kiwede, J. Tinka and G. Muhumuza). By relating the date that a mother was first seen with her infant to the last date to that which she had been seen without an infant, i.e. before its birth, I was able to calculate the oldest possible age of the infant when it was first seen. As a result of this cross-referencing of the three field assistants' notebooks I was able to age seven out of the nine infants to confidence intervals between 1 and 5 weeks (see Table 2.4). The remaining two infants (RA and ZL) could not be aged precisely as their mothers had not been seen within a reasonable time period before the birth. As a result RA and ZL had to be aged using the original estimated age made by the field assistants.

Table 2.3: Members of the Sonso community during the study period.

Name	ID code (mother's ID)	Name	ID code (mother's ID)
<i>Adult Females</i>		<i>Adult Males</i>	
Banura	BN	Black	BL
Harriet	HT	Bwoya	BY
Kalema	KL	Duane	DN
Kigere	KG	Jambo	JM
Kutu	KU	Kikunku	KK
Kwera	KW	Maani	MA
Mama	MM	Magosi	MG
Nambi	NM	Muga	MU
Ruda	RD	Njokjo	NJ
Ruhara	RH	Tinka	TK
Zimba	ZM		
Zana	ZN		
<i>Sub-Adult Females</i>		<i>Sub-Adult Males</i>	
Clea	CL	Andy	AY
Janie	JN	Bwoba	BW
Kewaya	KY	Nick	NK
Mukwano	MK	Zefa	ZF
Sara	SR	Zesta	ZT
<i>Juvenile Females: Stage 2</i>		<i>Juvenile Males: Stage 2</i>	
Muhara	MH (MM)	Gashom	GS (none)
Vita	VT (?)		
<i>Juvenile Females: Stage 1</i>		<i>Juvenile Males: Stage 1</i>	
Gonza	GZ (ZM)	Kidogo	KD (KG)
Grinta <sup>3</sup>	GT (RH)	Musa	MS (NM)
Shida <sup>3</sup>	SH (BN)	Bob	BO (RD)
<i>Infant Females: Stage 2</i>		<i>Infant Males: Stage 2</i>	
Bahati	BH (KL)	Kato	KT (KU)
		Kwezi	KZ (KW)
		Zalu	ZL (ZN)
<i>Infant Females: Stage 1</i>		<i>Infant Males: Stage 1</i>	
Nora	NR (NM)	Zig	ZG (ZM)
Bety	BT(BN)	Hawa <sup>4</sup>	HW (HT)
Rachel	RA (RD)		
Rose	RS (RH)		

<sup>3</sup> GR and SH were excluded from analysis as insufficient data were collected on these subjects.<sup>4</sup> HW was excluded from the study because his mother, HT, was so rarely seen.

**Table 2.4:** Calculations of the age of study subjects

<b>Infant</b>	<b>Mother last seen</b>	<b>Infant 1st seen</b>	<b>Earliest DOB</b>	<b>Oldest age when 1st seen</b>	<b>Age at begin. 08/97 (in months)</b>	<b>Age at begin. 03/98 (in months)</b>
RS	15/11/97	16/11/97	16/11/97	1 day	**	3.5
ZG	23/06/97	07/07/97	24/06/97	2 weeks	1.25	8.25
RA	17/05/96	09/07/97	?	2 months	3	10
BT	01/10/96	04/10/96	02/10/96	2 days	105	17 <sup>5</sup>
NR	31/01/96	08/03/96	01/02/96	5 weeks	18.2 <sup>5</sup>	25.25
ZL	not seen before	12/07/95	?	2 months	27 <sup>5</sup>	34 <sup>5</sup>
KZ	03/01/95	28/01/95	04/01/95	3 weeks	31	38
BH	02/12/94	16/12/94	03/12/94	2 weeks	32	39
KT	23/09/93	13/10/93	24/09/93	3 weeks	46	53

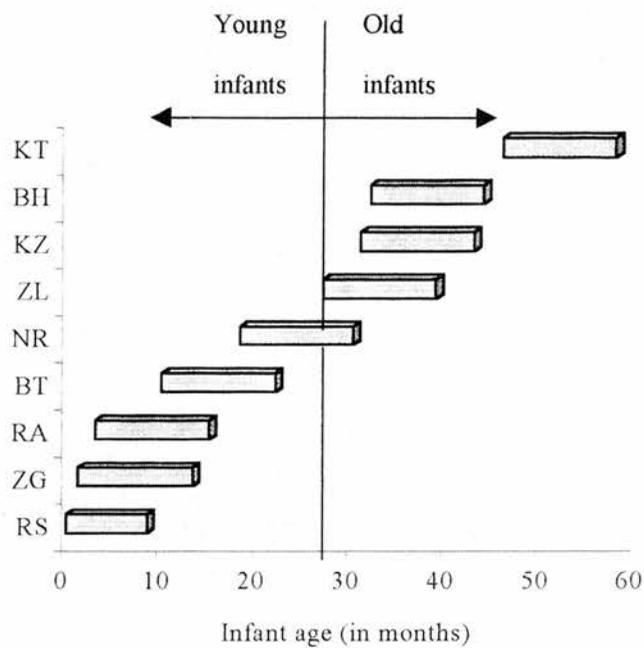
This study used a cross-sectional design, taking an integrated view of development and aimed to sample as many different infants at different ages as possible. There was sufficient overlap in the age spans of infants throughout the study period (see Figure 2.3)

<sup>5</sup> Ages are approximate.

Infants were divided into two groups:

- ‘Young’ infants (approximately equivalent to stage 1 infant, see Table 2.1 and Figure 2.3) mean age during course of study less than 2.5 years.
- ‘Old’ infants (approximately equivalent to stage 2 infant, see Table 2.1 and Figure 2.3) mean age during course of study more than 2.5 years.

**Figure 2.3:** Subject age throughout the study period



## **2.4 General Methods**

The following methods were common to the entire study. Methodologies specific to only parts of the study are described in the relevant chapters. Fieldwork occurred in two main phases. Preliminary observations were made during a 6 week pilot study in April to May 1997. During this period I was able to consider a broad range of behaviours and field-test observation criteria, methods of data collection, 'Observer' configurations and equipment. At the beginning of the main study in August, 1997 these methods, including the incorporation of the role of the field assistant, were refined and finalised. In addition, the categories of behaviour to be recorded were operationally defined and the sampling regime designed. Formal data collection began in mid-August and by this time the methods had been fully practised by both my field assistant and myself. Through the course of the study over 1200 hours were spent locating and observing chimpanzees.

### **2.4.1 Observation Methods**

#### **2.4.1.a Field Assistants**

BFP appoints a field assistant to all students who undertake long-term studies. In August 1997 I was assigned to work with Tinka John, a senior field assistant at the project. At this time he had over 6 years experience studying chimpanzees and in addition he was the project's botanical specialist. Sadly, in November '97 (three months into the study) Tinka became seriously ill. During this period of illness the Co-directors of BFP decided that I should be re-assigned to work with Kiwede T.

Zephyr, who is the head chimpanzee field assistant at BFP. He is in charge of compiling data collected by other field assistants and is usually exclusively employed to collect data for Professor Vernon Reynolds so, consequently, I am particularly grateful to Professor Reynolds for his generous understanding of the situation at that time. Although by February '98 Tinka had recovered and was back to work, the illness had left him with a partial paralysis of his right leg which meant that he had difficulty moving quickly through the forest. Hence, it was decided that I should continue to work with Zephyr for the remainder of the study.

#### **2.4.1.b Locating Chimpanzees**

A number of different strategies were used to locate chimpanzee mothers and their offspring. It was important to begin the search early, always soon after dawn, between 6.30 and 7am. The easiest way to find chimpanzees was to locate them by their calls. This method was most successful between the hours of 7 and 9am, as this is the main time when chimpanzees are vocalising and drumming (for calling frequencies see Sabater-Pi, 1979). However, females call less frequently than males (Ghigleri, 1984; Wrangham, 1977), they rarely initiate pant hoots (Goodall, 1986) and only males give pant-hoots on arrival at food patches (Ghigleri, 1984; Wrangham, 1977). Even as early as juvenility this sex difference in calling rates is apparent (Pusey, 1990). It is not surprising then, that when females were alone with young offspring and 'pant hoot' calls were heard nearby (even within 100m), they rarely responded by calling or approaching them (personal observation). In addition, compared to gregarious males, females with dependent offspring are often solitary (see section 2.1). A combination of their solitary nature and low calling rates seriously hampered efforts to locate females with young offspring. Difficulties with

habituation levels whilst females were travelling on the ground exacerbated the problem. This was the major difficulty in studying exclusively female chimpanzees with young offspring.

Dawn-to-dusk follows are often used as a strategy to increase hours of contact with subjects. This involves locating a particular chimpanzee on the first evening, nesting this individual, then re-locating the subject the next morning and attempting to follow this same subject all day. This method was tested in the pilot study but was discontinued for a number of reasons:

- Follows involve repeatedly sampling the same individual throughout the day, which was not appropriate for the cross-sectional design of this study where the number of subjects sampled per day had to be maximised.
- It was difficult to follow the mother as she left the nest the next morning, as the mother climbed onto the ground we invariably lost her (see section 2.4.1.c).
- Low light levels meant identification was rarely possible as the mother left the nest.

As a result the nesting method was only employed when under-sampled and high priority mothers were located in the evening.

If calls were not heard in camp before leaving for the forest, or if the sub-group located did not include any mothers, the next method was to check trees that were known to be in fruit and also the forest blocks where chimpanzees had recently been sighted. If at any point during this search, calls were heard then we would head

towards them and check the group to see whether any mothers were present by scanning all individuals. On locating a particular mother a decision would be made whether to stay and start a focal or whether to search for another mother (depending on how well sampled the subject had been that month, see section 2.4.3.d). Some adult females spent more time travelling with males and these mothers were the easiest to locate. The mothers that spent long periods of time alone or in female-only parties were the most difficult to locate and were the most liable to be under-sampled at the end of the month. At times it was necessary to target the search for particular mothers that had been under-sampled. Since chimpanzees calling loudly are usually in larger parties (Wrangham *et al.*, 1992), following calls was not usually a suitable way to locate these solitary mothers. Accordingly, we would search for such individuals by working round the system of trails and focusing the search on blocks with known fruiting trees, and then later monitoring other blocks with trees about to fruit. Sometimes we were able to focus our search on the basis of sightings of particular individuals by the two other students or other field assistants. Five months into the study, in January 1998, it was possible to communicate using VHF FM Transceivers (handset 'walkie-talkie' radios: Model: Yaesu SMC 517L10) and VHF FM Base Unit (Model: Yaesu FTL-2014). Handset-to-handset these walkie-talkie radios communicated over a distance of only about 600 metres. However, a message could also be relayed via the base radio which had a large aerial and using this method the radios worked over a distance of up to 2km.

Finally, if all else failed, we would resort to waiting at a fruiting tree for a subject to arrive. This proved to be a more productive method than simply traversing the grid system and searching randomly: chimpanzees were rarely located by chance. During periods when chimpanzees were particularly hard to locate and there were no

trees in fruit, then at this point we would concentrate our search on the edge of the grid system, where we would wait for and then follow any far-off calls.

#### **2.4.1c Habituation and Observation Conditions**

There were large differences in the level of habituation between male and female chimpanzees. Males were more confident and bold; they could easily be followed along the ground. A previous researcher at Budongo, N. Newton-Fisher, studied male chimpanzees and habituation efforts were focused on these individuals (Newton-Fisher, 1997). Females in general, and certain mothers in particular, were much shyer and nervous. In trees they were well habituated and could be routinely observed. However, mothers were difficult to observe on the ground, apart from when in the company of males when some mothers (e.g. NM, KW) could be observed whilst stationary, others could not (e.g. BN, RD). If travelling with males, some females would tolerate being followed at a distance. However, if alone and travelling mothers were extremely wary: if climbing down to leave a fruiting tree alone they would move away very fast and we invariably lost them in these circumstances. Once chimpanzees left the trail system and were moving fast the disadvantages of being a bipedal observer soon became apparent. The secondary forest of Budongo has a very thick under-storey of climbers that hampered bipedal movement and we were normally slower than chimpanzees, quickly losing them if we left the trail. In some cases we would be able to predict their route because they were heading for a known fruiting tree and we would be able to intercept an individual further ahead. Observation conditions and levels of habituation simply did not allow us to remain in visual contact with mothers when moving along the ground, unless they remained on the trail. As a result, the majority of observations

were made whilst chimpanzees were in the trees. Very few observations were made when mothers were feeding, travelling, resting or grooming on the ground. When such observations were possible I would approach the female alone (without my field assistant), as this appeared less alarming to them. The solitary nature of peripheral females is an obstacle to their habituation: it is likely to be considerably slower and more difficult to complete.

All observations were made with the aid of Zeiss DIALYT 10 x 40 Binoculars in my case and with Nikon Sport 8 x 40 binoculars in the case of my field assistant. Observations were suspended during rain because of possible damage to the hand-held computer and because of the effects on both activity and proximity.

#### **2.4.2 Recording Methods**

I used a hand-held computer to collect continuous focal data (see below). Hence, I was the only observer to collect continuous focal data and accordingly, there was no variation due to inter-observer differences for any analyses of continuous focal animal data. Intra-observer differences ('observer drift') throughout the length of the study was regarded as minimal because of objective standards imposed by the behavioural definitions drawn up at the beginning of the study (see definitions in section 2.4.5.b). The accuracy of my field assistant's estimates of proximity distances were tested, accuracy was at least 90% (see Appendix 1).

#### **2.4.2.a Hand-Held Computer**

Data were collected on a hand-held computer, which performed the role of a computer event recorder. A computer event recorder is simply a computer running suitable software that allows the researcher to record behavioural observations directly onto this computer. The software responds to the key pressed on the computer by storing a code representing the key and the time at which it was pressed. For this study it proved particularly useful because it allowed efficient recording of frequent and rapidly occurring events (such as bites of the same food type in the case of food intake rates).

In terms of hardware, the nature of the fieldwork determined that the device be not only portable and compact but also robust. The intention was to find a piece of equipment that was, as far as possible, resistant to high temperatures and protected from the effects of humidity and dirt. The Hewlett Packard range of palm-top computers had been used by previous personnel and met these requirements. The HP 200LX was used. This had 4MB of RAM and ran DOS-based programs. It ran on two AA size batteries. I used Ever Ready Rechargeable Nickel Cadmium 1.2V batteries and the Ever Ready FCH6 Fast Battery Charger. These batteries were charged by the solar panels in camp (see below). At the end of each day data were transferred from the Hewlett Packard 200LX palm-top (from here-on 'hand-held computer') to a Gateway 2000 CB486DX33 Colourbook laptop computer (from here-on 'laptop computer') at camp. An interface cable and the HP Connectivity Pack Version 1.02 software for HP100LX and HP200 LX to DOS-based PCs were used. The laptop computer was also charged from the solar panels in camp. These were four 6in. x 12in. Solarex MSX10 Solar Panels charged an acid-filled car

battery during the day. In the evenings the lighting in our houses ran off this power source but in addition the car battery was connected to a cigarette adapter. This cigarette adapter was in turn connected to a Mains Supply Converter (Handy Mains Adapter VPA Type), which brought the voltage up to 240V. This system was preferred because it allowed all UK standard electrical equipment to be charged from this source.

I used The Observer software package (Noldus Information Technology Inc., Wageningen, The Netherlands). This software has been designed as a universal system for the collection and analysis of observational data. It allows the researcher to create their own configuration for any of their (perhaps changing) needs. It is extremely flexible and nearly manages to achieve what the manufacturer claims of “support of all standard data collection methods and coding systems”. It fails on this on just one front – it is not possible to collect combined focal and instantaneous data samples. However, this was not critical to my needs because instantaneous sampling was recorded on a checksheet.

The Observer program is a modular system. The functions of the program are separated into individual sub-programs, or ‘modules’. These are the Program Manager, Configuration Designer, Event Recorder and Data Analysis Procedures. The Program Manager arranges all files belonging to the research project and is the starting point for running the other three modules. The Configuration Designer is used to devise the blueprint of the research project. The research design is constructed and can later be modified if required within this module. The behaviours to be coded, subjects to be observed, and independent variables to be

recorded are all specified here. These together then form what is referred to as the project configuration file. The project configuration file is run within the Event Recorder module to collect data, which is saved as an observational data file on the hand-held computer and transferred to the laptop computer in camp as described above. The data analysis procedures of Observer can be used for basic analyses. For additional computation, results can be exported to a spreadsheet program (such as Excel) and statistics package (such as SPSS).

All observations required binoculars. For this reason an unusual arrangement was required. The basic requirement was the ability to be able to key behavioural codes into the hand-held computer whilst observing the subject continuously through binoculars. This was achieved by positioning the hand-held computer on the top of the binoculars and securing it in place with 'Velcro'. In fact, the binoculars were positioned upside down so that the focusing wheel (located on the upper side of the binoculars) was available below the hand-held computer, for adjustment with the thumbs, leaving the fingers free to key in behavioural codes. Largely, observations were made of subjects at heights of 15-20 metres in trees. This meant that the binoculars and hand-held computer arrangement was a difficult and heavy apparatus to hold upright for continuous recording over long periods of time. For this reason, a 'chestpod' was also used. The chestpod is a T-shaped support used predominantly by birdwatchers to reduce the muscular strain caused by extended use of binoculars. It was possible to attach the binoculars/hand-held computer apparatus to the chestpod by way of a fitting usually used to attach cameras to tripods. The chestpod hangs around the neck and consequently the weight of the binoculars/hand-held computer apparatus is braced against the chest.

This allowed continuous observations of chimpanzees to be made even when they were at elevated heights within the trees.

#### **2.4.2.b Checksheets**

The checksheet used for data collection conformed to a basic grid, designed to meet three requirements: it was simple and straightforward to use, favoured quick and easy computer data entry and, finally, allowed a large amount of data to be recorded on a single A4 page. The first two weeks of the main study involved training and practising with my field assistant in the data collection methods. During this time there were subsequent improvements to the design of the checksheet.

#### **2.4.2.c Tape Recording**

A voice activated Sanyo Micro-cassette TRC-570M Recorder (or 'dictaphone') with a lapel attached Genexa Omnidirectional 33-3003 Microphone was used to record food sharing events when these were rapid. It also became necessary to use the dictaphone for continuous recording during one period when the hand-held computer failed (moisture had entered the computer and it took some time before a replacement could be sent from the UK). In both cases, tapes were transcribed soon after (if possible the same evening) that recordings were made. In the case of food sharing records, these were transcribed into a Word 6.0 file. For continuous records, the tape was transcribed and data entered in real time into the Observer program using the Observer Event Recorder module in the full program on the laptop computer.

#### **2.4.2.d Logbook**

A field logbook was also carried and used to note *Ad Libitum* observations, party composition and location, subject and time of focal observations.

#### **2.4.2.e Photography**

There were few opportunities for photography because of data collection and mothers and infants were rarely close enough to photograph. Photographic subjects were usually adult male chimpanzees. Despite very low light conditions the use of a flash-gun at any time would clearly have been inappropriate. This did however mean that the poor light levels within the forest made photography fairly impractical even with a very fast film speed. I used Fujii Provia 1600 ASA colour slide film supplemented with Fujii 400 ASA colour slide film. I used a Canon EOS 500N camera with two lenses: a Canon Zoom EF 75-300mm 1:4-5.6 II Lens and a Canon Wide Angle EF 28-80mm 1:3.5-5.6 IV Lens.

### 2.4.3 Sampling Methods

The focal animal sampling method was used to record behaviour (Altmann, 1974).

This requires that:

- All instances of specified behaviours are recorded for one individual, or a pre-determined number of individuals.
- Behaviours are recorded for a specified period of time and the time that the animal was out of view is noted.

It is important to note here the difference between sampling and recording rules. The sampling rule determines the target of the observation, whilst the recording rule determines the technique used to record behaviour. Hence, it is possible to use different recording rules simultaneously within the focal animal sample. This developmental study targeted particular individuals, focussing observation on infants, juveniles and mothers. Other sampling techniques, such as scan sampling, will provide data representing a broader range of subjects, which may be useful to examine ecological or social factors such as diurnal or seasonal changes across groups of individuals but it is limited in its power to examine age-related differences in behaviour. Clearly, for a developmental study focal animal sampling provided the best sampling method.

#### 2.4.3.a Focal animal samples

Within a focal sample period mother-offspring pairs were observed (either mother-infant or mother-juvenile). For one member of the pair behaviour was recorded continuously and instantaneously but for the other individual in the pair, behaviour

behaviour was only recorded instantaneously. For clarity, these individuals will be distinguished and referred to in the future as the 'principal focal animal' (behaviour recorded continuously and instantaneously) and the 'subsidiary focal animal' (behaviour recorded instantaneously).

The focal sample period was 20 minutes. Preliminary data collection during the pilot study had indicated that for mother-offspring pairs this shorter focal period was appropriate. There were three main advantages to a short sample period:

- It increased the likelihood that a larger number of individuals would be sampled each day (this was important to the sampling regime, see section 2.4.3.d).
- If longer focal periods were attempted there was a proportionally higher incidence of losing the subjects within the sample period because once a mother climbed down from a fruiting tree she was easily lost (see section 2.4.1.c).
- If subjects were lost within the sample period, a shorter sample period meant that the time wasted was minimised.

#### **2.4.3.b Continuous data collection**

Data were collected continuously on the principal focal animal using a hand-held computer (see section 2.4.2.a). This meant that all instances of the principal focal subject's behaviour were recorded during 20 minute focal sample periods, allowing accurate measurement of frequencies, duration and sequences of behaviour. The behavioural categories recorded are summarised in section 2.4.5.b. These reflect the

study's focus on feeding behaviour, although other behaviours, e.g. social behaviours, were also recorded.

#### **2.4.3.c Instantaneous data collection**

In addition to continuous data collection within the focal sample period, data were also collected at fixed intervals using the instantaneous sampling technique (Altmann, 1974). At the end of a pre-determined (usually short) period of time behaviour is sampled at that instant in time, or 'sample point'. This technique is most regularly used in conjunction with scan sampling, where a group of subjects is quickly scanned at fixed time intervals and an observation recorded for each individual at that instant. If the bout length of a behaviour is long relative to the interval time between samples, this technique is also frequently used sample the duration of behaviour.

In this study in addition to the continuous record of behaviour that was made on the principal focal subject, data were also collected instantaneously on both the principal and subsidiary focal subjects (i.e. both members of the mother-offspring pair) at 2 minute intervals. This fulfilled two objectives:

- To collect data on the proximity of mothers and their offspring.
- To collect data simultaneously on the activities of mothers and their offspring.

I collected continuous and instantaneous data on the principal focal subject and my field assistant was responsible for instantaneous data collection on the subsidiary

focal subject. For example, if my principal focal subject was the infant, then my field assistant observed the mother to collect data on her. When a 2 minute interval had elapsed both my field assistant and I were alerted to the sample point by the countdown timer on my field assistant's Timex Triathlon Ironman watch. In instances when I was further than 5 metres from my field assistant and could not hear the 'beep' from his watch, he would shout out to me to inform me of the sample point. I would then communicate the relevant information to my field assistant and he would record all the instantaneous data (for both the principal and subsidiary focal subjects) onto the checksheet.

#### **2.4.3.d Focal sampling regime**

In ideal conditions, focal animals should be selected on a random basis to remove possible bias in subject selection. It is possible to create a list, in which random permutations assign subjects to a particular order. For some studies this may be a workable solution. However early on, during the pilot study, this type of sampling regime was tested and rapidly abandoned because there were consistent problems with subject availability. The use of such a strict sampling schedule was not possible because of the considerable difficulties in locating mothers (see section 2.4.1.b). Nevertheless, attempts were made to limit the bias introduced by subject selection and increase the independence of consecutive observations, but this sampling regime centred on the objectives of the study. The focus of interest for this project is the development of behaviour and, in particular, pre-weaning foraging behaviour. Therefore, the following sampling objectives were identified:

- Objective (i): To obtain an equal number of focal samples on each subject in each month of data collection.

- Objective (ii) To maximise data on feeding bouts

Accordingly,

### Accomplishing objective (i)

This was attempted by dividing subjects according to how commonly they were observed. On this basis they were attributed a sampling priority (see Table 2.5). High priority subjects were always selected as focal subjects to be sampled, providing they had not been sampled in that week.

**Table 2.5:** The order of sampling priority for study subjects  
(1 = highest priority, 10 = lowest priority)

Priority	Mother	Infant	Juvenile
1	Ruhara	Rose	Grinta
2	Banura	Bety	Shida
3	Ruda	Rachel	Bob
4	Kutu	Kato	
5	Zana	Zalu	
6	Nambi	Nora	Musa
7	Zimba	Zig	Gonza
8	Kigere		Kidogo
9	Kalema	Bahati	
10	Kwera	Kwezi	

If a subject was found that had already been sampled that week then another subject was located. If there was no success in locating another subject by 11.00am<sup>6</sup>

<sup>6</sup> Previous experience on the pilot study had shown that after 11am the likelihood of finding another female with dependent offspring was extremely small. Hence, this was the 'cut-off' time decided upon. It should be noted that this rule did not prevent a subsequent search for other subjects in the afternoon.

then the original (already sampled) subject was sampled again but only in accordance with the rules outlined below (the same subject could not be continuously sampled more than once in one hour nor more than twice in one day). There were definite seasonal effects on the probability of finding some subjects. During some periods certain mothers were not sighted (by anyone, including other students and field assistants) for several weeks. In some instances this was attributed to very low food availability but at other times it was difficult to find a particular reason for the individual's extended absence. It is likely that the females designated high-priority constitute 'peripheral' females (Wrangham *et al.*, 1996).

After every focal was completed, a record was made. The aim was to balance this number of focal observations over a period of two weeks, and if this was not possible, then over a period of four weeks.

#### **Accomplishing objective (ii)**

If there were a number of potential subjects in view and available, and when the rules outlined in objective (i) had been met, the sampling decision was based on this objective. In this case, the mother-offspring pair that was feeding was selected as the focal animal.

At the end of the first focal sample on a subject recording was usually switched directly from this subject to the other member of the mother-offspring pair. For example, if a mother was the principal focal animal (behaviour recorded continuously and instantaneously) then when this focal terminated her infant became the principal focal subject and the mother became the subsidiary focal subject

(behaviour recorded only instantaneously). This meant that it was possible for two instantaneous focal samples and one continuous focal sample to exist for each subject within one hour. However, the following two rules were strictly adhered to:

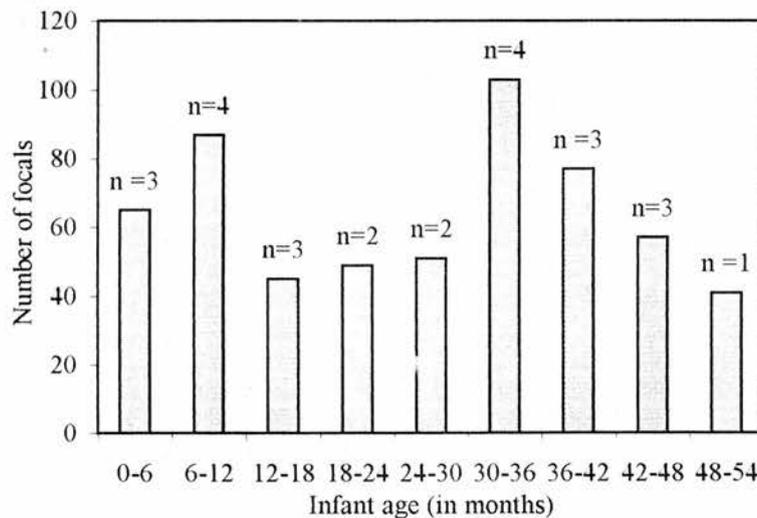
- No subject was sampled as the principal focal subject (behaviour recorded continuously) more than once in one hour.
- No subject was sampled as the principal focal subject (behaviour recorded continuously) more than twice in one day.

The sampling regime that resulted did not eliminate possible bias from the effects of diurnal variation, subject selection and consecutive observations. However,

- Within the possibilities and limitations imposed by subject availability, the regime reduced these effects as much as possible.
- None of these effects are integral to this study on development. Foraging behaviour is the focus of this project and interests do not extend to the diurnal variation in mother-infant activity, proximity or interaction.
- The possible bias introduced by sampling the same subject (up to a maximum of) twice in the same day was countered by the fact that the total number of samples for that subject would be balanced throughout each 4 week block of development.
- These biases would not be introduced in the comparison of different mother-infant or mother-juvenile pairs. The slow and extended period of development in chimpanzees accorded and justified a cross-sectional approach.

Despite the attempts to evenly sample subjects there was some variation in the number of focal samples per individual (see Appendix 3 for the total number of focal samples for each individual). Particular mothers (e.g. BN, RH) were more difficult to find and less habituated than others and as a result these mothers and their offspring tended to be under-sampled. Even in studies on well habituated chimpanzees researchers have been unable to equalise their observation time across mother-infant pairs (e.g. at Tai: see Boesch & Boesch, in press), presumably for the same reasons. However, when subjects were grouped according to the 6 month age block that they lie in, the sampling of infants is more balanced (see Figure 2.2).

**Figure 2.2:** Number of principal and subsidiary focal samples on infants grouped by age, n = number of infants within age block (each infant is represented in more than one age-block)



### 2.4.4 Statistical Methods

For all graphs, mean data values were calculated over each consecutive 6 month age period and plotted against age both because of the small number of subjects available for study and because this allowed the full pattern of development to be charted. However, for statistical analyses in age-trends data, were *not* pooled in this manner. Subjects were divided into four age categories: young infants, older infants, juveniles, and mothers and tested across these groups (see Table 2.6). This ensured statistical independence.

**Table 2.6:** Age categories used for statistical analysis

Age category	Description	Sample size
Young infants	Infants with a mean age of under 2.5 years during the study (infant stage 1)	N = 5
Older infants	Infants with a mean age of above 2.5 years during the study (infant stage 2)	N = 4
Juveniles	Juvenile stage 1	N = 4
Mothers	Adult females with dependent offspring	N = 9

All statistical tests were non-parametric and two-tailed. Sample sizes were close to the minimum requirements but fell within the prerequisites (Fowler & Cohen, 1992). In cases where  $df = 1$ , the  $\chi^2$  was corrected by the Yates' Correction for Continuity.

It is evident from the literature that large individual differences exist between mother-offspring pairs of chimpanzees (e.g. Plooij, 1984; Van de Rijt-Plooij & Plooij, 1987). These large individual differences and the small number of subjects available for study meant that extreme differences between age classes were required before tests produced statistical significance. Further, there was a potential source of bias in the sex ratio of subjects. The male-female ratio of young infants was 1:4., for older infants 3:1 and for juveniles 3:1 (see Table 2.2). It was possible that this difference in sex ratio, particularly between young and older infants, could have biased results.

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## 2.4.5 Behavioural Categories

### 2.4.5.a Configuring the Observer package to record behaviour

The behavioural codes were programmed into the Configuration Designer of the Observer software package. The sampling method (one-animal focal sampling), independent variables (subject two letter code and forest grid location), and duration for each focal (20 minutes elapsed time) were set and determined the entire configuration. Observer uses 'classes' to group behaviours, each class is a set of mutually exclusive behaviours, or 'behavioural elements', which can be either states or events. This means that within one class of behaviour, only one behavioural state can be active at one time. It is possible to associate a maximum of two 'modifiers' to each behavioural element. My modifiers included social partners, (e.g. playing or grooming partners) and positions of travelling behaviour (e.g. dorsal, ventral, etc.).

The manner in which behavioural elements and modifiers were coded and assigned to keys on the hand-held computer was crucial because it determined how quickly and efficiently behaviours could be recorded. Since behaviours had to be keyed into the hand-held computer 'blind' by touch-typing whilst looking through binoculars, their assignment had to be easy to memorise and conveniently located. For example, behavioural elements that were likely to occur in sequence were coded so that they were located near each other on the 'qwerty' hand-held computer keyboard. No behaviours were assigned to keys in the middle of the keyboard because they were too difficult to reach with assured accuracy. The choice of behavioural classes were also relevant to how efficiently behaviours were recorded,

because if designed carefully the number of modifier keys could be minimised. I chose to have three behavioural classes. One class contained all the subject's behavioural activities, another contained mother-offspring proximity distances and a final class contained all food species and parts. Thus, when a focal was started it was necessary to enter two independent variables (subject and grid location) and three classes information.

- Firstly, the three letter code for the species (usually a tree species) and a two letter code for the plant part that the subject was in or near (could potentially ingest) had to be entered. All activity (feeding) after this was assumed to have occurred on this species, and if the subject changed tree or moved to another potential food species then this code was immediately changed. The advantage of this scheme was that only 'start feeding' and 'bites' had to be coded, without having to enter a three letter plant species code and two letter plant part code every time the animal ingested a food item.
- Secondly, the physical distance that the subject was away from its mother/its offspring.
- Thirdly, the behavioural activity it was engaged in.

Once these three types of information had been inputted, Observer would start to run the event recorder and the focal began.

### 2.4.5.b Behavioural definitions

- Feeding:** Subject harvested, processed or in any other way manipulated an item in the hand or mouth, placed the item within the mouth, chewed and subsequently ingested the item. This included any orientation or movement if the subject still had the item within the hand or mouth and subsequently ingested the item. Terminated when the subject finished chewing the item, or when the subject started to harvest, process or manipulate a different item. Included **wadging**, where the subject had the item within the mouth for an extended period of time during which the lower lip was used to press the ball of food against the lower gums and teeth (to extract juice) and this food ball, or 'wadge' was subsequently spat out.
- This behavioural category had the highest priority and was recorded if the subject was feeding and concurrently engaged in another activity.*
- Playing with food:** Subject manipulated an item in the hand or mouth but the food item was not chewed when wholly within the mouth, nor was it ingested. Could involve several placements within the mouth if no chewing occurred.
- Playing with non-food:** Subject manipulated any physical object in the hand or mouth other than a potential food, e.g. a branch, a twig.
- Grooming:** One animal manipulated another animal's pelage involving the parting and examination of hair with periodic pauses during which time tiny items were

delicately removed.

**Social play:** The subject was playing with another individual and it involved one of the following elements: (1) Chasing play: subject was chasing, or being chased, by another individual, no physical contact was made. (2) ‘ Rough-and-tumble’ play: subject was playing with another individual in a highly physical and vigorous manner, included: embracing, thumping, wrestling, grappling, hitting, biting, or rolling on the ground. (3) Contact play: subject was playing in a more relaxed manner: included: mild stimulation: tickling, nibbling, and nuzzling.

**Solitary play:** The subject was playing alone, involved in some type of acrobatic or locomotory play. This involved one of the following elements: (1) Acrobatic play: subject was hanging or swinging by one or two limbs in branches. (2) Locomotory play: subject was ‘play walking’: back is rounded, stamping of feet, exaggerated swagger (Goodall, 1986).

**Moving:** Any locomotion that was not defined above included: independent walking, climbing and moving through trees and on the ground.

**Resting:** The subject was motionless and engaged in an activity not defined above.

#### 2.4.5.c Food type definitions

**Difficult foods:** Any food item that infants had difficulty harvesting and/or processing. This included embedded food items that were:

- Large and/or had hard shells that needed physical strength to open.
- Required dextrous manipulation and/or co-ordination to separate the edible portion efficiently.

**Easy foods:** Any food item that was easy for infants to harvest and/or process, this included:

- Small items without shells/with soft-shells.
  - Other small discrete items that were harvested and processed in one hand-to-mouth action.
-

# CHAPTER 3: SOCIAL & BEHAVIOURAL DEVELOPMENT

It is equally important to learn how chimpanzees become 'enculturated' into chimpanzee society

*Bard, 1993*

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## **3.1 Introduction**

The social environment in which a young primate matures will have profound consequences for its future development. The initial and principal relationship in the life of the immature primate is with its mother, who in the early stages of development provides all nutritional, protection and transport needs of the young infant. The mother also takes a primary role in the infant's socialisation; deprivation studies demonstrated all too clearly the damaging effects that separating an infant from its mother has on normal social development (e.g. Harlow & Harlow, 1965, 1969). Stressful conditions early in life have long term effects for chimpanzees that

include differences in temperament and deficits in cognitive performance (Bard & Gardner, 1996). Clearly, early social experiences will be important determinants of learning opportunities and behavioural development.

There are substantial field data on the mother-infant relationship in wild monkeys (e.g. for baboons: Altmann, 1980; Nicholson & Demment, 1982; for rhesus monkeys: Berman, 1982a,b; for vervet monkeys: Lee, 1986). Studies of mother-infant relations in the great apes are commonly undertaken in captive environments (e.g. Hoff *et al.*, 1981; Horvat *et al.*, 1980; Mellinger, 1983a,b; Miller & Nadler, 1981). There are less data on the development of wild apes (for mountain gorillas see: Fossey, 1979; Watts, 1985 and for orang-utans see: Bard, 1990, 1995). The small number of subjects available for study (the product of extended periods of development and long inter-birth intervals) discourages fieldworkers and observation conditions are often poor.

Long-term work at Gombe by Goodall has produced a complete description of the particularly intimate and long-lasting bond between chimpanzee mothers and their offspring in its longitudinal entirety (Goodall, 1967, 1986), particularly impressive considering that youngsters commonly remain with their mother for 9-12 years. Pusey (1983) illustrates the importance of the mother-juvenile relationship to healthy development by describing the adverse effects of the mother's death to young chimpanzees soon after being weaned. Two out of four juveniles orphaned before they were 6 years old showed aberrant, or at least inept, social behaviour for their age; another orphaned female juvenile failed to advance normally to sexual maturity (Goodall, 1983: cited in Pusey, 1983). Indeed, the juvenile life-stage is

commonly regarded as a hazardous time, since juveniles have not fully acquired the adult skills required to deal with all the social and ecological hazards within the environment (Janson & van Schaik, 1993). Mothers doubtless support juveniles in their acquisition of these adult skills (Goodall, 1986; Pusey, 1983) and, when orphaned, juvenile chimpanzees seek replacement close adult associates, who are commonly siblings (Nishida *et al.*, 1990; Pusey, 1983).

Pusey's (1983, 1990) detailed longitudinal data on juvenile and adolescent chimpanzees at Gombe National Park showed that only a considerable time after weaning (at about 9-10 years of age) was there an abrupt decline in the time that mother and offspring spent together (similarly, at Mahale: Hayaki 1988). Further, Pusey (1983) showed that these changes were not related to food shortage: she could not attribute the decrease in association to any increase in feeding competition occurring concomitant to offspring growth. In fact, the companionship of older offspring may be advantageous to mothers. Pusey (1983) suggests they might find food patches that their mother missed, assist in excluding other competing females, reduce time-budget constraints by grooming their mother, playing with younger siblings and in the event of their mother dying they would be available to adopt their younger brother or sister. Therefore, the decreasing attachment between mother and offspring is not the result of increasing rejection by the mother; rather, it appears that separation occurs as their individual reproductive strategies begin to diverge (Pusey, 1990, 1983).

In contrast to the quantitative data on the later developmental stages of juvenility and adolescence (Hayaki, 1985a,b; Hayaki, 1988; Pusey, 1979, 1980, 1983, 1990),

the description of the period of infancy in chimpanzees has tended to be qualitative in nature (e.g. see Clark, 1977; Goodall, 1967, 1968, 1971, 1986). Although Plooij (1984) and Van de Rijt-Plooij & Plooij (1987) provide quantitative data on behavioural development of Gombe chimpanzees, this is restricted to the first two years of life. More recently Brent *et al.* (1997) have analysed long-term data collected over a period of 30 years from Gombe, (involving 17 infants aged 6-24 months) to investigate the influence of siblings on social interactions of infants. At Mahale, quantitative studies on chimpanzee infants have concerned mother-infant grooming (Nishida, 1988), sex differences in ant eating and daytime nest making (Hiraiwa-Hasegawa, 1989), and alloparental behaviour (Nishida, 1983). However, there remains a lack of quantitative cross-sectional data on the basic social experiences of wild chimpanzees during the period of infancy.

Chimpanzee mothers with young offspring are the shyest of individuals, spending long periods feeding and moving alone (see section 2.1). In comparison to the temporary sub-groups that characterise the fission-fusion chimpanzee social organisation, a young chimpanzee exists in stable social unit, with mothers and their offspring forming the most fixed and stable sub-group over time (Goodall, 1967). The infant matures in this essentially constant (over several years) social unit. This long term social cohesion and permanency of attachment with its mother means that during its period of dependency an infant's predominate social companions will be its mother and, unless the infant was the first born, an older juvenile sibling (Goodall, 1986). Thus, the mother alone represents the major foraging model

available to a young chimpanzee<sup>7</sup>. Although the amount of investment and care a mother provides will vary as her infant matures and the dynamics of the mother-infant relationship will change over time (Trivers, 1974), the strong attachment between chimpanzee mothers and their offspring endures into adulthood (Goodall, 1986).

This chapter is concerned with both developmental changes in the nature of the mother-infant relationship, and the developmental changes in the behavioural budget of infants and juveniles. The first section of this chapter charts the modifications of spatial proximity between mother and offspring. This will determine the extent to which the mother is available to the infant as a foraging model: the opportunities that the infant will have for interaction and observation of its mother while she is feeding. The fine details of an infant's transition to social independence have not been investigated here. Singularly, the interest is in behaviours that may be important to foraging success and the increasing exploratory nature of the developing infant, its ability to interact with its expanding physical and social environment. The second section of this chapter provides a general overview and description of the infant's behavioural development throughout the pre-weaning years and in comparison to their juvenile siblings and mothers. Finally, the third and

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<sup>7</sup> An exception to this concerns infant chimpanzees living in Bossou, Guinea; these infants regularly observe and attend to adult females other than their mother (Inoue-Nakamura & Matsusawa, 1997). Hence, here there is the potential for other adult females to act as foraging models to young chimpanzees. However, this is in all likelihood specific to this community because of the unusually high level of interaction and affinity between females at Bossou (Sugiyama & Koman, 1979; Sugiyama, 1988).

fourth sections of this chapter investigate in more detail two positive forms of social interaction between mothers and their infants: grooming and play.

### **3.1.1 Proximity to mother**

The importance of early mother-infant contact is central to a young primate's normal development. Early work illustrated that physical contact between mother and infant is crucial to the healthy development of infant monkeys and apes (e.g. Mason *et al.*, 1968). Changes in the general pattern of infant development will be reflected by changes in the time infants spend at varying distances from their mother. Measurements of spatial proximity will be used to provide an index of the changes in the mother-infant relationship, as the offspring becomes increasingly independent. It is predicted that mothers provide their infants close physical proximity early in development but this is modified as the infant matures and extends the area it explores independently. Accordingly, specific predictions are:

- Younger infants will spend greater amounts of time in physical contact with their mother than older infants.
- Juveniles will spend greater amounts of time beyond arm's reach of their mother than infants.

Proximity measures alone will not establish the relative roles of mothers and infants in the maintenance of spatial relations. Researchers usually monitor these changes by applying Hinde and colleagues' method of observing the proportion of 'approaches' and 'leaves' over a pre-determined distance and recording the degree

to which either the mother or the infant was responsible for these changes (Hinde & Atkinson, 1970; Hinde & Spencer-Booth, 1967). However, this study was not concerned with the division of the responsibility for changes in proximity. The focus here is on quantitatively charting the dynamics of mother-infant spatial association across age in order to examine the possible value of physical closeness for learning at different stages of infant development.

### **3.1.2 Behavioural development**

Chimpanzee infants are nutritionally dependent on their mothers for a prolonged period of time and their passage to the independence is slow. They suffer high rates of infant mortality, pre-weaning mortality is 40% at Gombe (Goodall, 1986) and 53% at Mahale (Nishida *et al.*, 1990). An infant needs to reach a weight approximately four times its birth weight if it is to survive being weaned and grow once nutritionally independent (Lee *et al.*, 1991). However, reaching this optimum weight is energetically costly to the mother and delays her reproduction (Trivers, 1974; see Chapter 1). The infant's successful transition to independence critically depends on the infant's developing ability to feed itself. Chimpanzee infants start to eat solid foods at approximately 6 months of age although they continue to suckle for 4-5 years after birth (Clark, 1977; Hiraiwa-Hasegawa, 1990a). Throughout this period the energetic demands of infants change, as they progressively become able to feed independently.

The development of infant behaviour will be examined by comparing quantitative measures of four key behaviours (resting, feeding, socialising and moving). Following Wasser & Wasser (1995) the objective will be to chart the rate of behavioural change. Chapter 4 focuses in more detail on the infant's transition to independent feeding. Here, the aim is to provide a general overview of infant maturation. Descriptive statistics will be used to compare developmental patterns in the four major behavioural activities across the pre-weaning years to investigate the age-related change in behavioural activity as infants become increasingly independent.

The time allocated to different activities will also be investigated across the different age-groups by comparing infants' time budgets to those of their older siblings and their mothers. Infant dependency in terms of transport and nutritional requirements should allow them to spend more time resting and engaged in social behaviours than their siblings and mothers. Hence, the following specific predictions can be investigated:

- Infants spend more time engaged in social activities (playing and grooming) than their mothers and juveniles.
- Infants spend less time feeding than their mothers and juveniles.
- Infants spend more time resting than their mothers and juveniles.

### 3.1.3 Grooming

Two functions of social grooming are recognised. At least in part, this activity has important health benefits: functioning to remove or control external parasites and clean the skin (Hutchins & Barash, 1976). In chimpanzees, four such ectoparasites have been identified: two genera of lice, *Pediculus* and *Phthirus*, and two genera of tick, *Pangorillalges* and *Sacroptes* (Myers & Kuntz, 1972). In as much as allogrooming is focused on body parts that are not easily accessible for the groomee itself to reach, the health benefits of grooming in controlling parasite load are widely recognised (e.g. Goodall, 1986). A second, vital role of grooming is that it serves to establish, regulate and maintain social relationships (e.g. Simpson, 1973). At the same time, expression of this highly affiliative behaviour is considered evidence for social bonds existing between two individuals. It is expected that at different stages of development differences in the attachment (in terms of dependence) between mother and offspring and the offspring's body size, social and grooming experience will result in variations in the patterns of grooming observed between them. It is predicted that time is required to develop grooming skills, specifically:

- Older infants groom more than young infants.
- Juveniles groom more than infants.
- Mothers groom their infant more than they groom their juvenile offspring.
- Mothers groom their infant more than they receive grooming from their infant.
- Juveniles groom their mother more than infants groom their mother.

### 3.1.4 Play

Play is thought to prepare an immature primate for adulthood, providing it the opportunity to practise and perform behaviours in safe situations, outside circumstances where normally the same behaviours are used to enhance reproductive fitness (Fagan, 1993). It is a spontaneous, often inventive, behaviour that is thought to be important in providing exercise and physical training, and perhaps also the normal development of motor ability, social co-operation, communication, cognitive skills, establishing dominance rank, and promoting inter-individual affiliation and bonding (Baldwin & Baldwin, 1977). Social and solitary play characterises all primate species behaviour (Fagan, 1993) and will be investigated in this chapter. Object play may be important as part of early attempts at feeding behaviour and consequently is reserved for investigation in Chapter 5.

The frequency of play decreases dramatically, or may even be suspended completely, in times of stress (Fagan, 1981); for example, in times of food shortage juvenile vervet monkeys play at only very low levels (Lee, 1986). It is claimed that play has reproductive benefits (Fagan, 1993), although such claims remain debatable (Smith, 1992). Whether or not play has benefits to infants, it certainly has risks. It is physically demanding and thus costly in terms of time and energy expenditure but, perhaps more importantly, there is the additional danger of injury (Fagan, 1981). The predominant risk, at least for young chimpanzees, appears to be injuries sustained as a result of falling from trees and branches (Goodall, 1986; personal observation on Ngamba Island). Baldwin (1986) even suggested that the dangers of falling have been a powerful selection pressure in the evolution of play in arboreal

primates. Communicative signals have evolved functions in requesting, initiating and maintaining play behaviour and social communication during play is complex (Altmann, 1988). The play-face of chimpanzees is perhaps one of the most obvious and best-known play signals in primates (for a description see Goodall, 1986).

It is predicted that the physical benefits of play will be more important early in development and the social benefits will be more important as offspring grow older. Accordingly, specific predictions are:

- Infants play alone more often than they play with others.
  - Older infants and juveniles engage in more social play than young infants.
-

## 3.2 Methods

### 3.2.1 Definitions

In order to chart the dynamics of mother-infant spatial relations at different stages of infant development and increasing independence a number of distance categories were used. Van de Rijt-Plooij & Plooij (1987) made an important differentiation, they distinguished between those times that the mother supported the infant's body weight and the times that the infant independently supported its own weight. I have followed this concept. For example, under these definitions if an infant was playing with its mother which involved physical contact but the infant's body weight was not supported by its mother then this was scored as within arm's reach (see definitions below).

<b>Proximity</b>	<b>Definition</b>
Ventral contact	The offspring is in the ventral position (on the belly of) its mother so that most of the offspring's body is below or in front of the mother and is encircled by her arms and legs.
Dorsal contact	The offspring is in the dorsal position (on the back of) its mother so most of the offspring's body is above or behind the mother.
Other physical contact	The offspring is in any other position of physical contact with its mother so that its mother supports most of its body weight.

For example, the offspring may be on its mother's head, upper/lower arms, or upper/lower legs.

Within arm's reach	The offspring is within arm's reach of its mother so that if the mother extended her arm she could touch her offspring. This distance is approximately one metre.
Arm's reach – 3 metres	The offspring is out of arm's reach of its mother but within 3 metres.
3 - 5 metres	The offspring is further than 3 metres from its mother but within 5 metres.
5 – 10 metres	The offspring is further than 5 metres from its mother but within 10 metres.
10 – 20 metres	The offspring is further than 10 metres from its mother but within 20 metres.
More than 20 metres <sup>8</sup>	The offspring is greater than 20 metres from its mother.

Due to the difficult observation conditions it was rarely possible to observe that an infant was suckling or spending time on its mother's nipple. Initially, I defined 'suckling position' as not only those times that the mother's nipple was actually observed to be within the infant's mouth, but also those times when the infant was in such a position that suckling on the mother's nipple was likely. However, even with this refined definition it was rare that conditions permitted such clear observations to

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<sup>8</sup> Given the constraints of thick vegetation, this was regarded as the maximum distance over which mother and offspring would be visible. For this reason proximity distances did not exceed this value.

be made so I abandoned this activity category. In any case, empirical studies have shown that the time an infant spends on the nipple is not an entirely reliable measure of milk transfer (e.g. Mendl & Paul, 1989). Infants probably spend time on their mother's nipple in a variety of contexts that are non-nutritional in nature. For example, the infant may spend time on the nipple to be comforted: when both mother and infant are relaxed, resting or grooming, or in times of distress the infant may return to the nipple to be calmed. Consequently, time spent on the mother's nipple did not enter these analyses. For all behavioural descriptions see section 2.4.5.b.

For the subjects being studied (mothers, infants and juveniles) it was rare that the focal animal simultaneously groomed an individual whilst it was itself being groomed. In circumstances where such simultaneous and reciprocal grooming did occur, only bouts of grooming performed by the principal focal subject were recorded. A Similarity Index was used to investigate the balance of grooming between mother and offspring:  $G_A/G_{AB}$ , where  $G_A$  = % time that individual A grooms individual B and  $G_{AB}$  = % time that individual A grooms + % time that individual B grooms individual A.

### **3.2.2 Data collection**

Rain increases the probability that mother and infant are in contact in baboons, most likely providing warmth for mother and infant (Nicholson & Demment, 1982). This was also likely to influence proximity tendencies in chimpanzee mothers and

infants. Accordingly for this reason and because of the use of a hand-held computer observation had to be suspended during periods of rain.

### **3.2.3 Data analysis**

Data on mother-infant contact and distance measures, and behavioural activities were collected during 20 minute principal and subsidiary focal animal samples. Using these data extracted from instantaneous point sampling, the proportion for each individual subject was calculated for each 6 month age block they fell within. Subject means for each age block were then calculated and plotted against age for all graphs. In the case of the four major behavioural activities (feeding, resting, socialising and moving) data were fitted with one of five possible series of regressions. The best statistical fit was selected from linear, logarithmic, polynomial, power or exponential functions, to produce four behavioural descriptive developmental functions, as did Wasser & Wasser (1995) for baboons. Although parametric statistics were thought inappropriate for this study (see section 2.4.4), the only available method to plot such functions involves the use of parametric statistics. However, their use was warranted in this one case because these statistics were only being used descriptively, they were not been used for actual statistical comparisons.

All statistical tests were non-parametric and two-tailed. They were applied across the four age categories: young infants (n=5), older infants (n=4), juveniles n=4), and mothers (n=9). In cases where  $df = 1$ , the  $\chi^2$  was corrected by the Yates' Correction for Continuity.

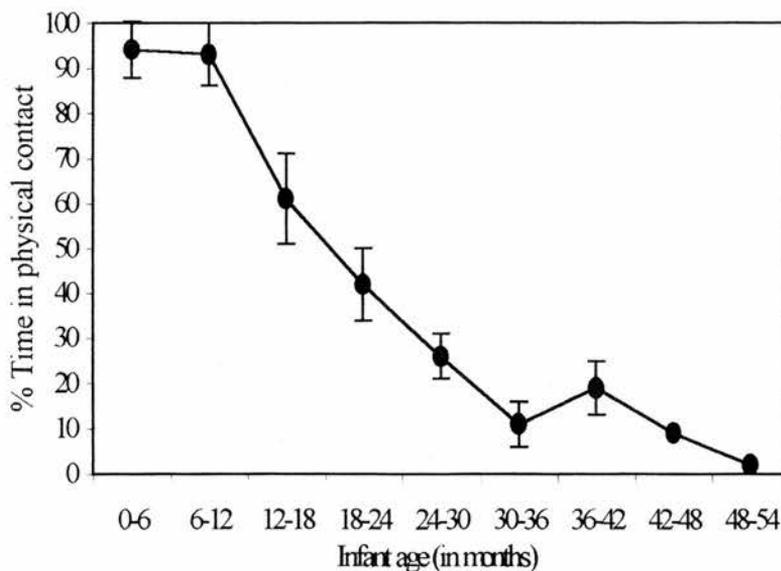
### 3.3 Results

Juveniles were observed within a 20m distance of their mother at some time during all (100%) focal observations. Hence, juveniles were observed to constantly associate with their mothers.

#### 3.3.1 Mother-infant proximity

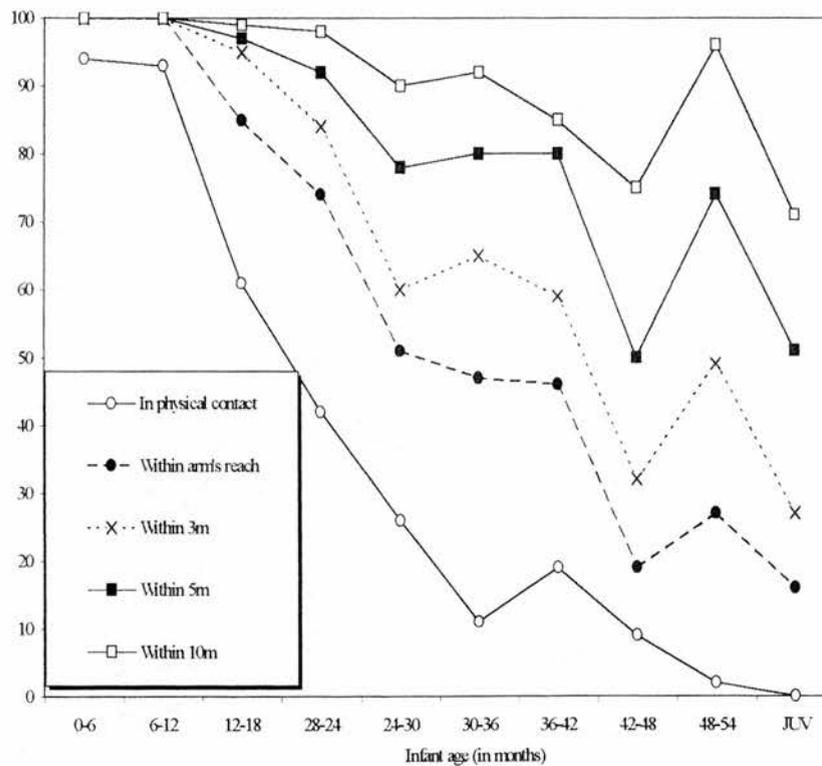
Post-weaned juvenile chimpanzees did not spend any time in physical contact with their mother (as definition, see section 3.2.1). Infants in their first year rarely broke physical contact with their mother. The mean time that infants spent having their body weight supported by their mother was 94% (SE=6) of the time (see Figure 3.1).

**Figure 3.1:** The proportion of time that infants spent in physical contact with their mothers. Data are pooled over 6 month age blocks and error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ).



In their second year chimpanzees started to move apart from their mother, and spent a greater amount, 48% (SE=7), of their time out of contact with their mother (see Figure 3.1). There was a highly significant difference in the time spent in physical contact with the mother between young and older infants (Young infants mean = 74 SE = 11.4, older infants mean = 17 SE = 2.6, Chi-squared test,  $\chi^2=6.05$ ,  $p<0.02$ ). Although infants in their second year increasingly spent more time out of contact with their mother, a substantial amount of this time was within arm's reach of her (Figure 3.2).

**Figure 3.2:** The cumulative percentage time that infants and juveniles spend at varying distances from their mother. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles.



As infants matured they increasingly spent time at greater distances from their mother, so that by 24-30 months infants were spending an average of 50% of their

time out of arm's reach of their mothers. The return to spending an average of 25% of time within arm's reach in months 48-54 may represent a retreat towards the mother prior to final weaning. Similar shifts to closer degree of proximity have been referred to as 'regressions' and defined as "the temporary return during early development of behaviours which were shown in an even earlier developmental period" (p.55, Van de Rijt-Plooij & Plooij, 1987). However, it is also possible that this was due to sampling error since there was only one infant in this age block.

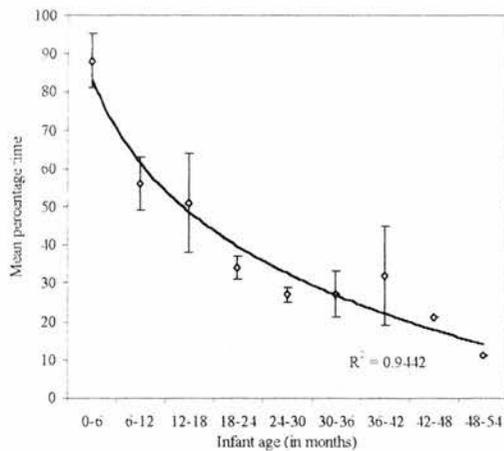
There were significant differences in shifts of proximity tendencies with age. When young infants, older infants and juveniles were compared, older infants and juveniles spent more time in the proximity categories 3-5 metres and > 5 metres than young infants (3-5m: young infants mean = 2 SE = 2, older infants mean = 19 SE = 1, juveniles mean = 24 SE = 5, Kruskal-Wallis test  $\chi^2=8.814$ ,  $p<0.01$ ; >5m: young infants mean = 1 SE = 1, older infants mean = 28 SE = 5, juveniles mean = 49 SE = 8, Kruskal-Wallis test  $\chi^2=10.326$ ,  $p<0.01$ ). Therefore the natural premise was supported: that older infants increasingly explore the space beyond their mother.

### **3.3.2 Behavioural development**

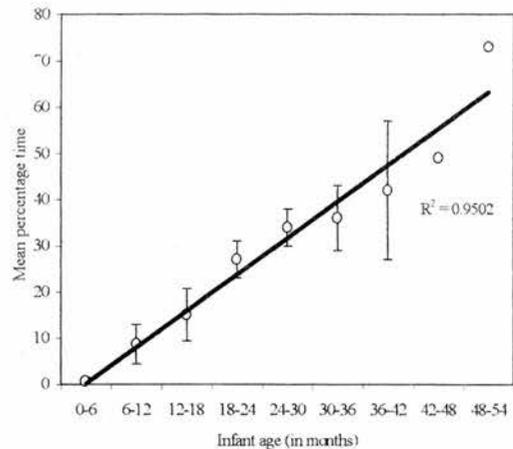
Trends in the behavioural development of individuals prior to weaning were examined (Figures 3.3, 3.4, 3.5 and 3.6). The descriptive statistic of functions was used to compare developmental rates across the pre-weaning years. The best (statistical) fit from a series of five possible regressions (linear, logarithmic, polynomial, power or exponential) was used to plot these developmental functions.

The mean time that infants spent resting decreased logarithmically with age, rapidly in the first six months from 88% (SE 7%) to 56% (SE =7%) in the second six months. Observation conditions did not allow time spent suckling to be distinguished from resting on the mother's ventral side, therefore it should be noted that this resting measure includes suckling time (but its change is not necessarily due to a change in suckling time). In the second year of life, the time infants spent resting decreased more slowly, levelling at 11% in the 48-54 month age block (see Figure 3.3). If this increase is calculated as a rate this is a decrease of 1.6% of time resting per month over these pre-weaning years.

**Figure 3.3:** Developmental changes in the proportion of time that infants spent resting. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ). The trendline fitted is logarithmic (r-squared value indicated on graph).



**Figure 3.4:** Developmental changes in the proportion of time that infants spent feeding independently. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ). The trendline fitted is linear (r-squared value indicated on graph).

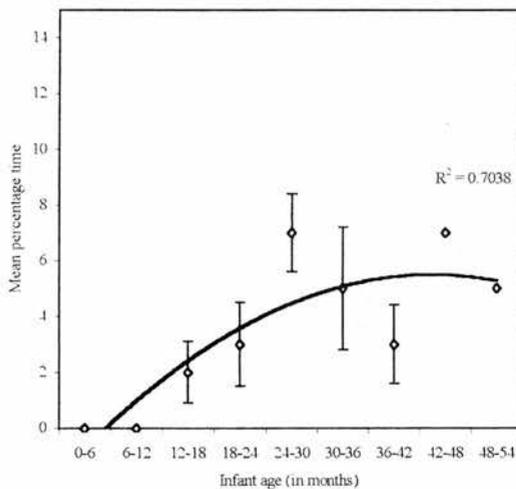


The mean time that infants fed independently increased linearly with age, from 9% (SE 4%) in the 6-12 month age block to 73% in the 48-54 month age block (see Figure 3.4). If this increase is calculated as a rate this is an increase of 1.3% of time

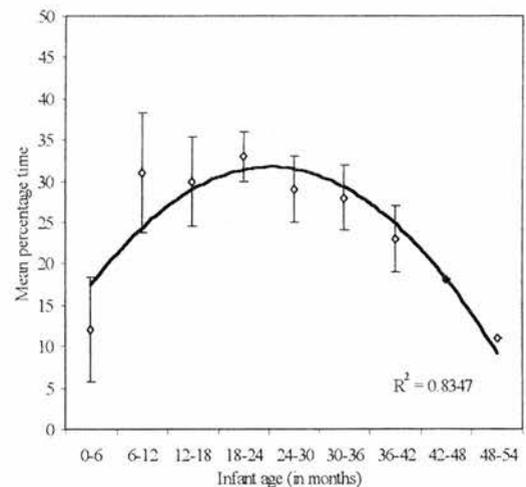
feeding per month, which almost equates to the corresponding decrease in resting time (see above).

Time spent moving increased with age but showed more variability (see Figure 3.5). Play and grooming were pooled into one category of social behaviour (these are investigated separately later in this chapter). Social behaviour showed the most variability across age, producing a curvilinear relationship with high values from 6 to 36 months (see Figure 3.6).

**Figure 3.5:** Developmental changes in the proportion of time that infants spent moving independently. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ). The trendline fitted is polynomial (r-squared value indicated on graph).

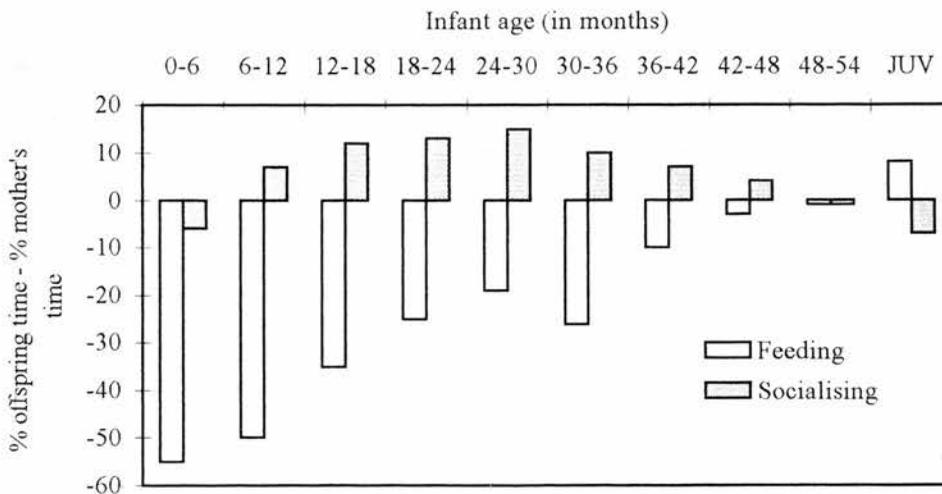


**Figure 3.6:** Developmental changes in the proportion of time that infants spent engaged in all social activities (grooming and playing). Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ). The trendline fitted is polynomial (r-squared value indicated on graph).



Infant activity budgets were then investigated in relation to their older offspring and mother's activity budgets. Infants spent less time socialising than their mothers in their first 6 months of life but the time they spent socialising gradually increased so that by 24-30 months infants spent 15% more time socialising than their mother (see Figure 3.7). This subsequently declined, so that by 48-54 months of age infants spent similar time socialising as their mother. Overall infants spent a significantly more time socialising than their mothers (Mann Whitney test  $U=12$ ,  $p<0.02$ ; see Figure 3.7) and their juvenile siblings (Mann Whitney test:  $U=3.5$ ,  $p<0.03$ ; see Figure 3.7). Juveniles spent significantly less time socialising than mothers (Mann Whitney test  $U=1$ ,  $p<0.05$ ; see Figure 3.7).

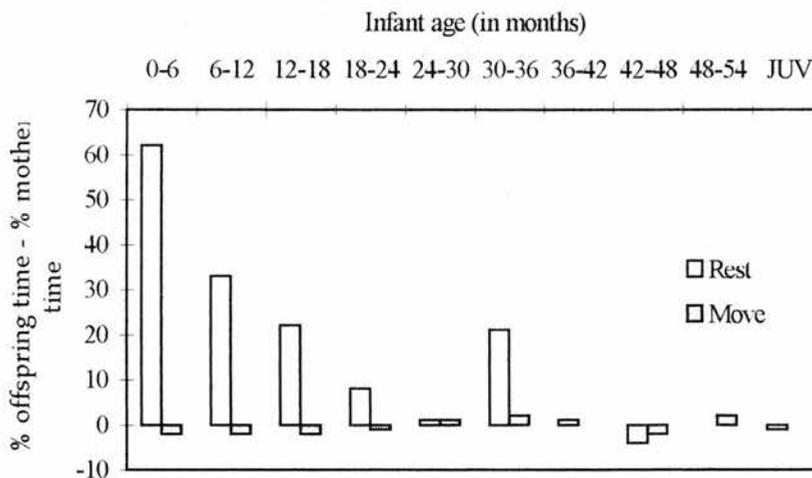
**Figure 3.7:** Infant and juvenile activity budget in relation to their mother's activity budget. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles. Then the proportion of time that offspring within these age blocks spent feeding and socialising was calculated and this was subtracted from the corresponding figure for mothers. Hence, bars below zero indicate that offspring were spending less time engaged in these behaviours than their mother and bars above zero indicate they were spending a greater amount of time engaged in these behaviours.



The reverse pattern was true of feeding. Infants spent less time feeding than their mothers (see Figure 3.7). This difference gradually decreased with age. By 48-54 months of age infants spent a similar amount of time feeding as their mother (see Figure 3.7). Overall infants spent significantly less time feeding than their mothers (Mann Whitney test:  $U=4$ ,  $p<0.001$ ; see Figure 3.7) and their juvenile siblings (Mann Whitney test:  $U=2$ ,  $p<0.015$ ; see Figure 3.7). Juveniles spent more time feeding than their mothers, but this was not a significant difference (Mann Whitney test  $U=3.5$ , *ns*; see Figure 3.7).

Differences in the time that infants, juveniles and mothers spent resting and moving were not so significant. Infants did spend significantly more time resting than their mothers (Mann Whitney test,  $p < 0.05$ ; see Figure 3.8). However, juveniles did not spend more time resting than mothers (Mann Whitney test:  $U=7$ , *ns*; see Figure 3.8). Infants, juveniles and mothers spent similar amounts of time moving (see Figure 3.8).

**Figure 3.8:** Infant and juvenile activity budget in relation to their mother's activity budget. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles. Then the proportion of time that offspring within these age blocks spent resting and moving was calculated and this was subtracted from the corresponding figure for mothers. Hence, bars below zero indicate that offspring were spending less time engaged in these behaviours than their mother and bars above zero indicate they were spending a greater amount of time engaged in these behaviours.



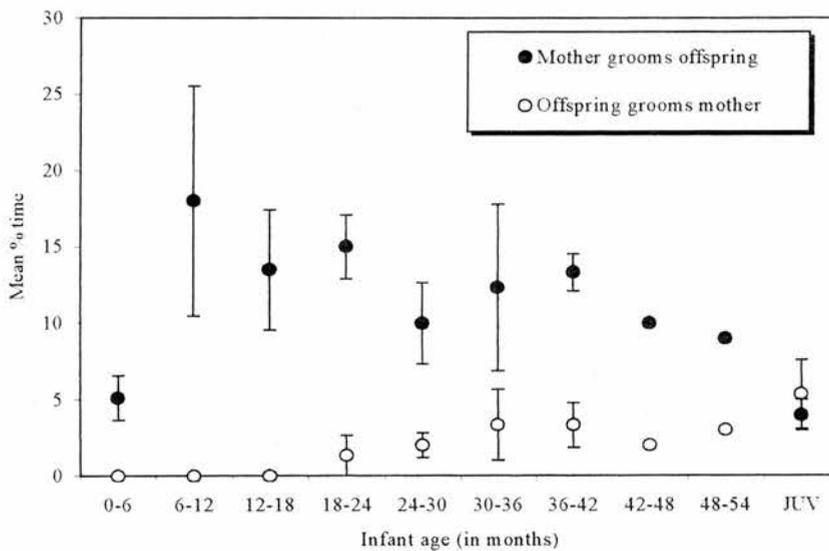
**Other variables**

There were various intervening variables that potentially could have been affecting results. Some variables, such as seasonal variations in food availability and the presence or absence of a sibling, were beyond the scope of this project to investigate. However, the effects of the infant's age and sex on its mother's feeding were investigated. Mothers with young infants might be expected to spend more time feeding than mothers with older infants. However, there was no significant difference in the time that mothers with young infants spent feeding in comparison to mothers with older infants (Mann Whitney test,  $U = 9.5$ , *ns*). Nor was there a significant difference in the time that mothers with daughters spend feeding compared to mothers with sons (Mann Whitney test  $U = 6.5$ , *ns*).

### 3.3.3 Grooming

The mean time that mothers spent grooming was 14% (SE=1). They directed most of their grooming towards their infants, spending a mean of 87% (SE=4) of their total grooming time grooming their infant. In comparison, mothers groomed their juvenile offspring for only 19% (SE=6) of their grooming time. Hence, mothers groomed their infants more than they groomed their juvenile offspring (Mann Whitney test  $U = 3$ ,  $p < 0.02$ ; see Figure 3.9).

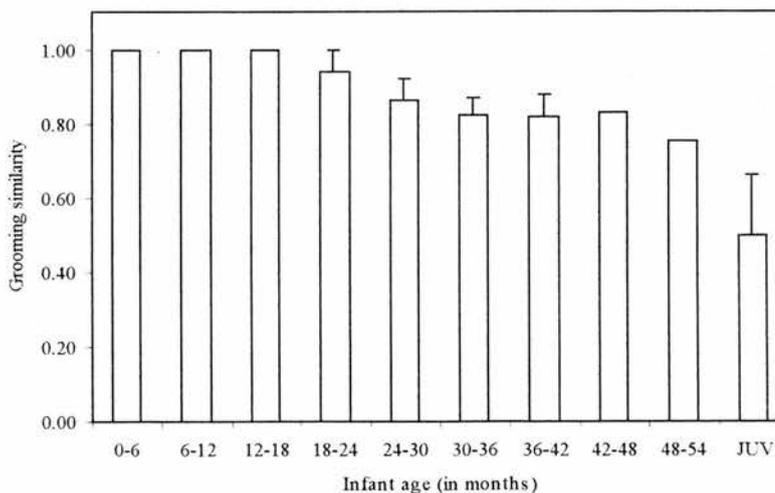
**Figure 3.9:** Mother-offspring grooming. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ).



There was a slight increase in the time that mothers groomed their infants after the infant's first six months of life but otherwise mothers groomed their offspring at similar levels throughout the period of infancy (see Figure 3.9). The time that older infants were groomed by their mothers was not significantly different from the time for younger infants (Mann Whitney test  $U = 7$ ,  $ns$ ).

Infants did not start to groom at all until they were at least 18 months old. Older infants groomed their mothers significantly more than younger infants (Mann Whitney test  $U=0$ ,  $p<0.02$ ) and juveniles groomed their mothers significantly more than infants groomed their mothers (Mann Whitney test  $U=4$ ,  $p<0.04$ ). Mothers groomed their infants significantly more than they received grooming from their infants (Wilcoxon signed-rank test  $Z = -2.666$ ,  $p<0.01$ ; see Figure 3.9). There was no such difference between the time that mothers groomed and received grooming from their juveniles (Wilcoxon signed-rank test  $Z = -1.214$  *ns*; see also Figure 3.9). This led to investigation of the similarity index, which is a measure of the balance of grooming between mother and offspring. In the first 18 months of an infant's life the index was 1.0, indicating that only the mother groomed the infant. The index gradually decreased throughout the infant's life to 0.75 in the infant's fourth year, indicating that the infant was now taking a more substantive role grooming its mother, although still not at a rate similar to the one at which she was grooming it.

**Figure 3.10:** Grooming similarity index of infants and juvenile offspring. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ).

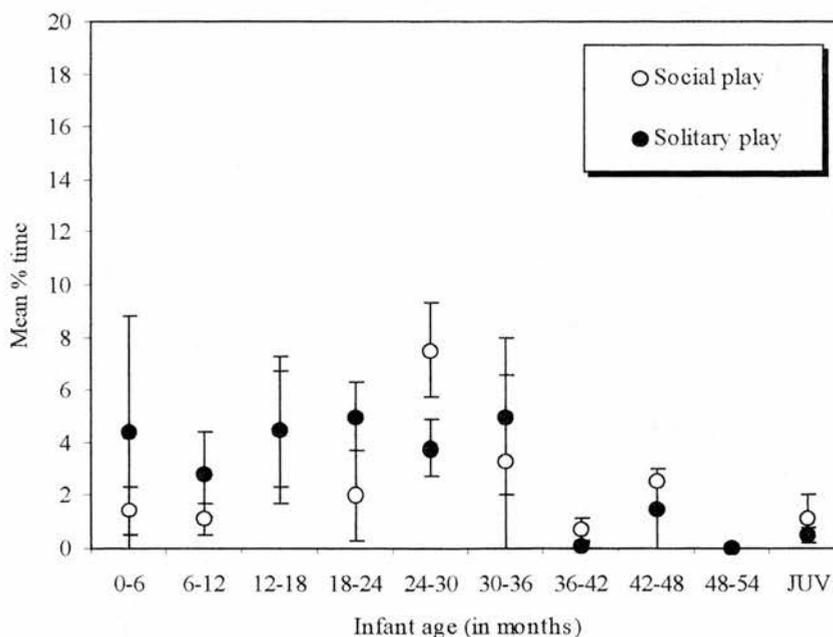


The negative correlation between infant age and the grooming similarity index was significant (Spearman's rank test  $R_s = -0.876$ ,  $p < 0.01$ ). Juveniles had a grooming similarity index of 0.5 ( $SE = 0.15$ ), indicating that they were approaching a reciprocal level of grooming with their mothers: in that they were grooming their mother approximately as much as their mother groomed them.

### 3.3.4 Play

The social play of infants involved playing with their mother, juvenile sibling or another infant. There was considerable individual variation in the time that infants engaged in solitary and social play, but they spent equivalent time engaged in each (see Figure 3.11).

**Figure 3.11:** Social and solitary play by age. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles. Error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ).



There were no clear trends in play behaviour but there was a possible peak in social play in the third year of infancy. However, overall across infant age groups there was no significant difference between the time that infants engaged in social and solitary play (Wilcoxon signed-rank test  $Z = -4.21$ , *ns*). There was no significant difference in time that young infants, older infants and juveniles engaged in social play, but younger infants (under the age of two years) spent a significantly more time engaged in solitary play (see Figure 3.11; Kruskal-Wallis test social play:  $\chi^2 = 2.432$ , *ns*; solitary play  $\chi^2 = 7.631$ ,  $p < 0.05$ ).

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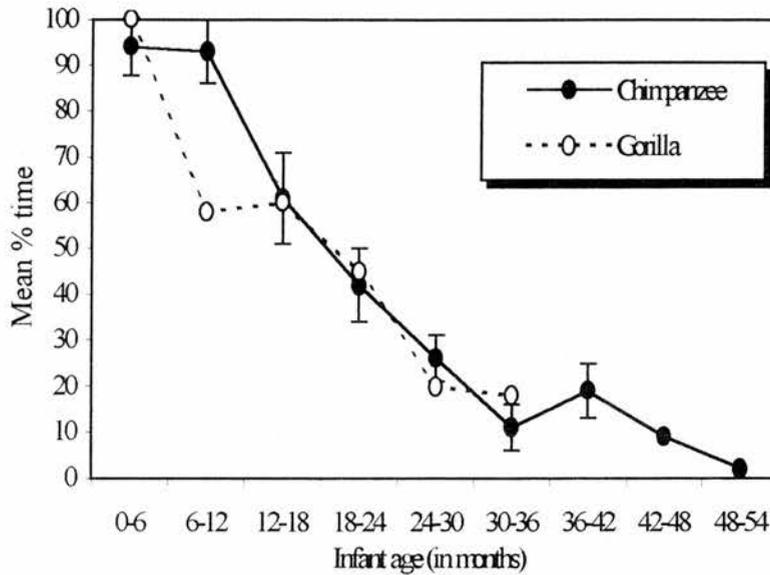
### 3.4 Discussion

The subjects of this study – mothers, infants and stage one juveniles - existed as constant social companions, they were always observed within 20m of each other within any focal sample. This is consistent with well-established data that both male and female chimpanzees that have been weaned continue to constantly associate with their mothers throughout the juvenile period (Hayaki, 1985b; Hayaki, 1988; Pusey, 1983). Hence, even though juvenile survival was not directly dependent on maternal nutritional provision, mothers determine the daily movement and travel pattern of juveniles, settling the initial foraging problem for juveniles of where to search for food. Only as a sub-adult, fully socially independent from its mother, will a chimpanzee need to make decisions concerning the location of food sources, which are complex because of the spatial reasoning and cognitive mapping skills required (Milton, 1981, 1988).

The close physical contact between a mother and her young offspring is both a feature and an indicator of the intensity of the mother-infant bond. The predictions regarding physical contact relations were supported. Older infants spent more time out of physical contact with their mother than younger infants. Infants in their first year were virtually in continual bodily contact with their mothers. This extended period of close physical contact reflects the highly dependent nature of the infant at this age and its need for security and protection, nursing, transport and warmth.

When compared to the available data for mountain gorillas (Fossey, 1979), chimpanzee infants spent longer in physical contact in their first year of life than mountain gorilla infants (see Figure 3.12).

**Figure 3.12:** The mean proportion of time that chimpanzee and mountain gorilla infants spent in physical contact with their mothers, data are pooled over 6 month age blocks. For chimpanzees, error bars indicate standard error about the mean (where no error bars are present  $n = 1$ ). Data on mountain gorillas are taken from Fossey (1979).



The reasons for this difference are likely to be manifold, but perhaps security is the obvious one. Chimpanzee infants have a greater risk of falling from high trees (Goodall, 1986) than mountain gorillas, who are largely terrestrial. No data are available for lowland gorillas but such data would be interesting since lowland gorillas, like chimpanzees, feed high up in trees and are much more arboreal than mountain gorillas (e.g. see Tutin & Fernandez, 1985, 1993; Tutin *et al.*, 1991b). Hence, the risk of falling to a young lowland gorilla would be expected to be similar to that for a young chimpanzee and, according to this hypothesis, lowland gorillas would be expected to reach spatial independence later than mountain gorillas, at a

time more equivalent to chimpanzees. Perhaps more likely is another explanation that concerns the differences in chimpanzee and gorilla social organisation. Young gorillas benefit from the security and protection of adult male gorillas within their group (Watts, 1990). This may release gorilla mothers from transport and protection costs and contrasts with the situation for chimpanzee mothers, who do not receive any form of paternal investment and are principally alone in protecting the safety of their infants (Tutin, 1994). Further, the risk of infanticide for gorilla infants is usually restricted to periods when adult male leadership changes, whereas for chimpanzee infants the risk of infanticide is a constant threat. Chimpanzee infants are at risk both from intra-group and inter-group infanticide, with the intra-group risk being high in the early months of life (mean age for a within-group infanticide = 5 months, Arcadi & Wrangham, 1999). These factors may explain the later spatial independence of chimpanzees in comparison to gorillas, with infant gorillas achieving earlier spatial independence from their mothers because they benefit from protection by adult males.

Chimpanzee infants began to explore space away from their mothers in their second year, so that by the beginning of their third year infants were spending half of their time beyond their mother's arm's reach. As infants matured there were successive increases in the time that they spent at greater distances from their mother. The increasing exploratory nature of infants in their second year corresponds to the time that mothers are beginning to gradually wean their infants by reducing access to the nipple (Clark, 1977; Goodall, 1968). This also coincides with the age that infants are increasingly starting to feed independently (see section 4.3.1, Chapter 4). Close physical contact also begins to be replaced by other forms of positive social interaction (e.g. play and grooming, see below).

Typically weaning of wild chimpanzee infants is gradual, with little maternal aggression towards the infant to prevent suckling until the third or fourth year (Clark, 1977; Goodall, 1968). Data on spatial proximity at 48-54 months in this study showed that there at this age there was a reversion to proximity levels that characterised earlier infant development and, accordingly, this may have represented a 'regressive period' (Van de Rijt-Plooij & Plooij, 1987). This may correspond to the time when mothers are beginning to resume sexual cycles, since the average inter-birth interval for wild chimpanzees is 68 months and resumption of oestrus cycles typically occurs 14-20 months prior to the next birth (Tutin, 1994). However, since there was only one infant within this age block, there was a possibility that this regressive period was due simply to sampling error. No firm conclusions could be made for this reason.

Captive chimpanzees break physical contact with their mother sooner than their wild individuals. Infants at Yerkes Regional Primate Centre were out of physical contact with their mothers for 50% of the time by the age of 11 months (Miller & Nadler, 1981); in this study wild infants away from their mother for this length of time were 24 months old. However, Miller & Nadler (1981) included passive forms of contact; so their 'within physical contact' included periods when the infant was touching its mother but independently sitting next to her. I had considered this as within arm's reach of the mother (see section 3.2.1). This difference in definition means that in direct comparison to my data, Miller & Nadler's (1981) measure is actually an over estimate of the time spent in physical contact. Indeed, it is clear that captivity will provide a more lenient and assenting environment, encouraging earlier physical independence of the infant. Although captive mothers manipulate their infants more than their wild counterparts, in natural environments close

physical contact between mother and infant is maintained up to two years longer than in captive conditions (Nicholson, 1977).

The proximity measures in this study were purely static; no attempt was made to examine the respective roles of mothers and infants in the maintenance of spatial relations. Van de Rijt-Plooij & Plooij (1987) at Gombe studied the spatial dynamics of chimpanzee mother-infant relations over the first 24 months of an infant's life. They found that mothers were solely responsible for maintaining ventral-ventral contact in an infant's first month of life but the infant initially became capable of re-establishing contact itself as early as its second month. From this age on, and increasingly over the next six months, the mother's role and responsibility in re-establishing ventral contact decreased. By the time an infant was six months old it had essentially taken over this role from its mother: the infant was principally responsible for maintaining this form of contact. When they were in the company of their mothers, older Gombe chimpanzees (post-weaned 5-12 year old offspring) were also responsible for actively sustaining close proximity to mothers (Pusey, 1983).

Descriptive statistics were used to produce overall developmental functions for the four major categories of behaviour: resting, feeding, socialising and moving. Following Wasser & Wasser (1995) age-related changes were investigated in the pre-weaning years. Resting (a measure that included suckling time, but did not necessarily reflect changes in suckling rate) decreased logarithmically with age, with a rapid fall in the proportion of time spent resting in the first six months and levelling at a more constant rate in the infant's second year. Infants gradually

became more responsible for feeding themselves, with the proportion of time spent feeding independently increasing steadily as a linear function with age. The proportion of time that infants spent moving independently increased as a polynomial function, levelling at a constant rate close to the time of weaning and indicating the development of infants' locomotory independence. However, it should be noted that because of the problems of habituation and observation conditions (see section 2.4.1.c) moving was largely a measure of infants' movement through trees, not travelling over large distances on the ground. The proportion of time that infants engaged in social activities (both play and grooming) showed the most variability and produced a curvilinear relationship over infant age, increasing early development, reaching a plateau at the end of second year and into the third, and decreasing as final weaning approached. Other reports also suggest that infants socialise less in the last stage of weaning (Clark, 1977).

Predictions for differences in the activity budget of infants in comparison to their juvenile siblings and mothers were supported. As might be expected infants spent significantly more time socialising and resting (a measure that included suckling time) but less time feeding than their mothers and older siblings. As infants became increasingly independent and started feeding for significantly greater proportions of time, they spent correspondingly less time socialising and resting. The amount of time that infants spent moving did increase with age but with some variability. As indicated previously, this was for the most part a measure of movement through trees, rarely was it possible to record infants travelling along the ground with their mother (see section 2.4.1.c). In contrast to their younger siblings, juveniles spent slightly more time feeding than their mothers, similar amounts of time resting and less time socialising. It is possible that juvenile nutrient intake requirements are

greater than their smaller body size indicates and they need to feed more to meet the metabolic demands of high growth rates (Janson & van Schaik, 1993). Although a more likely explanation may be that they have to feed for longer periods than their mother because they feed less efficiently: rates of feeding intake for infants, juveniles and mothers will be investigated later in Chapter 4 (see section 4.3.5).

Mothers began to groom their infants soon after birth. The predictions that mothers direct the majority of their grooming time towards their infant throughout its first 5 years of life, and groom their infant more than its older sibling were supported. Mothers groomed their infant more in the second six months of life than in the first six months of life, but the proportion of time that mothers groomed their infants did not increase further as the infants grew older. Similarly Hiraiwa-Hasegawa (1990a) found negligible differences in the proportion of time that mothers groom their infant before weaning.

Predictions regarding the development of grooming skills were supported. Older infants groomed more than younger infants did. At 18 months infants began their first grooming attempts. This is similar to Nishida's (1988) observation of a 20 month old infant grooming for 2 minutes. He also found that infants below the age of 2 years rarely groomed. As infants grew older there was evidence that they groomed their mother increasingly. However, infants were indiscriminating in the body parts they groomed (Nishida, 1988). Nishida (1988) notes that it is only with the onset of juvenility that youngsters obtain adult-like grooming skills and learn to focus grooming on inaccessible body parts. Data in this study showed that juveniles groomed their mothers more than older infants did and juveniles approached closer

to the levels where they groomed their mother as much as she groomed them. A complete balance in grooming between mother and offspring presumably occurs later, full reciprocity in grooming may only be achieved as late as adolescence (Nishida, 1988). In fact, in Nishida's study at about 11 years of age offspring often groomed their mothers more. He had larger sample sizes and was able to investigate sex differences, finding that female infants began to groom their mother earlier: there were 7 infants (1-2 year olds) and all 3 of the females groomed, whereas none of 4 males did (Nishida, 1988). Other studies lacked such convincing quantitative data but also suggest that immature females may first start grooming and groom more frequently than male immatures (Clark, 1977; Pusey, 1983). It seems youngsters continue to be dependent on kin to groom them until adolescence, with juveniles receiving over 90% of their grooming from their mothers and siblings (Pusey, 1990). Even as juveniles, then, individuals appear to be ineffective at attracting other non-kin grooming partners. Interestingly, Nishida (1988) found that the more offspring a female had, the greater grooming time that she apportioned to them, and immigrant mothers groomed their infants more than residents. Such long-term data are not available at Budongo and similar hypotheses could not be tested.

There are times when infants whose mothers have resumed cycling seem to use grooming as a form of social manipulation, to recover her attention when she was spending time with males (Nishida, 1988; personal observation). Moreover, a 44 month old female and 48 month old male have been observed to use grooming in attempt to scrounge food from adult males (Nishida, 1988) and three infants aged 48-58 months were observed to use grooming in attempts to suckle (Clark, 1977; Nishida, 1988). Therefore, it seems that before being weaned infants have, perhaps only in a clumsy manner, already learnt to use grooming as a type of social tool.

These attempts to manipulate others using grooming have to be regarded as clumsy because prior to weaning infants are not fully proficient and competent in their grooming skills.

In young animals play is conspicuous to an observer: it is often idiosyncratic and vigorous. Nevertheless, it commonly only constitutes a small part (1-10%) of the normal everyday time budget of mammalian youngsters (Fagen, 1981). Chimpanzee infants engaged in solitary and social play for similar proportions of time. During social play infants played either with their mother, a juvenile sibling or another infant but mother-juvenile play was infrequent. Similarly, at Gombe juveniles do not often play with their mother, preferring peers as play partners (Pusey, 1983).

The prediction that older infants and juveniles play more socially than younger infants was not supported. There was considerable variation between individual infants in the proportion of time they spent playing and consequently there were no clear age changes in the time spent in social play over the period of infancy and juvenility. In terms of solitary play there were more significant findings. The prediction that younger infants spend longer in solitary play was supported. The decline in solitary play later in infancy perhaps reflects the decreasing importance of practising locomotory and acrobatic skills as infants become older and more competent navigating the arboreal environment. Similarly, gorilla infants engage in solitary play more than they play with other infants (Fossey, 1979).

The large individual differences in the proportion of time that young infants at Budongo engaged in solitary and social play could have been due to numerous

factors that were beyond the scope of this project to investigate. Some of these have been investigated by others (e.g. Hayaki, 1985b; Pusey, 1990). Firstly, the availability of play partners was not investigated here. Clearly, the solitary nature of mothers makes the scope for playing with individuals other than juvenile siblings and mothers limited (Hayaki, 1985b; Pusey, 1990; Pusey, 1983). Even though the most frequent play partners of infants were their older siblings, Pusey (1983) found that in the company of peers, immatures favour playing with individuals of equivalent age and size. Further, a more recent study has shown that chimpanzee infants without siblings spent similar amounts of time socialising as those that had siblings, suggesting that if given the opportunity infants will seek out a certain level of social interaction (Brent *et al.*, 1997).

Neither was it possible to explore possible sex differences in play and partner preferences as part of this study. It is commonly suggested that as early as juvenility some sex differences may already be apparent, for example there is a sex differentiation in the pattern of making nests (Hiraiwa-Hasegawa, 1989). One prediction is that males might play more than females because as adults males are more gregarious and their reproductive success is likely to be more contingent on agonistic skills (Pusey, 1990). In most field studies sample sizes are too small to test such hypotheses. There are suggestions of trends in the direction predicted: at Mahale the two females observed spent slightly less time playing than the three males but this was not significant enough to conclude that there was a sex bias (Hayaki, 1985b). Neither were sex differences in interaction rates with the mother and other individuals conclusive (Pusey, 1983). In captivity males were slightly more inclined to more aggressive play, initiating chasing and rough-and-tumble play bouts at slightly higher rates than females (Markus & Croft, 1995). However, in this

captive study males were also more likely to engage in female-typical behaviours, such as play-mothering and infant tickling. Markus & Croft (1995) note that this may be because the young males were at the 'potential play-mothering age'. Pusey (1990) found that the two juvenile females studied did interact at a high frequency with their younger siblings and other infants but then again, equally, so did young males. This level of interaction decreased in adolescence and by late adolescence neither males nor females showed much interest in infants. Although there is anecdotal evidence that some young females at Gombe have been unusually attracted to infants (Goodall, 1971) and alloparental behaviour has been observed at Mahale (Nishida, 1983), some data point in the other direction. Goodall (1968) reports that two juvenile males actually played more with infants than the juvenile female. Although my data and sample sizes were insufficient to allow quantitative analysis and it was difficult to separate individual from age-related effects, my personal impression was that the sex of the infant was not an important determinant in the propensity for play or the vigour of play. I think it was likely that the large individual differences in play behaviour between infants was the result of differences in the sociability of mothers, as this determined the availability of peer play partners to infants. Further, I suspected that older, more experienced, more confident mothers encouraged their offspring to play more than other mothers, who were nervous and over-protective. Perhaps a possible way to unravel some of these questions in the future would be to combine relevant data across sites to create larger sample sizes for statistical analysis.

There are more convincing data on sex differences in behaviour at adolescence. For example, adolescent males appear to be more drawn towards others, separate from their mothers earlier and groom adult males at higher rates than females

# CHAPTER 4:

## FORAGING

## BEHAVIOUR

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### 4.1 Introduction

The common chimpanzee has been shown to have a diverse, predominately frugivorous diet at many different sites, in a variety of habitats across Africa. These range from McGrew *et al.*'s (1988) data from an open-savannah habitat, at Mt. Assirik in eastern Senegal; to extensive long term data from the savannah woodland-forest mosaics of Gombe, western Tanzania: (Goodall, 1986; Wrangham, 1977), and Mahale, western Tanzania (Nishida & Uehara, 1983; Nishida *et al.*, 1983), and the savannah woodland-forest mosaic habitat of West Africa: Bossou, Guinea: (Sugiyama & Koman, 1987; Yamakoshi, 1998). Data from seasonal semi-deciduous forest exists for Kibale, Uganda (Ghiglieri, 1984; Isabirye-Basuta, 1989; Wrangham *et al.*, 1991; Wrangham *et al.*, 1993); at Budongo there is an early description of diet (Reynolds & Reynolds, 1965) and more recently studies on feeding ecology (C. Bakuneeta, in preparation), female socio-ecology (K. Fawcett, in preparation) and feeding skills of injured chimpanzees (Stokes, 1999). Chimpanzee diet has also been studied in the tropical rainforests of Lopé, Gabon: (Tutin & Fernandez, 1993;

Tutin *et al.*, 1991b), Kahuzi-Biega, Democratic Republic of Congo: (Yamagiwa *et al.*, 1996), Nouabalé-Ndoki, Congo (Kuroda *et al.*, 1996) and Okorobiko Mountains, Equatorial Guinea: (Sabater, 1979).

The general picture that emerges is *Pan troglodytes*' diet is varied, consisting predominately of fruit, but supplemented with frequent intake of other plant material (such as leaves, seeds, pith, bark) and insects (ants, termites, etc). Occasionally, meat may also be consumed, but constitutes less than 1% (Teleki, 1973) or perhaps 1-3% (Busse, 1977) of the total annual diet. Nevertheless, it is a highly preferred food item (Teleki, 1973). Hunting is co-operative (Boesch, 1994) and in comparison to collection of safari ants the greater risks of hunting seem to be outweighed by the superior energy returns (McGrew, 1974). Meat is shared amongst adult males and with adult females, sometimes as voluntary offers of small and occasionally large portions of food (Boesch & Boesch, 1989; Teleki, 1975). Meat eating increases with age, whereas ant eating decreases after early adolescence and this cannot be explained by different rates of sociability of the males concerned (Kawanaka, 1990). Although Kawanaka (1990) notes that increasing meat consumption does not appear to substitute for ant-eating as males reduce their consumption of ants well before they near their highest rank and there is no consistency in the aggregate total intake of meat and ants from early adolescence and beyond. There are sex differences, with adult males consuming more meat than females, whilst females feed at higher rates on social insects (McGrew, 1979; Uehara, 1986).

During periods of low food abundance, optimal foraging theory predicts that an animal should widen its diet, decreasing its specialisation as its foraging costs

increase (Pyke *et al.*, 1977; Schoener, 1971). There is evidence that when choice fruits are not available, chimpanzees do broaden their diet in a general manner to more widely available, lower quality foods (Isabirye-Basuta, 1989). However, other studies have found that increases in dietary diversity during periods of low food abundance were not significant (Kuroda *et al.*, 1996; Tutin *et al.*, 1991b; Yamakoshi, 1998). This suggests that the increased intake of lower quality vegetation remains more selective than the predictions of optimal foraging models, which do not incorporate the concepts of absolute nutritional value, balance of essential nutrients, and avoidance of toxic secondary plant compounds in their specification of food value. Essentially, although chimpanzees consume a wide variety of foods they are selective, feeding on only a small proportion of food items from those that are potentially available. They spend a large amount of time feeding on a small number of key fruit species (Goodall, 1986; Tutin & Fernandez, 1993; Wrangham, 1977) and commonly, the feeding times on these important, preferred fruits basically corresponds to their availability (Tutin & Fernandez, 1993; Tutin *et al.*, 1991b). At some sites fig (*Ficus* spp.) fruits are continuously available throughout the year and are important fallback alternatives during periods of non-fig fruit scarcity (Kuroda *et al.*, 1996; Wrangham *et al.*, 1996), yet in montane forests where fruit diversity is lower, figs are the year-round preferred food (Yamagiwa *et al.*, 1996). During periods of fruit scarcity chimpanzees at Kibale and Lopé increase their intake of an assortment of vegetative foods including leaves and terrestrial herbaceous pith (Tutin *et al.*, 1991b; Wrangham *et al.*, 1996). At Bossou, Guinea and elsewhere chimpanzees increasingly exploit nuts of the oil palm during periods of low food availability, and the extraction of kernels of this species may have been an important selective pressure for subsistence tool use (Yamakoshi, 1998). The diverse feeding repertoire of chimpanzees is no doubt a response to variable fruit

production: chimpanzees have been described as 'opportunistic frugivores' (Tutin *et al.*, 1991b).

Chimpanzees at different sites have different feeding habits (McGrew, 1983; McGrew *et al.*, 1988; Nishida *et al.*, 1983). Many of these differences in feeding choices can be explained by differential regional availability, but in some cases the chimpanzees of one population consume a food that is readily available but not eaten by another population (McGrew *et al.*, 1988). However, as with patterns of tool use (see Chapter 1) it is difficult to untangle ecological and cultural factors. In the cases where there is no *apparent* valid ecological explanation for the difference in feeding choices, it is difficult (and we are unlikely to be able) to eliminate all possible environmental and ecological factors. This is particularly apparent in the case of feeding choice because foods may not be exploited by one population because another food source exists that is more nutritionally valuable, easily found, easily obtained, more abundant, etc.

In this study observation conditions were difficult and the majority of observations were made whilst chimpanzees were feeding in trees (see section 2.4.1.c). Thus, there is no suggestion here that this study represents the full range of food items that adult chimpanzees feed on at Budongo; levels of contact and observability of mothers simply did not allow this. Instead, a sub-set of feeding choices are examined and infant dietary selection is investigated by examining the food items eaten by infant chimpanzees and relating them to their mother's dietary composition. This will allow a direct comparison of feeding choices of infants and mothers under the same observation conditions. Hence, instead of considering a

food 'selected' from the environment because it was consumed at higher levels than would be predicted from its overall abundance, the likelihood of a young chimpanzee consuming an item is considered in relation to its mother's feeding profile. The infant's developing ability to feed itself may depend on the type and quality of foods available to it; suitable food items for the mother may not be suitable for the infant. Some foods will require further handling, or processing, so that the edible part of the food can be ingested. According to the type of food, this handling can be as little as simply detaching the item from a branch, through to more intricate manipulations to extract the edible portion of the item. On the basis of the complexity of this handling and processing, items were categorised as either 'easy-to-process' or 'difficult-to-process' (see section 2.4.5.c). Handling and processing of foods becomes the most complicated in the case of extractive foraging, where the edible portion is encased and needs to be separated from the inedible outer casing. The procurement of such embedded foods and the fact that many are only intermittently and seasonally available may have been an important selective pressure on the evolution of intelligence, stimulating progressive advancements in foraging techniques, eventually leading to "intelligent" tool use (Gibson, 1986; Parker & Gibson, 1977, 1979). In the case of these foods the edible portion of the food object may be particularly nutritious (e.g. seeds, nuts) but is effectively concealed because it is encased within an inedible matrix. The food is therefore on initial appearances inedible, yet the (unseen) contents are highly nutritious. Difficult foods should take longer to procure and process and it is predicted that:

- The feeding intake is greater for easy foods than difficult foods.

The ontogeny of food choices may depend not only on which food items are available, but also their suitability for ingestion. An item suitable to a mother or juvenile may not be suitable to the infant. I chart how food items that are included in the maternal diet are incorporated into the infant's dietary repertoire at different stages of development. It is predicted that:

- Easy to process foods will be the first items incorporated into an infant's diet as these represent suitable weaning foods.
- Infants eat significantly more easy foods than difficult foods.
- Juveniles do not eat significantly more easy foods than difficult foods.

Fieldworkers have usually investigated the feeding selectivity of primates by examining different plant parts and comparing those parts that are consumed, as opposed to those that are rejected. Studies on primarily folivorous primates have demonstrated that individuals maximise their intake of protein whilst minimising their intake of toxic secondary compounds such as condensed tannins: *Colobus guereza* (McKey *et al.*, 1981), *Alouatta palliata* (Milton, 1979), *Presbytis johnii* (Oates *et al.*, 1980) and *Gorilla gorilla beringei* (Watts, 1984). Frugivorous primates maximise sugar intake and minimise tannin intake *Pongo pygmaeus* (Leighton, 1993) and *Gorilla gorilla gorilla* (Rogers *et al.*, 1990). It has also been demonstrated that chimpanzees maximise their intake of sugars (and, hence, calories) by feeding on preferred ripe fruit pulp rather than the less preferred, usually unripe, fruits (Matsumoto-Oda & Hayashi, 1999; Reynolds *et al.*, 1998). It is predicted that:

- All individuals (infants, juveniles and mothers) spend a greater proportion of time feeding on ripe fruits than unripe fruits.

- Infants and juveniles spend proportionally more time feeding on ripe fruits than unripe fruits in relation to the time spent feeding on these items by their mother.

On the basis of young chimpanzees' experience and the difficulty involved in handling (procuring and processing) food items it is predicted that:

- Infants handle foods slower than juveniles and mothers.
- Juveniles handle foods slower than mothers.

And therefore:

- Infants consume less dry mass per unit time than juveniles and mothers.
- Juveniles consume less dry mass per unit time than mothers.

The development of actions used to procure food was also investigated. The frequency of simple procurement actions used by infants and how they emerged throughout development was documented.

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## 4.2 Methods

### 4.2.1 Definitions

For definitions of general behavioural activities see section 2.4.5.b. In cataloguing plant parts I followed Nishida and Uehara's (1983) plant part classification, which is only applied if the part was selectively eaten with other parts rejected. Categories were: mature leaves, young leaves, ripe fruit, unripe fruit, seed, bark (or cambium), wood, pith (inner unlignified tissue extracted from stem). Infants would sometimes only consume part of a food item and for this reason, in order to accurately measure feeding intake rate, it was important to record the fraction consumed in each single (hand-to-mouth) harvesting action. Given the difficult observation conditions, the fraction consumed had to be determined both by recording how many bites were taken from the item and by observing the size of any remnant portion that was discarded. The following categories were used in this scoring:

<b>Eat (can't see)</b>	One (hand-to-mouth) harvesting action observed but observation obscured (e.g. by vegetation, animal moving) and placement in mouth could not be confirmed.
<b>Eat whole</b>	Food item ingested intact and in its entirety.
<b>Eat half</b>	About one half of food item is ingested.
<b>Eat quarter</b>	About one quarter of food item is ingested.

Regularly used harvesting actions were categorised and scored as:

### **Unimanual Co-ordination**

- Pick-hold-bite** Subject picks food item, holds within one or two hands and repeatedly takes bites from item.
- One hand pull-mouth** Subject pulls branch towards itself and with a head movement takes food item directly with mouth.
- Pick-mouth** Subject picks food item directly from branch and places each single item into the mouth.
- Pick-gather** Subject repeatedly picks several food items to gather them into a bunch in one hand and places whole bunch in mouth.

### **Bimanual Co-ordination**

- One hand pull branch-pick other hand-mouth** Subject pulls branch towards itself with one hand and with the other hand removes food item.
- Two handed pull-mouth** Subject pulls branch towards itself with both hands (first hand pulls branch into reach, second hand pulls the branch nearer and stabilises), then with a head movement subject takes food item directly with mouth.

### 4.2.2 Data collection

Feeding bouts were recorded continuously to collect data on food species and part, feeding duration, frequencies of bites/food items consumed and simple harvesting actions. Samples of the major foods that were eaten by mother, juvenile and infant chimpanzees were collected in the field on the same day that the feeding observations were made and brought back to camp. The relevant food item was chosen on the basis of their condition (i.e. decaying or damaged items were not collected because chimpanzees did not consume these). It was possible to collect items equivalent to those consumed by chimpanzees from the ground because items were usually dislodged by chimpanzee activity and movement through feeding trees. The sample was separated according to the part(s) that was eaten and the part(s) that was rejected. For example, when chimpanzees fed on the pentagonal shaped fruit of *Entandrophragma angolense*, they stripped and discarded the outer pericarp, spat out the large seeds and fed selectively on the inner pulp. So in the case of this species, the fruit was separated into these three parts to be analysed weighed separately. Following Barton & Whiten (1993) the aim was to collect enough fresh material to give approximately 10g in dry mass. However, this was not always possible and in such cases as much fresh material as possible was collected. Two samples of fresh material were always collected and these were weighed separately to obtain wet mass values using a set of mechanical scales (kindly provided by Ohaus Ltd). These fresh samples were then dried over a period of approximately 1 week (depending on the sample). The samples were then re-weighed to obtain a dry mass measurement and sealed air-tight in a plastic bag for return to the UK in case further nutritional analyses were to become feasible.

### 4.2.3 Data analysis

Data on general feeding times and composition of the diet were collected during 20 minute principal and subsidiary focal animal samples. The difficulties of finding all subjects and balancing focal samples meant that in this data set there was a possibility that sampling biases existed between the feeding choices of different mother-infant pairs (see Chapter 2). Therefore, the feeding choices of infants and juveniles were analysed only in relation to their mothers' choices. This direct comparison removed the possibility of sampling bias between mother-infant pairs.

Data on feeding duration, food species and part, frequencies of bites/food items consumed and simple harvesting actions were collected continuously only during the principal focal animal samples. Handling rates were calculated as the number of food items per minute of feeding time. Feeding intake rates were calculated as dry mass (in grams) consumed per hour of feeding time. Both of these measures required calculation of the number of food items per unit time. For food items consumed in their entirety (e.g. leaves, small fruits), the dry mass intake per item for each individual was simply the mean dry mass of the plant sample divided by the number of food items ('whole eats') consumed per individual. In the case of small infants who tended to only take small bites of a fruit without consuming the whole food item, it was necessary to record the fraction of the food item consumed when the subject had ceased handling the item (e.g. 'eat quarter' or 'eat half' was recorded). This was also the case for larger food items when adults may only have consumed part of the item. For example in the case of *Desplatsia dewevrei* (a fruit that can be up to 20 cm long), adults sometimes only took a few bites, not even

consuming one quarter of the fruit. In these circumstances the 'eat whole' code was used to record the number of bites and when the fruit was separated at camp to be weighed into parts consumed and discarded, the total number of bites necessary to ingest the part consumed was estimated. In these cases the number of bites on a food item was divided by the total number of bites required to consume the whole large food item in order to give the fraction consumed. This fraction was then used in the calculation of individual rates of dry mass intake per food item per hour of feeding time.

All statistical tests were non-parametric and two-tailed. They were applied across the four age categories: young infants (n=5), older infants (n=4), juveniles n=4), and mothers (n=9). In cases where  $df = 1$ , the  $\chi^2$  was corrected by the Yates' Correction for Continuity.

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## 4.3 Results

### 4.3.1 Development of diet

No infant was observed to ingest a non-food item (defined as objects not normally part of the adult diet). However, infants did frequently play with non-food items by manipulating them in the hand or mouth (as per definition section 2.4.5.b), and this playing with food is later investigated as part of the social context of an infant's early foraging (see section 5.3.3, Chapter 5).

Foods were classed as 'easy-to-process' or 'difficult-to-process' in the field on the basis of the apparent amount of difficulty it required to procure or process the item (for definitions see section 2.4.5.c). For some foods the outer casings can be extremely tough and mechanically difficult to open, such that I was unable to remove food parts manually when I was collecting specimens for dry weights (see section 4.2.2). With these 'difficult-to-process' foods it was necessary for a human to use another device to open the fruit or other food. For example, in the case of some encased seeds a knife was required to open prise open the dry, thin tough husk. Some items encased in a hard shell were small enough to be opened with a knife, but others were very large fruits (e.g. *Desplatia dewereii*: 20 cm in diameter) and were hard to open even with use of a machete. Mothers were observed to open these food items usually with a co-ordinated use of hand(s) and teeth/mouth. This required a degree of manual dexterity and strength but typically the body part that was used for leverage and mechanical opening was the teeth.

Data on mothers' feeding time and number of food items consumed were pooled to calculate processing and intake rates for the two different classes of food item: 'easy-to-process' and 'difficult-to-process'. These data were then used to investigate whether my impression (from the field) that the processing times of easy and difficult foods were significantly different (see Table 4.1).

**Table 4.1:** Maternal processing and feeding intake rates of 'easy-to-process' and 'difficult-to-process' food items

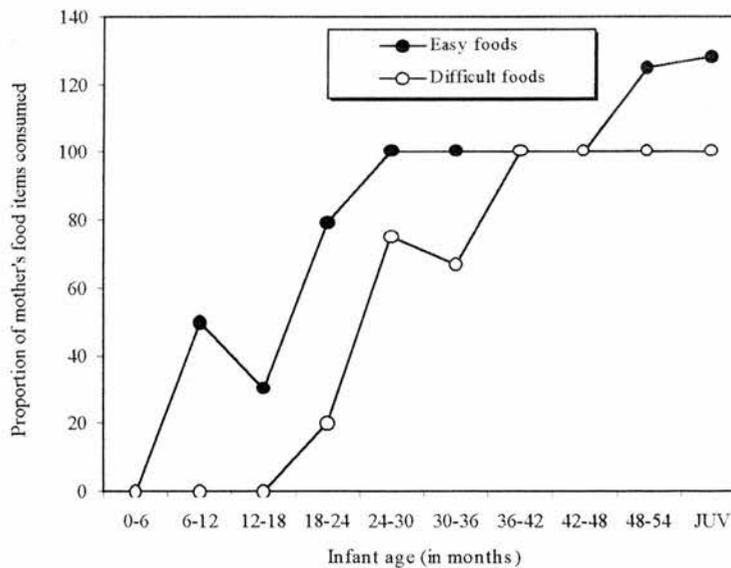
Food item		Hand-mouth actions per min	Number of actions required to consume food item	Number of food items per min	Food item dry weight (in grams)	Dry weight consumed per min
<b>'Easy-to-process'</b>						
<i>Broussonettia papyrifera</i>	Unripe fruit	1.72	1	1.72	1.12	1.93
<i>Broussonettia papyrifera</i>	Ripe fruit	3.04	1	3.04	1.36	4.13
<i>Broussonettia papyrifera</i>	Flowers	10.33	1	10.33	0.31	3.18
<i>Ficus mucoso</i>	Ripe fruit	2.52	1	2.52	2.53	6.38
<i>Ficus mucoso</i>	Unripe fruit	6.07	1	6.07	1.64	9.95
<i>Ficus sur</i>	Unripe fruit	4.53	1	4.53	0.63	2.83
<i>Ficus sur</i>	Ripe fruit	7.53	1	7.53	0.93	7.02
<b>'Difficult-to-process'</b>						
<i>Broussonettia papyrifera</i>	Young leaves	11.51	1	11.51	0.09	1.08
<i>Cordia millenii</i>	Unripe fruit	1.58	1	1.58	1.21	1.91
<i>Cynometra angolense</i>	Seeds	5.88	1	5.88	0.16	0.97
<i>Erythrophleum suaveolens</i>	Seeds	1.91	1	1.91	0.35	0.67
<i>Milicia excelsa</i>	Ripe fruit	3.79	4	0.95	0.39	0.37
<i>Mildbraediendron excellsum</i>	Ripe fruit	0.25	5	0.05	8.80	0.44
<i>Platyserium angolense</i>	Mature Leaves	1.09	20	0.05	1.61	0.09

These data confirmed my impression that the processing times of easy and difficult foods were significantly different. Mothers' intake rate for easy foods (dry mass per minute consumed) was significantly higher than for difficult foods (see

Table 4.1; Easy: mean = 5.06 SE=1.08, Difficult: mean = 0.79 SE=0.23 Wilcoxon matched-pairs signed-ranks test  $Z = -2.366$ ,  $p < 0.02$ ).

As infants start to feed independently they supplement their intake of milk with an increasing number of solid food items. These early independent feeding attempts by infants were investigated in relation to their mother's pattern of feeding. The number of food items that an infant consumed independently was calculated in relation to the number of food items that its mother consumed (see Figure 4.1). These data refer to the infants' initial independent feeding attempts (this is to be distinguished feeding on shared food items: see Chapter 6 for these investigations).

**Figure 4.1:** Proportion of mother's food items consumed by infants. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles.



Infants fed independently on significantly more of the easy foods consumed by their mother than the difficult foods she had consumed (Easy foods: mean = 68

SE=14, Difficult foods mean = 40 SE=15; Wilcoxon matched-pairs signed-ranks test  $Z = -2.366$ ,  $p < 0.02$ ; see Figure 4.1). By the beginning of their third year infants were consuming all the easy foods eaten by their mothers, but were not able to consume all difficult foods until the beginning of their fourth year. Conversely, juveniles did not differ significantly in the number of easy and difficult foods they consumed, (Easy foods: mean = 128 SE=11, Difficult foods mean = 100 SE=0; Wilcoxon matched-pairs signed-ranks test  $Z = -1.604$ , *ns*; see Figure 4.1). In fact juveniles fed on a more diverse range of easy foods than their mothers, but consumed a similar number of difficult foods.

Fruit was the most important dietary component for all subjects. Mothers spent a mean of 82% (SE=4) of their time feeding on fruits, juveniles 79% (SE=10) and infants 85% (SE =5). Since chimpanzees fed predominantly on fruit, fruit-feeding patterns were further investigated. For each individual infant and juvenile the time spent feeding on ripe and unripe fruits was calculated in relation to their mother's feeding times on these items and compared for each individual.

**Table 4.2:** Proportion of mother's feeding time that infants feed on ripe and unripe fruits

Infant	% of mother for ripe fruit	% of mother for unripe fruits
Young RS	0	0
Young ZG	1	0
Young RA	12	0
Young BT	19	0
Young NR	41	25
Older ZL	56	49
Older KZ	65	28
Older BH	71	28
Older KT	94	52

**Table 4.3:** Proportion of mother's feeding time that juveniles feed on ripe and unripe fruits

Juvenile	% of mother for ripe fruit	% of mother for unripe fruits
BO	107	100
MS	167	156
GZ	104	98
KD	87	94

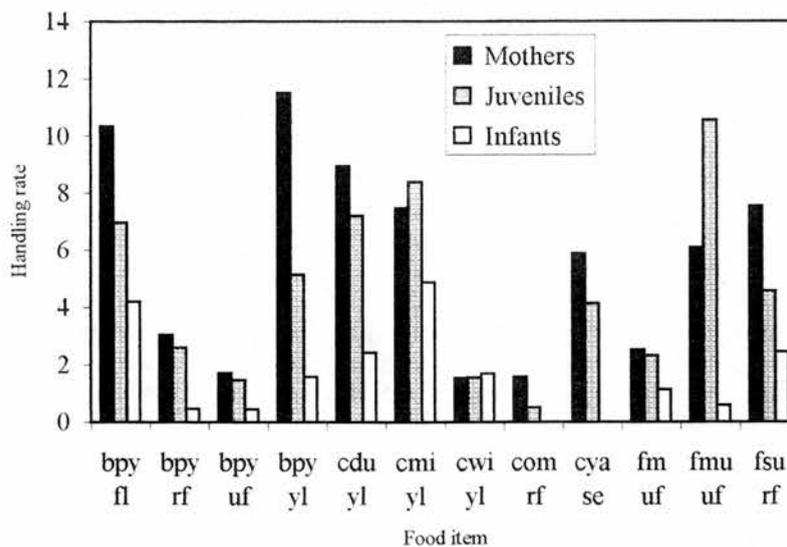
When infants' feeding time on ripe and unripe fruits was investigated as a proportion of the time that their mothers fed on these items, infants fed on ripe fruits significantly more often than they fed on unripe fruits (ripe fruit mean = 40 SE=11, unripe fruit mean = 20 SE=7, Wilcoxon matched-pairs signed-ranks test  $Z = -2.521$ ,  $p < 0.01$ ; see Table 4.2). Infants began to feed on ripe fruits earlier than unripe fruits. Only one infant, the eldest of the young infants (NR) consumed unripe fruits, whereas the three infants younger than NR (ZG, RA, BT) all consumed ripe fruit

(see Table 4.2). In contrast, juveniles were not significantly more likely to feed on ripe fruits (ripe fruit mean = 116 SE=17, unripe fruit mean = 112 SE=15, Wilcoxon matched-pairs signed-ranks test  $Z = -9.21$ , *ns*; see Table 4.3).

### 4.3.2 Processing rates

The processing rates of the top 12 foods (in terms of feeding times) were investigated. Data within each age-class were pooled. Since the quality and size of individual food items is not identical and this may affect feeding rate, comparison between individual chimpanzees would be difficult. Consequently, the mean handling and feeding intake rates for infants, juveniles and mothers were calculated for the 12 food items with the highest feeding times (see Figure 4.2; Table 4.4).

**Figure 4.2:** Mean handling rates (number of food items consumed per min) for mothers, juveniles and infants on the 12 major food items. The food codes on the x axis refer to the species and part of the food item, see Table 4.4



Infants processed foods slower than mothers and juveniles (see Figure 4.2) and so consumed less dry mass per unit time (see Table 4.4). The handling rates, and consequently dry mass intake rates, of mothers and juveniles did not differ substantially but for some food items juveniles did have lower handling and intake rates than their mothers (see Figure 4.2 and Table 4.4)

**Table 4.4:** Handling and feeding intake rates for mothers, juveniles and infants.

Species	Part	Code	Dry mass per item	Mean handling rate (number of food items per min)			Mean feeding intake rate (grams per hour)		
				Mothers	Juveniles	Infants	Mothers	Juveniles	Infants
<i>Broussonettia papyrifera</i>	Flowers	Bpy flo	0.31	10.33	6.96	4.2	192	129	78
<i>Broussonettia papyrifera</i>	Ripe fruit	Bpy rf	1.36	3.04	2.61	0.46	248	213	38
<i>Broussonettia papyrifera</i>	Unripe fruit	Bpy uf	1.12	1.72	1.46	0.45	116	98	30
<i>Broussonettia papyrifera</i>	Young leaves	Bpy yl	0.09	11.51	5.15	1.58	62	28	9
<i>Celtis Durandii</i>	Young leaves	Cdu yl	0.07	8.92	7.2	2.42	37	30	10
<i>Celtis mildbraedii</i>	Young leaves	Cmi yl	0.08	7.46	8.37	4.87	36	40	23
<i>Celtis Wightii</i>	Young leaves	Cwi yl	0.05	1.54	1.56	1.7	5	5	5
<i>Cordia millenii</i>	Unripe fruit	Com uf	1.21	1.58	0.51	--	115	37	--
<i>Cynometra alexandri</i>	Seeds	Cya se	0.16	5.88	4.14	--	56	40	--
<i>Ficus Mucoso</i>	Ripe fruit	Fmu rf	2.53	2.52	2.32	1.13	383	352	172
<i>Ficus Mucoso</i>	Unripe fruit	Fmu uf	1.64	6.07	10.55	0.57	597	1038	56
<i>Ficus Sur</i>	Ripe fruit	Fsu rf	0.93	7.53	4.57	2.45	420	255	137

### 4.3.3 Development of harvesting actions

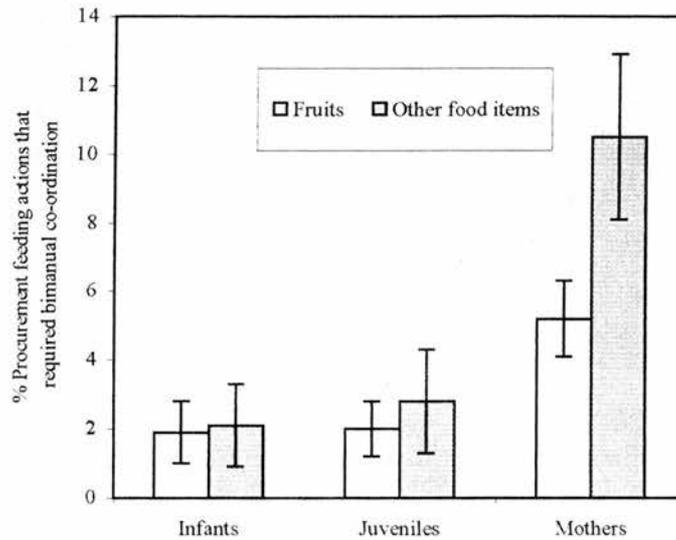
The use of different harvesting actions as they emerged throughout development was investigated. Juveniles and mothers used all harvesting actions but not all infants did. Those harvesting actions that only required the use of one hand emerged first in development, with bimanual harvesting actions not emerging until the infant was in its third year of life (see Table 4.5).

**Table 4.5:** Emergence of harvesting actions during infancy

Harvesting actions	Infant age (in years)				
	1	2	3	4	5
<b><u>Unimanual Co-ordination</u></b>					
Pick-hold-bite	✓	✓	✓	✓	✓
One hand pull-mouth	✓	✓	✓	✓	✓
Pick-mouth	✓	✓	✓	✓	✓
Pick-gather			✓	✓	✓
<b><u>Bimanual Co-ordination</u></b>					
One hand pull branch-pick(other hand)-mouth			✓	✓	✓
Two handed pull-mouth				✓	✓

The proportion of harvesting actions used that required bimanual co-ordination was investigated for infants, juveniles and mothers (see Figure 4.3).

**Figure 4.3:** Mean proportion of feeding actions that required bimanual co-ordination. Error bars indicate standard error about the mean.



Infants did not differ in the proportion of bimanual harvesting actions for fruits and non-fruits (Fruit mean = 1.9 SE=0.9, Other food items mean = 2.1 SE=1.2, Wilcoxon matched-pairs signed-ranks test  $Z = 0$ , *ns*; see Figure 4.3). Nor did juveniles differ in this respect (Fruit mean = 2.0 SE=0.8, Other food items mean = 2.8 SE=1.5, Wilcoxon matched-pairs signed-ranks test  $Z = -0.736$ , *ns*; see Figure 4.3). Mothers, however, used bimanual harvesting actions significantly less often for fruits than for other food items (Fruit mean = 5.2 SE=1.1, Other food items mean = 10.5 SE=2.4, Wilcoxon matched-pairs signed-ranks test  $Z = -1.992$ ,  $p < 0.05$ ; see Figure 4.3). There was no significant difference in the number of bimanual harvesting actions used between infants and juveniles either for fruits (Infants mean = 1.9 SE=0.9, Juveniles mean = 2.0 SE=0.8; see Figure 4.3) or other food items (Infants mean = 2.1 SE= 1.2, Juveniles mean = 2.8 SE=1.5; see Figure 4.3).

Mothers used bimanual harvesting actions significantly more often than infants for fruits (Mothers mean = 5.2 SE=1.1, Infants mean = 1.9 SE= 0.9, Mann Whitney test  $U= 14$ ,  $p<0.02$ ; see Figure 4.3) and other food items (Mothers mean = 10.5 SE=2.4, Infants mean = 2.1 SE=1.2, Mann Whitney test  $U= 16$ ,  $p<0.02$ ; see Figure 4.3). Mothers also used bimanual harvesting actions significantly more often than juveniles for fruits (Mothers mean = 5.2 SE=1.1, Juveniles mean = 2.0 SE=0.8, Mann Whitney test  $U= 6.5$ ,  $p<0.05$ ; see Figure 4.3). Mothers also used bimanual harvesting actions more often than juveniles for other food items but this only approached significance (Mothers mean = 10.5 SE=2.4, Juveniles mean = 2.8 SE=1.5, Mann Whitney test  $U=8.5$ , $p= 0.10$ ; see Figure 4.3).

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## 4.4 Discussion

It was not possible to regularly follow subjects on the ground (see section 2.4.1.c) and, as a result, the majority of observations were made of mothers and their offspring feeding arboreally. Accordingly, the feeding choices for offspring were not choices between species; rather they were choices about the part of the food species to be eaten given the tree the mother was in. In many respects any infant will be limited in the number of feeding choices available to it because it remains so near its mother (see Chapter 3). If the infant is in close proximity to its mother, the likelihood that it will choose to feed on the same food type as her is increased. Hence, infants' feeding behaviour will largely be determined by the infant's close spatial proximity to its mother.

Infants began to feed independently and supplement their milk intake with solid food in the second half of their first year. Also in their first year, infants obtained a large proportion of their solid food from their mother (food sharing: investigated in Chapter 6). Infants did not ingest anything unsuitable, although they did frequently play with food as a precursor to normal feeding behaviour (investigated in Chapter 5, see section 5.3.3). Similarly, gorilla infants manipulate food and non-food in the hand and mouth frequently, but have not been recorded to ingest any food items not eaten by their mother (Watts, 1985).

The independent feeding behaviour of young chimpanzees was investigated in relation to their mother's feeding choices. Juvenile chimpanzees, being nutritionally independent, ate all the foods that their mothers ate and in fact ate a greater variety

of easy food species than their mother. Young infants gradually included their mother's food items into their diet and consumed a significantly greater proportion of easy items in comparison to difficult items. By the beginning of their third year, infants were eating on all the easy food items that their mother fed on, but only by the beginning of their fourth year were infants feeding on all the difficult food items that their mother fed on. Although, on the whole, difficult food items did not require complicated handling techniques to open, they did require a degree of physical strength. Quantitative measurement of maternal processing and feeding rates confirmed that the difference between easy and difficult foods was significant: easy foods were consumed at higher dry mass intake rates.

So by their fourth year infants were feeding on all the food items that their mother was feeding on and had acquired the same feeding patterns as their mothers at least in rudimentary form. Therefore, it seemed that at this age infants were able to identify most food items in the diet of adults. Although given the large inter-annual variability in chimpanzee diet (e.g. Nishida & Uehara, 1983) there may still be some food items not yet encountered by a 4 year old chimpanzee. However, at this age the development of efficient handling of foods is probably more important than identification of items since infants were significantly less efficient at processing food items compared to their older siblings and mothers. Consequently, infants consumed less dry mass per unit time. This is likely to be due to various factors such as their smaller body size, lack of strength, experience, motivation, etc (further discussed below). In the second half of their fourth year infants began feeding on some food items that their mothers were not observed to feed on but these food items were still concurrent with normal adult food choices. Such

'asynchronous' feeding is further investigated in the next chapter. Generally, though, the diet of infants was simply a sub-set of their mother's.

Mothers juveniles and infants all fed predominately on fruit. When infants' feeding was investigated in relation to their mother's, infants fed on ripe fruits significantly more often than they fed on unripe fruits, but juveniles were just as likely to feed on either. Hence, infant chimpanzees consumed proportionally more ripe fruit and proportionally less unripe fruit when compared to their mothers and older siblings. Infants were therefore maximising their intake of sugars but minimising their intake of toxic secondary compounds such as tannins (Reynolds *et al.*, 1998). The relatively small portion of the infant diet that consisted of leaves and unripe fruits suggests that infants may be inefficient or physiologically unable to detoxify large quantities of tannins and perhaps other secondary compounds. However, since some ripe fruit species, particularly figs, contain a relatively high tannin content (Reynolds *et al.*, 1998) and young chimpanzees do consume small quantities of unripe fruit and leaves, infants must be able to at least tolerate some level of toxicity. Perhaps animals should not be expected to completely avoid low concentrations of tannins: Gottlieb (1996) noted that "tannin-promoted astringency may even stimulate ingestion, or in the case of humans, induce processing of otherwise nutritious plant parts to lessen their tannin content" (p.195). One of the effects of tannins is that they attach to proteins and reduce their digestibility but Reynolds *et al.* (1998) note that this effect may be countered by the production of salivary muco-proteins. The ability to tolerate tannins may in part be dependent on the concentration of these enzymes in the saliva; if so this has implications for mothers' sharing of material they have half-chewed with their infants (see Chapter 6). Similarly, extensive wadging of fig fruits may serve to minimise toxicity levels

since the seed, pulp and fibrous portion of figs is compressed and chewed for a long period of time during wadging. Only the juice, which contains high levels of water-soluble carbohydrates, is ingested (Reynolds *et al.*, 1998; Wrangham *et al.*, 1993).

In contrast to their younger siblings, juveniles spent slightly more time feeding than their mothers did (Chapter 3). The slightly lower (although not significantly different) handling rates (and consequently dry mass feeding intake rates) of juveniles in comparison to their mothers suggests that they consume on average less dry weight per unit time than their mothers and perhaps they therefore need to spend longer feeding than their mother. Other authors have also described their impression that despite being fully nutritionally independent, juveniles are less efficient foragers than adults are (e.g. Altmann, 1980). Janson and van Schaik (1993) reviewed data on white-fronted capuchins and other quantitative data on macaques, baboons, brown capuchins, siamangs, white-handed gibbons and mantled howler monkeys. They concluded that juveniles have lower foraging success than adults do and have enhanced foraging effort. Similarly, although infant howler monkeys spend a similar time foraging for invertebrates as older monkeys, they use a less accomplished technique (Boinski & Fragaszy, 1989). Instead of using older individuals' techniques for manually catching arthropods, infants would more often use an easier but less effective technique of scraping the foliage so that "an arthropod is gnawed, chewed or licked from the substrate" (p.417: Boinski & Fragaszy, 1989). Boinski & Fragaszy (1989) note that this elementary method of procuring arthropods required no hand-eye co-ordination. However, these authors lacked data on actual feeding intake rates and were unable to determine whether infants, by concentrating their efforts on scraping foliage, were able to consume a greater quantity of arthropods than adults using the same technique, or whether this

was simply an inferior technique as they suspected. There were other indications that suggested young monkeys were less proficient in their processing of other prey. For example, adults tended to prise apart the non-preferred parts (e.g. skin, peel, seeds) of some of the larger (1-5mm) fruit to avoid ingesting these but Boinski & Fragaszy (1989) note that infant faecal samples frequently contained these non-preferred parts unremoved from the whole fruit. Although juvenile chimpanzees at Budongo had slightly lower feeding intake rates than their mothers this was not a significant difference, and feeding on fruits did not appear to require any particular searching skills or complicated handling methods. In this case a more convincing argument is that juvenile chimpanzees have lower feeding rates than their mothers because they encounter higher levels of social competition at food patches. Although I have no quantitative data to test this suggestion my general impression was that juveniles were more frequently displaced from feeding sites and this is likely to have interfered with their foraging efficiency. These data on juvenile chimpanzees are consistent with Janson and van Schaik's (1993) suggestion that juvenile primates are more vulnerable during periods of low food availability.

Typically, chimpanzees open difficult food items with the co-ordinated use of their hands and mouth, with the teeth providing the physical means to break open the food item. The inclusion of difficult food items into the diet of infants marks improvements in the infant's foraging competence. The infant needs to grow in strength, co-ordination and familiarity with various food items before being capable of feeding on the full range of these difficult food items, which does not occur until their fourth year of life. It is difficult to isolate the importance of each factor. Clearly, only with age will infants develop the strength and co-ordination necessary to deal with difficult food items. A key developmental feature will be adequate

dentition, since teeth will be required to open all of these difficult food items, some of which are encased in particularly tough shells. Chimpanzee infants have two incisors and their first molars by the age of 5 months but their second upper and lower molars do not emerge until 12-13 months (Conroy & Mahoney, 1991). It is at this age that the young infant will have its complete set of primary ('milk') teeth. However, it is probably only with the development of the larger and stronger permanent dentition, and particularly the incisors which emerge at about 36-39 months (Conroy & Mahoney, 1991), that infants can open these extremely hard-shelled items. In addition, bite strength and force is likely to increase with age, both as the muscles of the jaw grow (increasing power) and the skeletal anatomy of the jaw matures (increasing load and leverage). The delay in dental development and other aspects of chimpanzees' physical development is likely to limit the ability of young chimpanzees to feed themselves at an early age. This places a large burden on mothers (Trivers, 1974) and perhaps explains mothers' willingness to share food with their infants, particularly difficult foods at a young age (Fragaszy & Bard, 1997; see Chapter 6). Finally, difficult food items probably also require a greater familiarity on the part of the infant than easy food items because they are embedded (or 'hidden') within an inedible casing (Parker & Gibson, 1977, 1979) and sensory cues will not indicate immediately that they are suitable to eat. They also have to be removed from these outer parts. The infant's experience near its mother whilst she is feeding may be salient in providing infants experience with these food items (to be investigated in Chapter 5).

It is not clear what the rate-limiting step in processing and harvesting food is, but for fruits and leaves at least it is likely to be the search time and picking rate. However, the rate-limiting step may not always reflect the efficiency with which the

food is harvested and processed. For example, for other less digestible vegetative food items the rate-limiting step may be chewing time, as indicated by Uehara's (1990) study of age-differences in pith eating of adult and adolescent chimpanzees at Mahale. Uehara noted that the feeding actions used to strip the outer parts of the stem away to expose the inner pith were accomplished in a regular manner, continuously without repetition. He suggested that this stage of the technique, the harvesting (pulling the stem from the ground) and processing (stripping the inedible parts away), were not the source of variation in intake rates. Instead, Uehara (1990) suggested that adults differed in the time that they spend chewing the (fully processed) pith and not any idiosyncrasy in the expertise of their technique. These chimpanzees extract pith from two species, *Aframomum sp.* and *Pennisetum purpureum*. Both species pose the same level of processing complexity and chimpanzees employ the same technique. Yet, when adult feeding rates on the two pith species were compared, individual within-species variation was greater for *Aframomum sp.* than for *Pennisetum purpureum*. In the case of *Pennisetum purpureum*, chimpanzees consistently selected only the softer part of the stem. Uehara (1990) therefore hypothesised that individual males varied less in their intake rate of *Pennisetum purpureum* because the level of mastication required would be invariably low, whereas for *Aframomum sp.* feeding rates would vary according to the hardness or rigidity of the pith being consumed. It is perhaps surprising that chimpanzees would not *always* select the softer part of the stem when eating pith, no matter what species they are consuming. Indeed, they have a tendency towards younger (softer and less fibrous) rather than older stems (personal observation; personal communication Kiwede T. Zephyr). However, Uehara (1990) suggested that stems of *Aframomum sp.* do not differ in density and flexibility along the length of the stem whereas *Pennisetum purpureum* does. Adult male

chimpanzees have higher mean feeding rates than adolescent males on both pith species studied, *Pennisetum purpureum* and *Aframomum sp.* This is unlikely to be due to differences in the biting power or shearing strength of adolescent and adult males but, instead, Uehara (1990) suggests it is more probably attributable to the higher frequency of social displacement that adolescent males experience.

Chimpanzees at Budongo co-ordinated the use of hands and teeth/mouth to remove embedded food items. Asymmetric bimanual co-ordination is the term given to a two-handed task that requires the use of one hand to perform one action whilst the other hand performs a different, but complementary, action on the same object. This is a particularly complex form of manipulative ability because it requires the planning and implementation of a co-ordinated and sequential set of different motor programs to achieve the same goal (Byrne & Byrne, 1991, 1993). Detailed studies in this area have been undertaken at Budongo (Stokes, 1999) and R. Byrne and N. Corp are conducting further studies at Mahale. The procurement actions briefly investigated here demonstrated there is a difference in the simple manipulations required to pull a food item into reach. Infants did not start to use both hands to procure foods until their third year. While juveniles did use these actions they used them less frequently than their mothers did. It is possible that the greater strength of mothers allows them to pull larger branches into reach to pick food and that they use both hands to do this. Or perhaps their larger size and weight of mothers prevents them from reaching food on the end of branches and they are only able to reach these outlying branches by using one hand and then the next to rake the branch in. Conversely, juveniles and infants, being lighter, are able to travel further along these branches and are able to pick these less accessible food items straight from the tree without the use of two hands. Another alternative is that

infants and juveniles lack the degree of bimanual co-ordination required to utilise these procurement techniques whilst faced with the various other spatial challenges involved in arboreal travel which can be complex (Povinelli & Cant, 1995; Russon, 1998).

Tool using is a method of food acquisition that requires great technical skill and represents the last feeding technique to be acquired by a young chimpanzee (Boesch & Boesch, in press). Some one-handed tool tasks, such as fishing for termites (*Macrotermes spp.*) at Gombe, involve can involve full lateralisation of hand use. McGrew & Marchant (1999) compared chimpanzees that solely used one hand for this task (fully lateralised) to those that were ambi-lateral, or incompletely lateralised, in that they did not use one hand exclusively. The fully lateralised individuals were significantly more successful, obtaining more termites per probe withdrawal than the incompletely lateralised individuals. Fully lateralised individuals were also more efficient at fishing for termites, gathering more termites per unit time, and they made fewer withdrawals in which no termites were acquired, but for these measures the difference was not significant between the two groups. McGrew & Marchant (1999) note that their study is foremost in establishing that laterality of behaviour is beneficial under natural and ecologically relevant conditions.

There is one particularly intriguing feature of chimpanzee behaviour that relates to the discussion of how young chimpanzees learn to forage. Chimpanzees are known to use foods not for their nutritional value, but also to exploit the medicinal properties of plants (for a review see Huffman & Wrangham, 1994). For example,

detailed field observations revealed how one female suffering from gastrointestinal illness recovered within 24 hours after picking young shoots of a *Vernonia amygdalina* plant, carefully removing its leaves and outer bark to expose the inner pith, then chewing and sucking the uncommonly bitter juice (Huffman & Seifu, 1989). This plant has a wide range pharmacological activity; it contains sesquiterpene lactones, which have anti-parasitic, anti-fungal and anti-tumour properties (Ohigashi *et al.*, 1991), and steroid glucosides, which show broad-spectrum anti-parasitic activity (Huffman *et al.*, 1996). Chimpanzees also swallow some particularly abrasive and hairy leaves whole without ever chewing them (e.g. *Commelina spp.*, personal observation; *Aspilia spp.* Wrangham & Nishida, 1983). These leaves are extremely rough sided and are defecated whole as they are ingested, still folded and undamaged. They are also swallowed at particularly high rates during periods when chimpanzees are suffering high parasite loads, with whole leaves usually found in those dung samples that contained parts of intestinal parasites (Wrangham, 1995), suggesting that these leaves are swallowed to remove intestinal parasites (Wrangham & Goodall, 1989). The origin and acquisition of these medicinal plant use behaviours is interesting. They must be particularly unpleasant and distasteful to consume because of the inherent bitterness and abrasiveness that characterises them (Huffman & Wrangham, 1994) so chimpanzees would be unlikely to discover their value by trial-and-error sampling and tasting of these plants. Effective self-medication also requires an assessment of the correct time for ingestion, specific dosage and any specialised techniques required to extract and activate the medicinal properties of the plant. Huffman and Wrangham (1994) argue that timing and dosage can be accomplished if chimpanzees directly associate particular and unusual tastes with these plants and their pharmacological properties, and then when they are ill they either actively find these plants or they become less

averse to their taste. They also note that if chimpanzees learn to use plants medicinally after watching another chimpanzee they would need to perceive their own illness in relation to other afflicted chimpanzees. Studies of medicinal plant use of Budongo chimpanzees are now being undertaken (P. Pebsworth, in preparation).

Finally, in conclusion, infant diet differed from that of their older siblings and mothers in that it contained, comparatively, a greater number of soft-shelled ripe fruits, which represent easily obtainable and processed foods. Infants began feeding on these easy foods earlier than difficult foods, which they had trouble opening either because they were too inexperienced or because they lacked the physical strength. Young infants ate easy foods significantly more often than difficult foods and these easy items were the first to be incorporated in the diet, serving as the first solid food alternatives to the still nutritionally dependent infant. These easy foods probably represent good 'weaning foods' in that they have low processing costs. For example, in humans there is a major reduction in suckling rates, termination of lactational infertility and resumption of menstrual cycling in women when their infants begin to feed on easily procured and digested foods (Bonagaarts, 1980; Short 1984; Tay, *et al.* 1996). Similarly, the early consumption of easily procured food items by chimpanzee infants would reduce their mother's lactation load. The availability of these easy food items is likely to be important to young infants and their rate of progress in consuming these easy foods will be crucial to survival since infants appear too inexperienced or lack the physical strength to open or process 'difficult' food items effectively.

The following chapter, Chapter 5, investigates the role that social factors play in the development of the feeding behaviour and the possible cues or influences that infants use to learn food choices.

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# CHAPTER 5:

## SOCIAL CONTEXT

### OF FORAGING

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#### **5.1 Introduction**

The development of a primate's discriminative ability to identify food is generally assumed to have its origin in the infant's early experiences of its mother's food. The close physical proximity of mother and infant whilst the mother is feeding regularly exposes the young primate infant in a passive way to the relevant olfactory and visual cues. It is further argued that the infant may be active in this process, approaching and attending to its mother whilst she is feeding in a manner that suggests observation is instrumental to the infant's subsequent food choices and acquisition of adult feeding habits (Box, 1984; King, 1994; Watts, 1985; Whitehead, 1986). In the case of wild chimpanzees there are even indications that mothers may directly intervene to (positively or negatively) reinforce their infant's behaviour in a manner that suggests the mother is guiding her infants' feeding choices. There are reports of mothers actively encouraging their infants to feed, and occasions where without any discernible action on the part of the infant, mothers appear to actively donate food to their infants (this is further investigated in Chapter 6). More

extensive in the literature are observations of mothers intervening to actively discourage infants handling, or attempting to feed, on items that are not normally part of the adult diet. One of the earliest descriptions of this kind was by Wrangham (1975, cited by Goodall, 1986) who reported that when a year-old infant began mouthing the seed of a fruit which adults spit out or swallow without chewing his mother responded by flicking it away from his mouth. Goodall (1971) described three similar incidents at Gombe and Nishida *et al.* (1983) described two occasions at Mahale when mothers snatched food from their infants' mouths, and discarded it. Hiraiwa-Hasegawa (1990b) reported in more detail the response of one mother to the attempts of a 9 month old infant to touch apparently unpalatable *Ficus exasperata* leaves. Hiraiwa-Hasegawa (1990b) noted that although leaves of *Ficus exasperata* are sometimes eaten by chimpanzees at Mahale, at the time of this interaction no individuals were feeding on, and actually appeared to be avoiding, the leaves of this particular tree. The infant (PN) repeatedly touched the leaves and at first her mother (FT) took PN's hand and moved it away from the leaves. As PN continued to touch and pull the leaves towards her mouth FT took the leaves from PN's hand, plucked all the leaves from the stems that were within PN's reach and finally dropped them to the ground. A smaller number of similar examples exist for gorilla mothers. Watts (1985) reported one incident where a young infant reached for an unidentified stem and pulled it toward itself but its mother pushed it away. Fossey (1979) described how a mother similarly intervened when a 7 month old infant reached out and tried to pick up faeces.

It could be argued that these cases of maternal intervention are analogous to teaching, meeting Caro & Hauser's (1992) functional definition. Caro & Hauser (1992) considered teaching as the capacity of an experienced individual to support a

naïve individual in some way to acquire knowledge, not necessarily involving intentional instruction by the teacher, although they stipulate intentionality is integral to some forms of teaching. Examining Caro & Hauser's (1992) criteria (in italics):

- *The naïve individual's behaviour was modified.*

The infant refrained from eating the non-food item

- *The experienced individual appeared to gain no proximate benefit from this behaviour.*

The mother was not protecting her food source because she prevented the infant feeding on a non-preferred food part and the intervention probably detrimental to her own feeding efficiency.

- *The naïve individual potentially acquired information that would improve its expertise in the future.*

The infant was prevented from eating something harmful and would have learnt to avoid that item in the future.

Beyond basic feeding behaviour, mothers might be expected to intervene and instruct their young when food extraction is particularly complex or intricate, for example when the use of tools is required. Chimpanzees of Tai Forest, Ivory Coast, use a hammer and anvil to crack open nuts and this has been extensively studied (e.g. Boesch & Boesch, 1981, 1983, 1984a,b, c, 1985, 1990; Boesch *et al.*, 1994). It is known that this behaviour is attained later than any other tool using technique; only as adults do individuals reach full proficiency (Boesch & Boesch, in press). Although very rare compared to the total number of observations made, there were

two observations made by Boesch (1991b) on this population that would qualify as teaching according to Caro & Hauser's (1992) working definition. Within the literature, Boesch's (1991b) two anecdotes are probably the most convincing reports of a wild non-human primate mother teaching its offspring. However, parsimonious explanations exist for these reports (e.g. Call & Tomasello, 1996) and it is clear that single anecdotes will not provide emphatic evidence. This is problematic for all field studies, but perhaps especially for those on the great apes where these reports are concentrated, because it is usually not possible to observe individuals precluded from these forms of instruction. In the first of Boesch's (1991b) examples, a mother was watching her 6 year old male offspring crack nuts and when he placed a nut badly on the anvil she intervened, picked up the nut, cleaned the anvil and then re-set the nut in better position. The male juvenile then successfully opened the nut. In the second example a 5 year old female was having difficulty with an unusually shaped hammer and when the mother approached the juvenile gave her the hammer. With her daughter watching her, the mother slowly turned the hammer to re-orientate it with a more suitable grip and hammering action. The young female then persevered using the same grip she had watched her mother use and was able to crack open nuts. However, other studies that have focused on development of the use of stone tools to open nuts have not reported any incidences of demonstrative teaching (Matsuzawa, 1994; Inoue-Nakamura & Matsusawa, 1997). Despite long-term studies of chimpanzees (that have revealed an extensive range of tool use behaviours, see Whiten *et al.*, 1999), reports of direct and active mother-infant intervention of this type are surprisingly rare.

Systematic investigations of the influence of not only mothers but also other social partners on feeding choices in free living populations are concentrated mostly

on monkeys: mantled howling monkeys, (Whitehead, 1986), squirrel monkeys (Boinski & Fragaszy, 1989), spider monkeys (Milton, 1993), vervet monkeys (Hauser, 1994) and yellow baboons (King, 1994). One of the great apes has been studied, mountain gorillas (Watts, 1985). The acquisition of adult feeding preferences in infant mantled howling monkeys (*Alouatta palliata*) appeared to require some socially-mediated learning, but the importance of these social influences was contingent on the type of food (Whitehead, 1986). This study focused on two mother-infant pairs and classified food items into two categories: leaves and fruits/fruit-like objects. Together, these two categories made up 99% of feeding time. A fruit-like object was 'any plant part with columnoid or spheroid shape' (p. 111) and so included galls, seeds, flowers, etc. These monkeys fed on 16 types of leaves but only 6 fruit-like objects. The study occurred over a period of 3 months but Whitehead (1986) only focussed on these two mother-infant pairs for one month, although there were excellent observation conditions (she notes that Glander (1975) working on the same population had subjects in view 94% of the time). Whitehead's (1986) criteria for socially dependent learning are summarised below:

*(a) Infant is attentive to its nearest neighbour and waits for this individual to ingest a food item before they attempt to feed themselves.*

*(b) Infant watches experienced model before starting to feed.*

*(c) Infant synchronises feeding and confines its feeding activity to the time that this adult model is feeding.*

*(d) Adults actively intervene to prevent infants feeding on plant parts that*

*adults do not normally feed on.*

*(e) Infants do not ingest plant parts that are avoided by adults.*

*(f) Infants that do not follow adult models will show indications of digestive illness.*

Whitehead (1986) found that in the case of infants feeding on leaves, all of these criteria appeared to be supported. By contrast in the case of infants feeding on fruits, or fruit-like objects, only one criterion, (b), was upheld indicating that learning processes independent of social factors were operating. When infants were feeding on fruits they did not remain in close proximity to, or watch, older individuals, nor did they delay feeding until the adult had begun. Rather, infants appeared to taste fruits that were not part of the adult diet. Whitehead (1986) linked these results to the higher concentrations of toxic compounds present in leaves than fruits. He proposed that infants observed and attended to social partners when they were feeding on leaves to avoid the risk of ingesting toxins. He suggested that when feeding on fruits, such a risk-aversion strategy was superfluous and instead infants sampled fruits, presumably learning through individual trial-and-error. Whitehead's (1986) study is probably one of the most systematic attempts to investigate learning conditional on experiences with older group members. However, the study was short and involved only two mother-infant pairs so only in the case of the first criterion (waiting for adult model to feed first) was a statistically significant difference in the data demonstrated. All other observations, (b) – (f), were supported by the 'majority of observations' (p.109) and no frequencies or proportions were given. This chapter will more rigorously test some of Whitehead's (1986) predictions for chimpanzee infants.

There is also counter-evidence suggesting that the early social context of foraging is not key in acquiring differential selection of food items and normal adult food preferences. For example, wild infant squirrel monkeys (*Saimiri oerstedii*) spent only small amounts of time close to their mother (less than 15% of their time within 1m of her by their third month: Boinski & Fragaszy, 1989). Moreover, they were also less likely to be close to an older individual if it was feeding, suggesting that competition over feeding resources was a more important effect than the need to observe a more experienced conspecific. When infants did approach others feeding this was just as likely to be a fellow infant as experienced adult or sub-adult (Boinski & Fragaszy, 1989). Hence, these data did not support the concept that infants were watching more experienced individuals to learn adult feeding habits. There were four anecdotal observations of where adults intervened, seemingly to alert infants to the presence of noxious prey (urticaceous caterpillars). In the case described, an adult paused to inspect a caterpillar and then continued. Later, as four infants approached the same caterpillar the adult returned to this same spot, emitted barking vocalisations and placed himself between the infants and the caterpillar. However, the authors noted that adults exhibited the same barking vocalisation and intervention to warn other individuals when they encountered opossums, snakes and owls. It therefore seems more likely that this type of adult behaviour is effective in warning about the presence of any potentially dangerous animal and not specifically transmitting information to infants about harmful food. Similarly, chacma baboons have been reported to avoid potentially dangerous food as a result of threats from a knowledgeable higher ranking male (Fletemeyer, 1978).

Milton's (1993) study of a group of immature spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island in Panama adds weight to the idea that a species-typical

diet can be attained by individual learning processes, independent of social observation, interaction and learning from more experienced individuals. A group of five young monkeys was introduced onto this island. Despite the lack of adults in the group, all of these young monkeys became competent independent foragers and fed predominately on ripe fruit, a diet which was akin to those of wild populations of adult spider monkeys studied in other parts of Panama. There were no experienced spider monkeys to guide the released immatures. Other primates on the island were primarily foliovorous (howler monkeys) or insectivorous (tamarins, capuchin monkeys, night monkeys), so the spider monkeys did not learn foraging habits from other primate species, nor did they try to exploit other available food resources. Milton's initial assumption that these foraging behaviours developed in the absence of opportunities to observe and interact with more experienced individuals may, however, be unjustified. The foraging experiences prior to capture, and even the age, of these introduced monkeys was not known. Although Milton stated that it was likely that all the monkeys released were small infants, she also reported Eisenberg (1976) noted that in 1964 five monkeys survived the introduction and that these monkeys ranged in age from 1.5 - 5 years. Since spider monkeys are weaned by the age of 3, it is likely that at least a proportion of the introduced monkeys were already feeding independently and had developed adult foraging patterns. There is the chance that one, or more individuals, provided experienced foraging models for the other released monkeys to observe, interact with and learn basic feeding patterns from. Without knowing the full history of the released individuals prior to capture and their level of foraging competence at the time of release, it cannot be proved unequivocally whether the released monkeys learnt feeding patterns by social means (either before or after release) or, as Milton suggested, by individual trial-and-error learning.

This chapter will investigate the social context of the early foraging of chimpanzee infants at different stages of development and examine these as opportunities for social learning. The aim is to identify whether a social element (in terms of the mother's behaviour) is functional or important to the infant's early foraging experiences and whether infants alter their behaviour to increase the likelihood of acquiring information from their mother. Clearly, to observe its mother feeding an infant must be close to her and attending. In Chapter 3 the time that infants spent in close proximity to their mother was investigated. In a similar manner the time that infants spend within arm's reach to their mothers to observe and interact with them is examined, but within the context of the mother's feeding activity. Whilst it is predicted that younger infants will have more opportunities to interact and observe their mother whilst she is feeding than older infants, if infants do spend time close to their mother in order to observe her feeding behaviour the following predictions should be supported:

- Infants spend more time within arm's reach of their mother whilst she is feeding compared to when she is engaged in non-feeding activities.
- Infants will spend more time within arm's reach of their mother when she is feeding on difficult foods compared to when she is feeding on easy foods.
- Young infants attend at higher rates to their mothers feeding than older infants and juveniles.
- Infants attend to their mothers at higher rates when they are feeding on difficult foods than when they are feeding on easy foods.

- Infant attention to their mother's food will precede the infant's first attempts at feeding: there will be a negative correlation between infant attention to mother's food and infant feeding behaviour.

There were anecdotal suggestions from early studies that the initial foraging attempts of primate infants begin with infants feeding synchronously with their mother on the same food items as she does (chacma baboons: Hall, 1963; ring-tailed lemurs: Sussman, 1977; mantled howling monkeys: Whitehead, 1986). Quantitative data suggest that vervet infants that synchronise feeding with their mother survive longer (Hauser, 1994) and synchrony may also be important to acquisition of food preferences in infant baboons (King, 1994), and infant gorillas (Watts, 1985). If infants synchronise the timing of their feeding with their mothers to learn appropriate food choices the following predictions should be supported:

- Young infants who are not yet feeding independently play with food more often when their mother is feeding than when she is engaged in non-feeding activities.
- Infants synchronise their feeding bouts with the times that their mother is feeding but juveniles will not be constrained to feed at the same time periods as their mother.
- Infants will be more likely to feed on the same food item as their mother is feeding on as opposed to the other food items available. However, the feeding choices of juveniles will not show such high levels of correspondence with their mother.

- Within the same feeding bout older infants and juveniles will be more likely to feed at times that their mother is not feeding and more likely to feed on a food item that their mother is not feeding on.
  - Infants will be more likely to synchronise their feeding with their mother when she is feeding on difficult foods.
-

## 5.2 Methods

### 5.2.1 Definitions

For definitions of general behavioural activities see section 2.4.5.b. In addition the following behaviour is specific to this chapter.

**Attention to mother's food:** Subject was in physical contact or within arm's reach of its mother and looking at (orientated towards) its mother's food (the mother must have physical contact with the food item) for more than 3 seconds. This involved food that the mother was processing, whether the food was in the hand or mouth. This was distinguished from a passive solicitation, which is a request or appeal for food. To be scored as a passive solicitation for food the infant's head had to be extremely close (within 20 cm of its mother's food) or the infant made some type of other begging gesture (see section 6.2).

Clearly, an infant's solicitations for food could be considered a particular type of attention to food but a solicitation for food is distinguished by its intensity, rather than being simply inquisitive behaviour, it is a real attempt to obtain food. For this reason these episodes are analysed in Chapter 6.

Authors have used different terms in describing feeding synchrony. For example, King (1994) divides Hauser's (1994) 'feeding synchrony' into co-feeding (feeding at the same time on the same item) and feeding synchrony (feeding at the same time but on a different item). I chose the following terminology:

<b>Synchronous feeding:</b>	Mother and infant were both feeding and they were feeding on the same food item.
<b>Discordant feeding:</b>	Mother and infant were both feeding but they were feeding on different food items.
<b>Asynchronous feeding:</b>	Only the offspring was feeding, the mother was engaged in some other type of non-feeding activity.

### 5.2.2 Data collection

Data were collected *Ad libitum* for any observations of maternal intervention, either encouragement or discouragement. All other data were extracted from continuous and instantaneous point samples.

### 5.2.3 Data analysis

The time that infants spent within arm's reach whilst their mother was foraging was investigated as a measure of 'opportunity' that infants were close enough to interact and observe their mother while their mothers were feeding. The proximity feeding

index was calculated as  $MFE_{\text{war}}/MFE$ , where  $MFE_{\text{war}}$  was the maternal feeding time whilst the infant was within arm's reach and  $MFE$  was the total maternal feeding time.

Maternal activity was divided into three proportions to investigate infant proximity:

$$MFE_{\text{war}}/T_{\text{war}}$$

$$MSO_{\text{war}}/T_{\text{war}}$$

$$MOT_{\text{war}}/T_{\text{war}}$$

Where:  $MFE_{\text{war}}$  = Maternal feeding time whilst the infant was within arm's reach.

$MSO_{\text{war}}$  = Maternal socialising time whilst the infant was within arm's reach.

$MOT_{\text{war}}$  = Maternal time spent resting or moving whilst the infant was within arm's reach.

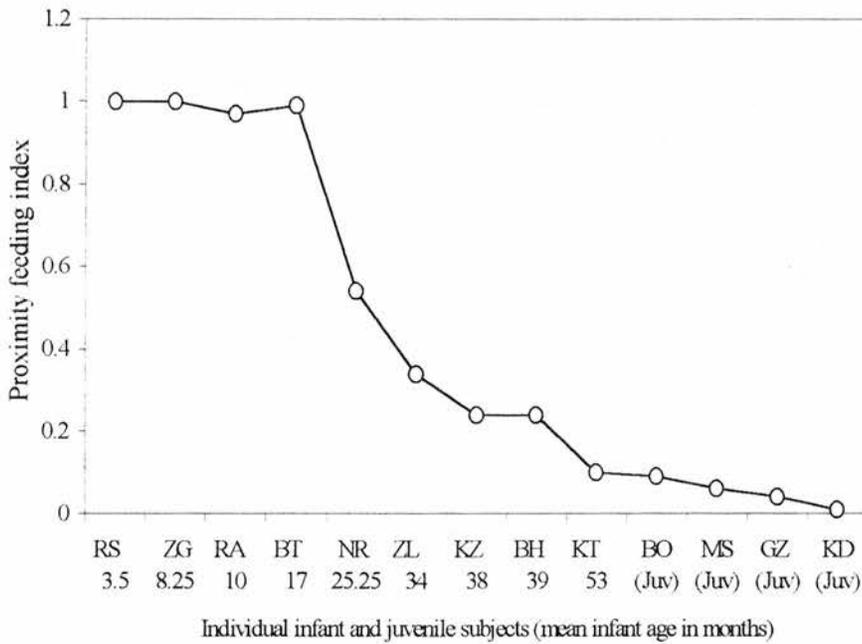
$T_{\text{war}}$  = Time that the infant spent within arm's reach.

Data on feeding synchrony were extracted from instantaneous sample data on mothers, infants and juveniles. The start of each infant or juvenile feeding bout was scored as synchronous, asynchronous or discordant according to the definitions. All statistical tests were non-parametric and two-tailed. They were applied across the four age categories: young infants (n=5), older infants (n=4), juveniles (n=4), and mothers (n=9). In cases where  $df = 1$ , the  $\chi^2$  was corrected by the Yates' Correction for Continuity.

### 5.3 Results

With the exception of food sharing events (to be investigated in Chapter 6), no cases of direct maternal encouragement or discouragement of infant or juvenile behaviour were observed. The feeding proximity index was investigated to determine the period of development over which the infant was spending more time with its mother whilst she was feeding and plotted as a function of mean age (see Figure 5.1).

**Figure 5.1:** The proximity feeding index of individual infants, with mean age, and juveniles.



There was a strong negative correlation between the proximity feeding index and infant age (Spearman's Rank Correlation  $R_s = -0.975$ ,  $p < 0.001$ ; see Figure 5.1). As the infant became older its opportunity to observe and interact with its mother whilst she was feeding thus decreased. In the infant's third year the feeding proximity

index fell below 0.5, indicating that infants were no longer spending more time within arm's reach of their mother whilst she was feeding than at greater distances. By the end of infancy, individuals were spending similar amounts of time near their mother whilst she was feeding as juveniles (KT, mean age 53 months, feeding proximity index: 0.10; juvenile mean feeding proximity index: 0.05, SE=0.016).

### 5.3.1 Maternal activity and proximity

Maternal activity was divided into feeding and non-feeding activities (socialising, resting and moving).

**Table 5.1:** Percentage time that infants and juveniles spent within arm's reach of their mother when she was feeding ( $MFE_{war}$ ), socialising ( $MSO_{war}$ ) or involved in other activities, resting and moving ( $MOT_{war}$ ).

Age Category	Individual	Mean age (in months)	$MFE_{wa}$	$MSO_{war}$	$MOT_{war}$
Young infant	RS	3.5	45	21	34
Young infant	ZG	8.25	40	23	36
Young infant	RA	10	64	14	17
Young infant	BT	17	61	15	23
Young infant	NR	25.25	26	14	27
Older infant	ZL	34	15	20	22
Older infant	KZ	38	12	15	12
Older infant	BH	39	12	12	15
Older infant	KT	53	5	12	12
Juvenile	BO	JUV	3	12	4
Juvenile	MS	JUV	3	5	5
Juvenile	GZ	JUV	1	12	3
Juvenile	KD	JUV	0	17	4

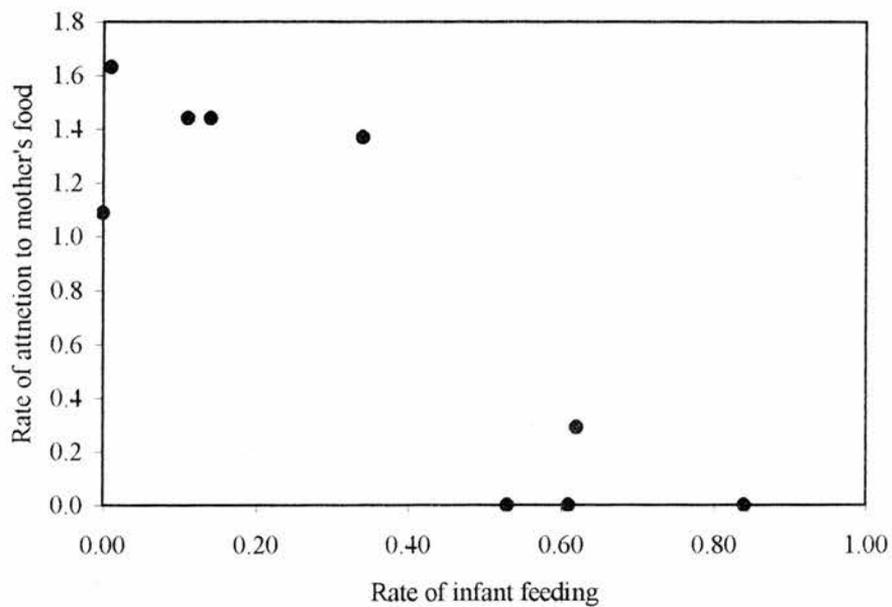
Overall, testing across all infants (i.e. young and older) offspring were not more likely to be within arm's reach of their mother when she was feeding than when she was resting or moving (see Table 5.1; Wilcoxon matched-pairs signed-ranks test All infants:  $Z = -0.841$ , *ns*). Nor were they more likely to be within arm's reach of their mother when she was feeding than when she was socialising (see Table 5.1; Wilcoxon matched-pairs signed-ranks test All infants:  $Z = -1.680$ , *ns*). However, testing young infants alone showed that in their early years infants were significantly more likely to be within arm's reach of their mother when she was feeding than when she was resting or moving (see Table 5.1; Wilcoxon matched-pairs signed-ranks test: Young infants  $Z = -2.023$ ,  $p < 0.05$ ). These young infants were also more likely to be within arm's reach of their mother when she was feeding than when she was socialising but only at levels that approached significance (see Table 5.1; Wilcoxon matched-pairs signed-ranks test  $Z = -1.753$ ,  $p = 0.08$ ). Hence, young infants did selectively spend more time close to their mother when she was feeding compared to when she was resting or moving, although older infants did not.

### 5.3.2 Attention to food

Infant's attention to their mother's food was calculated as a rate (frequency of infant's attention to its mother's food per hour of mother's feeding). Infants did not display a high rate of attention to their mother's food (see Figure 5.2: less than 2 events per hour of mothers' feeding time). There was no significant difference in infant's attention to difficult foods and attention to easy foods (Wilcoxon matched-pairs signed-ranks test  $Z = -0.105$ , *ns*). Therefore for subsequent analyses foods were not separated into easy and difficult.

Young infants attended to their mother's food significantly more often than older infants (Young infants mean = 1.39 SE=0.09, Older infants mean = 0.07, SE=0.07; Mann U Whitney test,  $p < 0.02$ ). In addition, there was a negative correlation between the rate at which infants attended to their mother's food and the time they spent feeding independently (Spearman Rank Correlation  $R_s = -0.711$ ,  $p < 0.05$ ; see Figure 5.2).

**Figure 5.2:** Offspring's rate of attention to mother's food (frequency of infant's attention to its mother's food per hour of mother's feeding) as a function of the rate of infant's feeding (infant feeding time as a proportion mother's feeding time).

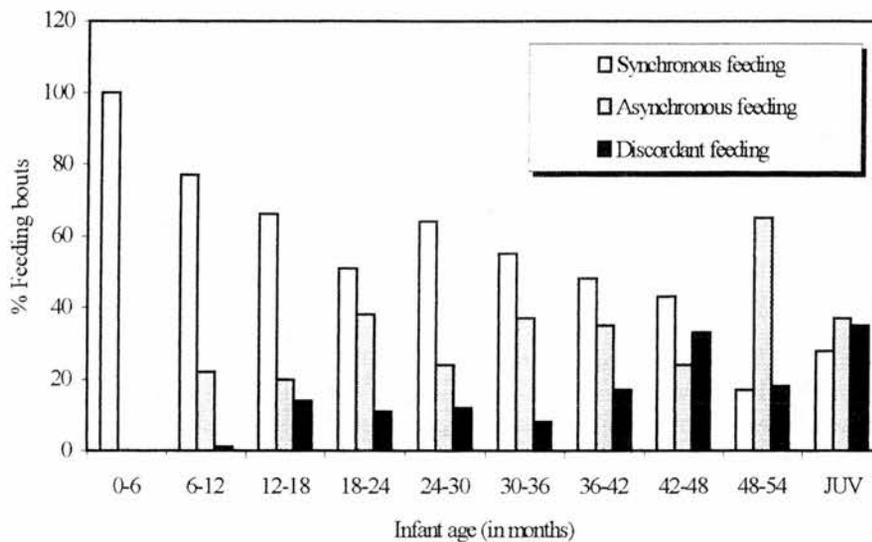


### 5.3.2 Feeding synchrony

There were no significant differences between easy and difficult foods for feeding synchrony (Easy: mean = 54 SE=7, Difficult: mean = 53 SE=10, Wilcoxon matched-pairs signed-ranks test  $Z = -0.510$ , *ns*), feeding asynchrony (Easy: mean =

29 SE=3, Difficult: mean = 22 SE=6, Wilcoxon matched-pairs signed-ranks test  $Z = -1.021$ , *ns*), or discordant feeding (Easy: mean = 16 SE=4, Difficult: mean = 25 SE=9, Wilcoxon matched-pairs signed-ranks test  $Z = -0.534$ , *ns*). Hence, foods were not separated into easy and difficult for these analyses.

**Figure 5.3:** Synchronous, asynchronous and discordant feeding. Data were pooled within 6 month age blocks for infants and into a single post-weaned category ('JUV') for juveniles.



In their first attempts at feeding independently infants always fed when their mother was feeding and on the same food item as their mother (synchronous feeding: see Figure 5.3). As they matured, infants started to feed at times their mother was not feeding (asynchronous feeding) and in their second year sometimes fed on food items that their mother was not feeding on (discordant feeding). On the whole, throughout their period of nutritional dependence, infant chimpanzees were significantly more likely to feed when their mother fed than at times when she was not feeding (Synchronous feeding: mean = 66, SE=7; Asynchronous feeding: mean = 25, SE=4; Wilcoxon matched-pairs signed-ranks test  $Z = -2.549$ ,  $p < 0.02$ ; see

Figure 5.3). They were also more likely to feed on the same food item as their mother (Synchronous feeding: mean = 66, SE = 7; Discordant feeding: mean = 9, SE=3; Wilcoxon matched-pairs signed-ranks test  $Z = -2.668$ ,  $p < 0.01$ ; see Figure 5.3). Conversely, juveniles were not more likely to feed when their mother was feeding (Synchronous feeding: mean = 27, SE=3; Asynchronous feeding: mean = 39, SE=5; Wilcoxon matched-pairs signed-ranks test  $Z = -1.826$ , *ns*; see Figure 5.3), nor were they more likely to feed on the same food item as their mother (Synchronous feeding: mean = 27, SE=3; Discordant feeding: mean = 35, SE=3; Wilcoxon matched-pairs signed-ranks test  $Z = -1.826$ , *ns*; see Figure 5.3). For older infants, particularly in the 48-54 month age block, these patterns of feeding synchrony, feeding asynchrony and discordant feeding more closely resembled that of juveniles, who were not attuning their feeding with their mothers (see Figure 5.3). Age-differences were further investigated. Older infants and juveniles fed asynchronously and discordantly more than young infants, this was a significant for discordant feeding and not significant, but approaching significance, for asynchronous feeding (Kruskal-Wallis test feeding discordant:  $\chi^2 = 9.219$ ,  $p < 0.05$ ; asynchronous feeding:  $\chi^2 = 5.442$ ,  $p = 0.066$ ). Young infants spent significantly more time feeding synchronously than older infants and juveniles (Kruskal-Wallis test feeding discordant:  $\chi^2 = 9.270$ ,  $p < 0.05$ ).

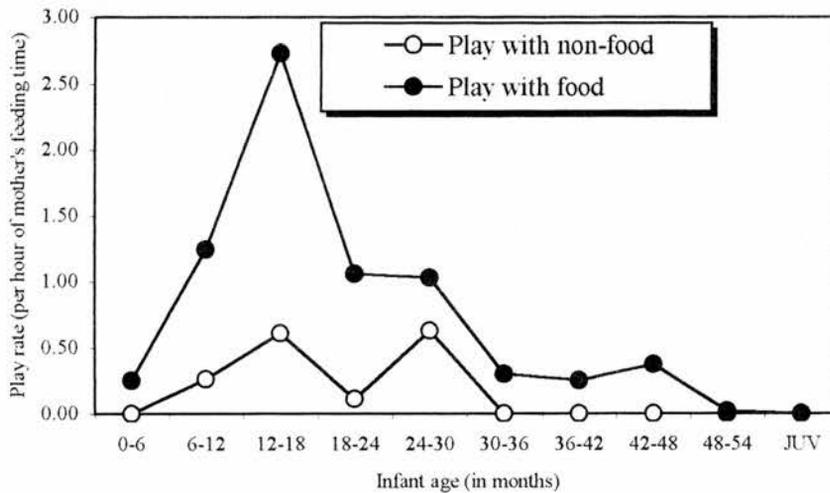
### 5.3.3 Playing with food

When playing with easy and difficult foods was expressed as a rate per hour of mother's feeding on those foods, infants did not play with easy foods more often

than they played with difficult foods (Wilcoxon matched-pairs signed-ranks test  $Z = -0.210$ , *ns*). Therefore data for easy and difficult foods were pooled.

As might be expected, younger infants played with food significantly more often than older infants and juveniles (Kruskal-Wallis test  $\chi^2 = 8.695$ ,  $p < 0.02$ ; see Figure 5.4). When the rate of playing with foods was compared to the rate of playing with non-foods, infants played with foods significantly more often than they played with non-foods (Wilcoxon matched-pairs signed-ranks test  $Z = -2.521$ ,  $p < 0.02$ ; see Figure 5.4).

**Figure 5.4:** Playing rate with non-food items and food items per hour of mother's feeding time



It is likely that infants' playing with food was facilitated by their own mother's feeding activity, because across subjects infants were significantly more likely to play with foods when their mother was feeding than when she was engaged in any other activity (Chi-squared test  $\chi^2=28.7$ ,  $p<0.01$ ; Table 5.2).

**Table 5.2:** Frequency of bouts for infants playing with food

<b>Infant</b>	<b>Whilst mother is Feeding</b>	<b>Whilst mother is resting, socialising or moving</b>
ZG	1	0
RA	7	0
BT	4	3
NR	6	0
ZL	1	0
KZ	0	3
BH	2	1
KT	1	1

## 5.4 Discussion

The period of development when an infant had the greatest opportunity to observe and interact with its mother over food appeared to be limited to the first two years of life. During this time infants spent more time than not within arm's reach of their mother whilst she was feeding. As the infant matured it increasingly explored the area further from its mother (see Chapter 3). So, as expected, as infants became older the time they spent near their mother whilst she was feeding gradually declined. By the end of infancy, individuals were close enough to interact and observe their mother for only one-fifth of her feeding time.

In order to acquire feeding skills chimpanzee infants might be expected to selectively spend time near their mother when she is feeding compared to those times that she is engaged in other activities. This was the case with young infants (those infants under the age of 2.5 years), who spent significantly more time within arm's reach of their mother when she was feeding compared to when she was resting or moving. Since infants at this age are quite dependent on their mother for transport, it was particularly noteworthy that they should spend more time within arm's reach of their mother when she was feeding compared to when she was moving. In contrast, older infants did not appear particularly interested in their mother's feeding behaviour: they were no more likely to approach close to their mother when she was feeding than they when she was engaged in other activities. Although it was possible that mothers deter older infants from spending time near them when they are feeding, no overt aggressive interactions were observed between mothers and their infants of a sort that would suggest such an effect. In fact mothers

are characterised by their extremely tolerant attitude to their infants within the context of feeding, often allowing infants to scrounge their own food (see Chapter 6). Since infants in their second year are beginning to feed independently (see Chapter 4), it was more likely that these older infants were engaged in their own foraging attempts whilst their mother was feeding (supported by the feeding synchrony data below).

Although infants did show some direct attention to their mother's food (definition, section 5.2.1, distinguished from and an infant passively soliciting food, for definition see section 6.2.1), this occurred at low rates. Infants did not selectively attend to foods that they could not procure or process independently, suggesting that they were not directing their interest where they had the most to learn from their mother. However, young infants did attend to their mother's food at significantly higher rates than older infants and juveniles, and there was a negative correlation between the rate at which infants attended to their mother's food and the amount of time they spent foraging independently. Young infants also played with food at significantly higher rates than older infants and juveniles. Thus, if infants' interest in their mother's food and their own playful handling and mouthing of food are important determinants in cueing the infant to appropriate food, their effect will only be significant in an infant's first two years of life. Indeed, watching the mother and playfully handling and mouthing food may be precursors to infants becoming competent foragers, only at a later age with the development of sufficient dentition and jaw musculature are infants able to ingest these foods (see section 4.4).

The visual inspection, manual investigation, and mouthing or tasting (without ingestion) of potential food items by playing with them were opportunities not only to glean visual and olfactory cues but also other, further sensory cues (e.g. astringency, bitterness). Infants would not be able to experience all of these cues by simply spending time close to their mother whilst she was feeding, nor by watching her. Handling and mouthing food would allow individual appraisal of the visual and mechanical properties of suitable items, attributes that probably include size, texture, colour, and density. Such individual experience with different items is probably more important in the early stages of foraging than attending to the mother as a foraging model because observation of her feeding behaviour will not help in these discriminations. The physical features of the item are key not only to make perceptual judgements about whether a particular item is suitable to eat, but also in the refinement of foraging decisions. The infant's subsequent foraging efficiency within the same food patch will be conditional on its ability to assess the quality of individual items, their sweetness and astringency, before ingestion. These early playful attempts may allow discrimination of the ripeness of the item and its level of toxicity without any of the nausea inducing consequences of ingestion.

The early playful behaviour with different food items is consistent with the general impression that infants are naturally more inquisitive and curious when they are younger. The consequences for a young chimpanzee in making errors and ingesting an unsuitable item are not likely to have serious, at least not fatal, effect because such small quantities are consumed. In any case these, seemingly small, risks may be outweighed by the benefit and importance of sampling potential foods in a constantly changing environment, which is particularly the case for chimpanzees. The diversity of chimpanzee diet both within populations (e.g.

Nishida & Uehara, 1983) and across different populations (e.g. McGrew, 1983; McGrew *et al.*, 1988; Nishida *et al.*, 1983) is indicative of chimpanzees' dietary opportunism. Foods vary in availability both across the year and between years and this uneven distribution and unpredictability of food sources requires dietary flexibility. Sampling new species as environmental conditions change to incorporate them into the diet is important in order to respond rapidly to changing environmental conditions. Not only would this optimise feeding habits to the current environmental condition but it would also favour adaptation to the wide geographical range and diversity of habitat types that chimpanzees have managed to colonise. Hence, it is likely to be an important and prominent feature of their feeding patterns and behaviour. The tendency to sample novel foods appears to be most conspicuous in immature chimpanzees as it is in infant gorillas (Watts, 1985) and infant capuchin monkeys (Fragaszy *et al.*, 1997a,b). Young chimpanzees are more likely to adopt new foods (Nishida *et al.*, 1984) and evidence suggests that new feeding habits seem to be started by juveniles (Takasaki, 1983), as are a broader range of behavioural innovations (Kummer and Goodall, 1985).

To some extent maternal feeding activity appeared to facilitate infants' interest in handling and mouthing (i.e. playing and tasting but not ingesting food), since infants were more likely to initiate this type of behaviour when their mother was feeding. This pattern of social facilitation probably also explains why playful handling and mouthing of objects was more often directed towards foods than non-food items. It is suggested that in some free-ranging monkeys there is a general neophobia towards new foods, which prevents ingestion of toxic substances and is specific to those plant foods with the highest concentrations of these (Glander, 1982; Milton, 1993; Whitehead, 1986). Studies in captivity also demonstrate social facilitation of

feeding habits. For example, juvenile and adult capuchin monkeys are more likely to feed on novel foods if they feed with social partners in comparison to conditions when they feed alone, and the same effect does not occur with familiar foods they encounter everyday (Visalberghi & Fragaszy, 1995). However, Fragaszy *et al.* (1997b) later found that infant capuchin monkeys are not cautious towards novel foods and in fact fed on novel foods more frequently than familiar foods in either condition – alone or with social partners. They suggested two alternatives for this difference between the two studies: (i) an age difference in the avoidance of novel food items – older animals are neophobic but infants are not, or (ii) group-specific difference in the avoidance of novel food items. A third is also possible. Fragaszy *et al.*'s (1997b) definition of 'eat' is somewhat puzzling. They recorded three feeding-related behaviours: 'interest', 'picks up food' and 'eat'. They note: "If the subject put the food in its mouth, it was labelled as Eat. A new bout of eating was scored only after the previous piece of food had been consumed or abandoned" (p.1340). Clearly, infants frequently pick up various food items and manipulate them for a varying amount of time without ever subsequently ingesting them (see before). This includes not only manipulating the food item within the hand but, more commonly, within the mouth. Fragaszy *et al.*'s (1997b) definition of 'eat' would include this infant 'mouthing' behaviour. Infants in their study may have been picking up food items and 'eat' being recorded without the infant ever having ingested any of these items. This is perhaps supported by the fact that the frequency of eating a food was independent of age in this study, a surprising result. It remains possible, then, that these infants were 'mouthing' novel foods as often as familiar foods but not ingesting them as frequently. Since the juvenile and adult monkeys will only ingest food and not 'mouth' them in this playful infant manner, then it is

possible that this difference qualifies as an alternative explanation to the apparent divergent results.

It is argued that if in their first attempts at feeding infants synchronised their feeding with their mother then they would be maximising opportunities to gain relevant feeding cues (Hauser, 1994; King, 1994; Watts, 1985). Infant chimpanzees did attune their early feeding attempts in both timing and food choice to their mothers feeding. Hiraiwa-Hasegawa (1990b) similarly found that infants in their first and second year always fed on the same food item as their mother but after their third year infants often fed on a different food item to their mother. Chimpanzees showed a clear developmental trend in feeding synchrony. The feeding of younger infants was more likely to co-occur and correspond with their mother's feeding than was the case of older infants and juveniles. Hiraiwa-Hasegawa's (1990b) found likewise asynchronous feeding increased with infant age, these Mahale chimpanzees were feeding asynchronously for about 50% of the time at 5 years old. This figure is similar to the corresponding figure for Budongo infants (65% asynchronous and discordant feeding in the first half of their fifth year). Similarly, young gorillas coincide their first feeding attempts with the periods when their mothers are feeding, and so ingest the same food item that their mother was feeding on, or one that she had ingested earlier but within the same feeding bout (Watts, 1985). Further, Watts (1985) found that in those times that infants did not synchronise their feeding with that of their mother (for example, they fed as their mother was resting) the infant was significantly more likely to select a plant part that did not normally comprise part of the adult diet. Hauser's (1994) study suggested that feeding synchronously with the mother has direct benefits, not just to an infant's foraging success but ultimately its reproductive success. He studied 30 mother-infant pairs of vervet

monkeys over a two year period and found that vervet infants that fed synchronously and on the same food item as their mother survived longer. This was despite the fact that Hauser found no significant differences in the survival rate with the likelihood of encountering predators or habitat quality. Because there was variation both between individual infants and between groups he did find that infants aged over 4 months living in high quality habitats had a higher percentage of same food-synchronous feeding bouts. For this reason he cautioned that the feeding synchrony effect was difficult to separate from that of habitat quality, recognising that further data on infants living in the same habitat would be required to confirm this result.

Some caution is needed regarding inter-species comparisons. In primates that feed principally arboreally, infants will usually be feeding in the same species of tree as their mother and therefore feeding choices will be confined to food parts of that species. In the case of primates that feed on the ground, (baboons, for example), infants close to their mother will be surrounded by a wider selection of species, and it may be particularly important for these primate infants to synchronise their feeding with their mothers. Unfortunately, in this study very few feeding observations were made on the ground (see section 2.4.1.c). Otherwise, it would have been interesting to have been able to investigate the degree of feeding synchrony for chimpanzee infants when they were feeding on the ground in comparison to when they were feeding in trees.

Feeding preferences can be influenced by co-feeding (Hikami *et al.*, 1990). When mother-infant Japanese monkeys (*Macaca fuscata*) were placed in a paired-feeding condition they increased the similarity of their feeding choices. Foods that

had been consumed by either the mother or infant before they were placed in a paired feeding situation came to be consumed by both and continued to be consumed by both throughout this paired situation, whereas those foods eaten by neither were never consumed. In an experimental test infants were conditioned to avoid two foods, whereas mothers to avoid just one. When placed in the paired feeding situation the infant then began feeding on the food that its mother continued to feed on despite the infant having previously been artificially conditioned to be aversive to it.

Data from this study showed that infant feeding synchrony was not contingent on the type (difficulty) of food being eaten. The hypothesis that infants would be more likely to synchronise feeding with their mother when she was feeding on difficult foods was rejected. This is perhaps surprising considering that in her study of savannah baboons, *Papio cynocephalus*, King (1994) found that infants were more likely to feed at the same time and on the same food item to differing extents depending on the food type. They would synchronise both the periods of feeding and select to feed on the same food at the highest rates on corms, intermediate rates on fruits, seeds and tree gums, and at the lowest rates on leaves and stolons. This seemed to correlate with the level of processing required for each of these food types. Corms are particularly difficult for young baboons to procure and process because they need to be pulled out of the ground and infants lack the strength and expertise to remove them effectively until they are about 6 months old. Leaves and stolons are easy for young baboons to process and infants did not synchronise their feeding at such high rates on these food items. King (1994) doubted that this was an artefact of corms being aggregated and clumped in their distribution, forcing individuals to feed together on them. Instead, she found it more likely that infants

synchronised their feeding with adults because somehow it allowed them to watch other individuals whilst practising at the same time to pull up corms themselves (King, 1994).

So far the parameters investigated in this chapter offer no convincing evidence that infants' observation of their mother's feeding behaviour was critical to their early foraging experiences. Although young infants did selectively spend time within arm's reach of their mother whilst she was feeding, in other respects they did not modify their behaviour in a manner that demonstrated they were actively increasing the likelihood of acquiring feeding information from their mother. For example, they did not attend to their mother's feeding behaviour at high levels, nor did they focus their observation on foods that they had difficulty opening. More striking was the general manner in which infants' initial foraging attempts were facilitated by maternal feeding activity, which seemed to initially direct infants towards playful handling and tasting of food items rather than non-foods and later infants attuned their feeding with their mothers. However, it was noteworthy that infants were no more likely to do this with foods that they lack the skill and knowledge to process.

It is possible that social learning is only evident when particular tasks need to be learnt. If this is so, social learning should be particularly adaptive in situations where complex or novel behaviours have to be learnt, perhaps specific to the domain of learning more technical skills, such as tool use (Byrne & Russon, 1998). This thesis has been concerned with basic foraging behaviour because no tools are used in the feeding context at Budongo (personal observation; also see Whiten *et al.*, 1999).

However, where apprenticeship is considerably longer, as in the case of tool use (e.g. 6-7 years to learn to crack nuts: Boesch & Boesch, 1983), it might be expected that learning from the mother is particularly important (Parker, 1996). However, the evidence suggests that chimpanzees learn to use tools to crack nuts by piecing together sequences of actions in an idiosyncratic manner, sometimes using actions that are non-functional in opening the nut (Inoue-Nakamura & Matsusawa, 1997; Matsuzawa 1994). For example, in their first year chimpanzees begin with various single-object manipulations: touching, hitting and rolling the stone and playful mouthing of nut, obtaining food from their mother. By the age of two years the young chimpanzee has begun to push the nut against the stone, place the nut on the stone, hit the nut with the hand or foot, hold the stone and push the nut against it. Typically, youngsters were recorded to reiterate each action several times at this age but only as 3 year olds did they begin to combine these object-association manipulations in an increasingly ordered manner, for example placing the nut on the anvil stone and hitting it with the hand. Finally, when it is in its fourth year the chimpanzee's co-ordination had increased sufficiently for it to suitably incorporate these various actions into an ordered sequence, successfully using one stone as the anvil, and one as the hammer to open the nut. At this age the young chimpanzee was still using the one hand to complete the entire task, with the same hand placing the nut on the anvil, as holding the hammer to strike the nut, as retrieving the kernel from the opened nut. Infants required further practice to achieve the same bimanual co-ordination and proficiency as the adult technique (Inoue-Nakamura & Matsusawa, 1997; Matsuzawa 1994). However, in acquiring the final refined ability Inoue-Nakamura & Matsusawa (1997) note that youngsters "did not copy the motor patterns or the way to relate nuts with stones which were shown in the tool use by mothers" (p. 172). It is difficult to separate deficiencies in performance due to

insufficient motor co-ordination and incomplete functional comprehension of a technical task (Boesch & Boesch, in press). Nonetheless, it is striking that mothers did not appear to be critical to the learning process. For example, one young female never learnt to crack nuts even though her mother was one of the most skilled nut crackers within the group. This seemed to be because the young female sustained a snare injury which disabled her for a period and although she recovered the full use of her limb the injury had prevented her practising these tool using techniques (Matsusawa, 1994). It is clear that even in tasks that were cognitively demanding and required complicated technical skill, individual experience was important and may have been more effective than observation in acquiring the correct technique. Social learning limits assimilation of information to the confines of the visual perspective and does not provide information about the physical properties (such as the size, shape, weight, hardness) of the tools being used (Boesch, 1996a). Individual experience is important to assess the strength required to complete the task, particularly given it will need in the future to be repeated under different circumstances with different tools that vary in these qualities (Boesch, 1996a). In complicated tasks it may be more appropriate for an inexperienced individual to break down sequences, perfect single elements and recombine them to complete the task in the most effective way for itself. It has been argued that imitation can still occur in such circumstances because the hierarchical organisation of actions and the higher level of program is copied (Byrne & Russon, 1998).

There is distinctive food-related interaction that we have not considered in this chapter: mother-infant food sharing. King (1994) argued that infants scrounging food from their mothers are acquiring not only a nutritional subsidy but also

information that may improve their future discriminative ability. The next chapter investigates this phenomenon as an opportunity for social learning.

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# CHAPTER 6:

## FOOD SHARING

The robb'd that smiles,  
steals something from the thief

*Shakespeare*

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### 6.1 Introduction

Many mammalian species, but particularly social carnivores and primates, have been reported to share<sup>9</sup> food items between individuals both in the wild and in captivity (for a review see Feistner & McGrew, 1989). In captivity there are many more reports of this behaviour, but this is perhaps explained by the intense social spacing, abundant food resources which are available on predictable schedules, and a correspondingly high probability of food-related interactions. Clearly, observation conditions in field settings are more difficult, but in the wild, food sharing does

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<sup>9</sup> In this chapter I will continually be referring to 'sharing' of food. I agree with Feistner & McGrew (1989) that in nearly all cases this behaviour is better described as one animal *tolerating* the *food scrounging* behaviour of another. However, I use the phrasing 'food sharing' synonymously with 'food transfer' for ease of wording. I recognise that definition is important and in section 6.1.1 classification of different types of food sharing and transfer are discussed.

appear to be more limited, occurring predominately between mothers and their offspring. There are numerous anecdotal reports of this behaviour in primates, but it is only in chimpanzees and a sub-family of New World monkeys, the *Callitrichidae*, that food sharing appears to be a well-developed and typical feature of infant development. Hence, evidence suggests that in these species food sharing may be a particularly important evolutionary adaptation.

Across all non-human primates the only notable exception to the characteristic food sharing across mother-infant dyads, is the inter-adult sharing of animal prey and occasionally artificially provisioned plant foods by chimpanzees (Boesch, 1994; McGrew, 1975). It is, however, highly unusual for adults to share any naturally occurring plant food items (McGrew, 1975). On the rare occasions this has been observed it has involved uncommon (and seemingly 'prized') large fruits (Bethell *et al.*, in press; personal observation). Bethell *et al.* (in press) suggested that this rare type of adult-adult plant food sharing resembles meat sharing in terms of adaptive benefits to individuals (for a discussion of the social benefits of sharing meat see Boesch, 1994). Work with captive primates suggests that such individual benefits also underlie inter-adult plant food sharing in chimpanzees as these studies suggest that a reciprocal mechanism operates by which food is shared in exchange for grooming (de Waal, 1989, 1997). Whilst such mechanisms have not been documented in natural conditions, it is apparent that adult-adult sharing of food in the wild is unique to chimpanzees and differs from mother-infant food sharing. Firstly, adult-adult sharing in chimpanzees is much less frequent and secondly, it is restricted to highly-valued, contested food items (Boesch, 1994; McGrew, 1975; Silk, 1978). Consequently, adult-adult food sharing is likely to have a different

adaptive function and selective advantage than the more common mother-infant food sharing.

Like the common chimpanzee, bonobos share both plant and animal foods but in contrast to the common chimpanzee, adult female bonobos frequently share large plant foods (Kano, 1980; Kuroda, 1984; White, 1994). This bonobo female adult-adult plant food sharing parallels the meat sharing of common chimpanzees in a functional manner, such that food is shared on a reciprocal basis and often in return for future sexual access (Kuroda, 1984). The fruits shared are very large; at Lomako only three large fruits (weighing 0.9–8.9 kg) were shared (White, 1994) and interestingly one of these was *Treculia africana*, the same species involved in the sharing events recorded by Bethell *et al.* (in press). Consequently, White's (1994) first suggestion that the more common adult-adult plant food sharing among bonobos is related to the occurrence of large fruits in central Zaire may not hold. These appear to be available at least to some populations of *Pan troglodytes*, although whether at similar levels of availability it is not known. Her second suggestion probably holds more weight, that the difference reflects the major distinction in social organisation between common chimpanzees (male-bonded: Wrangham, 1987) and bonobo chimpanzees (female-bonded: Kuroda, 1979, 1980; White, 1988, 1992). Hence, the close relationships between males in common chimpanzees means that on the rare occasions when adult-adult sharing of plant food is observed, it occurs between males (Bethell *et al.*, in press). Similarly, the more common meat sharing occurs most frequently between males or from males to other adult females (Boesch, 1994). In bonobo chimpanzees the high affinity between adult females results typically in female-female sharing. White (1994) documented that out of a total of 90 observations adult female-female sharing was most frequent

(n=52), followed by adult female to adult male sharing (n=30), while sharing amongst adult males was rare (n=7). Although female bonobo chimpanzees also share food with their offspring, this mother-infant food sharing comprises only 30% of the total food transfers in bonobo chimpanzees and these tend to be, (84 out of 85 observations), smaller plant items (White, 1994).

In the New World monkeys some type of food sharing occurs in all genera of the sub-family *Callitrichinae* (Feistner & Price, 1991; Price & Feistner, 1993). All species of this group are monogamous, co-operative breeders. Fathers and older siblings co-operate with the mother in the care of infants and sharing is, as a result, intra-familial. Infants are the usual recipients of food but reproductive females, juveniles or older offspring carrying an infant also receive food from other group members. For the different types of food sharing that occur within these species see Table 6.1.

**Table 6.1:** Food sharing in *Callitrichinae*. Species can be divided according to the type of food sharing that occurs within the breeding group. On the whole, infants initiate any transfer by 'begging' for food from an older individual. A far less common form of food transfer occurs in the species in the right hand column. Individuals in these species also volunteer food without any solicitation on the part of the infant. In this case of 'offering', infants are attracted by a special high-pitched food call which is notably absent from the species in the left hand column, which do not offer food.

ONLY BEGGING	BEGGING AND OFFERING
<b>Marmosets</b>	<b>Marmosets</b>
<i>Callithrix jacchus</i> (Feistner & Price, 1991)	<i>Cebuella pygmaea</i> (Feistner & Price, 1991)
<i>Callithrix geoffroyi</i> (Feistner & Price, 1991)	<i>Callithrix flaviceps</i> <sup>10</sup> (Feistner & Price, 1991; Ferrari, 1987)
<i>Callithrix argentata argentata</i> <sup>10</sup> (Feistner & Price, 1991)	
<b>Tamarins</b>	<b>Tamarins</b>
<i>Callicebus torquatus torquatus</i> (Starin, 1978)	<i>Leontopithecus rosalia</i> (Feistner & Price, 1991; Price & Feistner, 1993)
<i>Saguinus nigricollis</i> (Izawa, 1978)	<i>Leontopithecus chrysomelas</i> (Feistner & Price, 1991; Price & Feistner, 1993)
<i>Saguinus labiatus</i> (Feistner & Price, 1991)	<i>Leontopithecus chrysopygus</i> (Price & Feistner, 1993)
	<i>Saguinus oedipus oedipus</i> (Feistner & Chamove, 1986; Feistner & Price, 1991; Wolters, 1978)
	<b>Callimico</b>
	<i>Callimico goeldii</i> (Feistner & Price, 1991)

<sup>10</sup> These small New World monkeys are particularly difficult to study in the wild and as a result only in two of the cases above, *Callithrix flaviceps* and *Callicebus torquatus torquatus* were the records made in free-ranging groups (Ferrari, 1987; Starin, 1978).

### 6.1.1 Classifying food sharing

Feistner & McGrew (1989) noted that published reports of primate food sharing:

“cover a whole range of behaviour from active donation of food to another individual, to unresisted or at least unsuccessfully resisted theft, to intimidation of one individual by another to usurp food” (p.22).

As a result, Feistner & McGrew (1989) defined food sharing as: “voluntary transfer of defensible food items by food motivated individuals” (p.23). This definition rests on the word ‘*voluntary*’. In other words, the behavioural disposition of the possessor of the food determines the interaction. Further, they distinguish that:

- The food must be *items*. This determines that only solid food is included, since it is transferable in distinct quantities. Lactation is excluded.
- The food must be *defensible*. Feistner & McGrew (1989) refer to ‘ownership’ of the food item. Explicit to this is that the possessor, beyond having physical contact with the food item, must also have authority over the food item. These authors consider that if the food item is small it is likely to be defensible. However, they also warn that in cases where a higher-ranking animal attempts to take food from a subordinate it will not be possible to differentiate (any level of) sharing from theft – the higher-ranking animal may have simply displaced the possessor of the food item. Accordingly, it is difficult to consider that a subordinate animal feeding can ever have any real ‘ownership’ over food if a higher-ranking individual subsequently approaches this animal. If we consider a study by Hauser (1994), this point is well-illustrated. He measured the distance at

which infants, juveniles and adults abandoned different quality food items when approached by a higher-ranking individual. There was a significant difference for juveniles and adults but not for infants. Whilst it could be that infants were not able to distinguish between, or respond shrewdly, to differences in food quality it could also be that infants, when approached by a higher ranking individual, always choose to abandon. As Hauser (1994) points out “[in this case the] behavioural assay used to assess developmental changes in ecological experience (i.e. abandon difference) is insufficient”.

- The possessor must be *food motivated*. Presumably, in wild populations feeding competition and limited food availability ensures that whilst feeding all individuals are food motivated. However, in captivity this may need to be clarified. Captive animals may be supplied with food abundant to their requirements and they may not, as a result, be food motivated. In this case, the nutritional costs of sharing will be diminished and its biological significance is questionable. However, work on captive *Saguinus oedipus oedipus* showed that high adult food motivation resulted in an increase in food sharing rates (Feistner & Chamove, 1986).

Boesch & Boesch (1989), studying meat sharing, also applied an operational definition that centred on the motivational state of the possessor of the food item (see Table 6.2).

**Table 6.2:** Boesch & Boesch's operational definition of meat sharing: Six levels of increasing intention to share by the food owner (taken from Boesch & Boesch, 1989)

Category	Definition	Interpretation
S1 Theft	B forcefully takes part or all of A's food.	Sharing takes place against A's will: A shows opposition.
S2 Recovery	B takes part of the food that A has dropped on the ground or placed there.	Sharing without intention of A and merely tolerance of B's proximity if close.
S3 Passive sharing	B takes part of the food that A is holding. A makes no movement to facilitate nor avoid B's action.	A passively tolerates B's action but may accept that B holds the food pooled in common for some time.
S4 Active-passive sharing	B takes part of the food that A is holding. A makes a movement to facilitate B's action.	A actively tolerates B's action and expresses it by withdrawing its hand or by bringing the food toward B.
S5 Active sharing	A gives part of its food to B either by cutting off a piece it by holding a piece towards B.	A makes an explicit action showing its intention to B.
S6 Gift	A gives a part at least three times larger than its own remaining piece to B.	A's generosity seem to show a greater sharing intention than the category.

Therefore, authors have emphasised that the importance of food sharing lies in the tendency of possessors to accord other group members a high level of tolerance and this is interpreted as a willingness to share with them. In the case of mother-infant food sharing, if a mother does not resist an attempt from her (less dominant) infant, then implicit to this is the mother's propensity to *allow* the infant to take the

food and it is concluded that a level of sharing has occurred (Feistner & McGrew, 1989).

In sum, previous definitions have regarded the motivational state of the mother (or other possessor) – the ‘degree of volition’ (Feistner & McGrew, 1989) or the ‘level of increasing sharing intention’ (Boesch & Boesch, 1989) - as critical in classifying, measuring and recording food sharing behaviour. I argue that in addition, in order to completely clarify the food sharing issue, the part an infant (or other animal attempting to obtain food) plays needs to be considered more fully. If we think of food sharing as a social commerce between mother and infant, then the infant’s role in the interchange will be important - the intensity of infant’s solicitation, persistence, etc. Indeed, others have already argued that infants themselves are effective elements in their own socialisation and particularly within the realm of interactions over food (e.g. King, 1994).

Thus, my aim is to build on Feistner & McGrew’s (1989) and Boesch & Boesch’s (1989) definitions to propose a new classification. I refer to the case of mother-infant food sharing but the scheme can equally be applied to all other types of sharing and, indeed, it is important that a system be universally applicable. The progenitors of sharing (solicitation or offering) are referred to throughout the literature and in some cases they are defined thoroughly (e.g. Feistner & McGrew, 1989). A simple way to grade food sharing is to consider it as the product of the type of infant solicitation and the type of maternal response (see Table 6.3). King (1994) stressed that in studying the transfer of social information the ‘relative roles’ of both mothers and infants should be examined. Here, I follow this approach.

Hence, I classify food sharing as a dyadic interaction: in terms of not only how willing the mother is to share the food but also how active the infant is in attempting to acquire it.

By classifying food sharing in a table the different categories can be easily distinguished. Here, I have considered both the 'degree of volition' (Feistner & McGrew, 1989) or 'sharing intention' (Boesch & Boesch, 1989) as previous authors, but I have also considered the action of the infant, or what could be referred to as the 'level of demand'. Hence, the table allows the interaction to be considered in its entirety.

**Table 6.3:** Classifying food sharing. In almost all cases the infant will initiate the transfer by soliciting food from its mother. This can be a passive solicitation or an active solicitation. A mother in response to solicitation can show a varying degree of willingness to share food: she can respond positively, neutrally or negatively. For full definitions see section 6.2.1.

Infant	Mother's Response		
	Positive <i>Active donation</i>	Neutral <i>Ignores solicitation</i>	Negative <i>Resists solicitation</i>
<u>No Solicitation</u> <sup>11</sup>	Active sharing		
<u>Passive Solicitation</u> Infant makes no physical contact with mother's food <ul style="list-style-type: none"> <li>• Extends begging hand</li> <li>• Stares at food within 20cm</li> </ul>	Passively solicited donation	Unsuccessful solicited transfer	Resisted solicited transfer
<u>Active Solicitation</u> Infant actually makes physical contact with mother's food <ul style="list-style-type: none"> <li>• Touches food</li> <li>• Places mouth over mother's mouth</li> </ul>	Actively solicited donation	Tolerated scrounging	Resisted pilfering

 Not applicable

 Food transfer is always successful if infant persists

 Food transfer is never successful

<sup>11</sup> Usually a food transfer is initiated by a solicitation from the infant. However, in rare cases this may be absent. Clearly, if there is no infant solicitation, there will not be a maternal response. But here, for the purpose of this table, I consider that the mother always 'responds positively' in the case of no infant solicitation - of course, this is not really a 'response', the mother is simply donating the food to her infant.

Other authors have not examined the behaviour of the potential recipient prior to transfer. For example, de Waal *et al.* (1993) examined food sharing by brown capuchin monkeys that were separated by a wire-mesh barrier but failed to describe any movement towards the barrier, gesture, or vocalisation that may have been a request for food. The importance of considering the actions of both the possessor and the recipient is demonstrated by examining a paper by Bethell *et al.* (in press). They used Boesch & Boesch's (1989) meat sharing levels for their description of inter-adult plant food sharing (although Feistner and McGrew, 1989 provided a clear definition they did not provide a classification of the different levels of sharing). This meant that within this paper Bethell *et al.* (in press) recorded active sharing [S5, Boesch & Boesch, 1989] between MG (possessor of food item) and MU (recipient of food item) even when immediately preceding the food sharing event the following observations were made.....“MU stared hard at MG's face and at the fruit, separated by a distance of only about 30cm. This continued for several minutes (p.3)”. This would qualify as passively solicited donation under the present classification, not active sharing. Clearly, this is qualitatively different from an instance where, for example, MG approached MU, sat within arm's reach of MU and handed over food without any solicitation or other discernible “request” for food from MU (this would qualify as active sharing under present classification). Boesch & Boesch's (1989) classification does not make this distinction between these two types of sharing but the present one does. It is clear that the possessor's (or mother's) behaviour should be considered as a response to any possible action by the potential recipient (the infant). This will be important, not only to describe infant strategies and persistence, but also to examine the possible cost and benefit levels of subsequent denouement of the interaction by mothers.

### 6.1.2 The functions of food sharing

We have seen that mother-infant food sharing is a common developmental experience for both chimpanzees and the *Callitrichinae*. We assume, then, that this is a behavioural adaptation that has some selective advantage in these species. For chimpanzees it is thought that this advantage must in some way facilitate, or even speed up, an infant's passage from dependent suckling to independent foraging (Silk, 1978; Lefebvre, 1985; Hiraiwa-Hasegawa, 1990c).

According to evolutionary theory a mother should wean her infant as soon as possible whilst assuring its growth and survival (Trivers, 1974: see Chapter 1). By continuing to invest and nurse her current offspring the mother will delay the production of future potential offspring (Altmann *et al.*, 1978) and hence this reduces her future reproductive success (Trivers, 1974). As offspring mature their nutritional requirements increase and at the same time, in a parallel to these changing needs, the costs to the mother of providing *all* infant care (not only meeting nutritional needs but also providing locomotion and protection) also increase and parent-offspring conflict intensifies. Trivers' (1974) parent-offspring conflict theoretical framework is often examined within the context of lactation and weaning (see Chapter 1) but it could be equally applied to the case of food sharing (Silk, 1979). Food sharing may be an alternate investment strategy. By sharing solid food with her infant a mother would reduce her lactation load whilst still providing the infant with sufficient nutrients prior to it foraging independently (McGrew, 1975; Silk, 1978 ), thus allowing the mother to give birth earlier than she

would otherwise have been able to do. From here on I refer to this as the 'nutritional supplement hypothesis'.

Chimpanzee diet is characterised by being diverse, frugivorous and opportunistic (see section 4.1). Many of the food types are produced seasonally, so there may only be a short window of time for infants to gain experience with such food items. Food sharing may provide the opportunity for infants to obtain information about various foods (Silk, 1978; Lefebvre, 1985; Hiraiwa-Hasegawa, 1990c). This information would allow them to learn not only which of these foods are suitable to eat but also the extractive foraging skills needed to acquire the edible part. From here on I refer to this as the 'food learning hypothesis'.

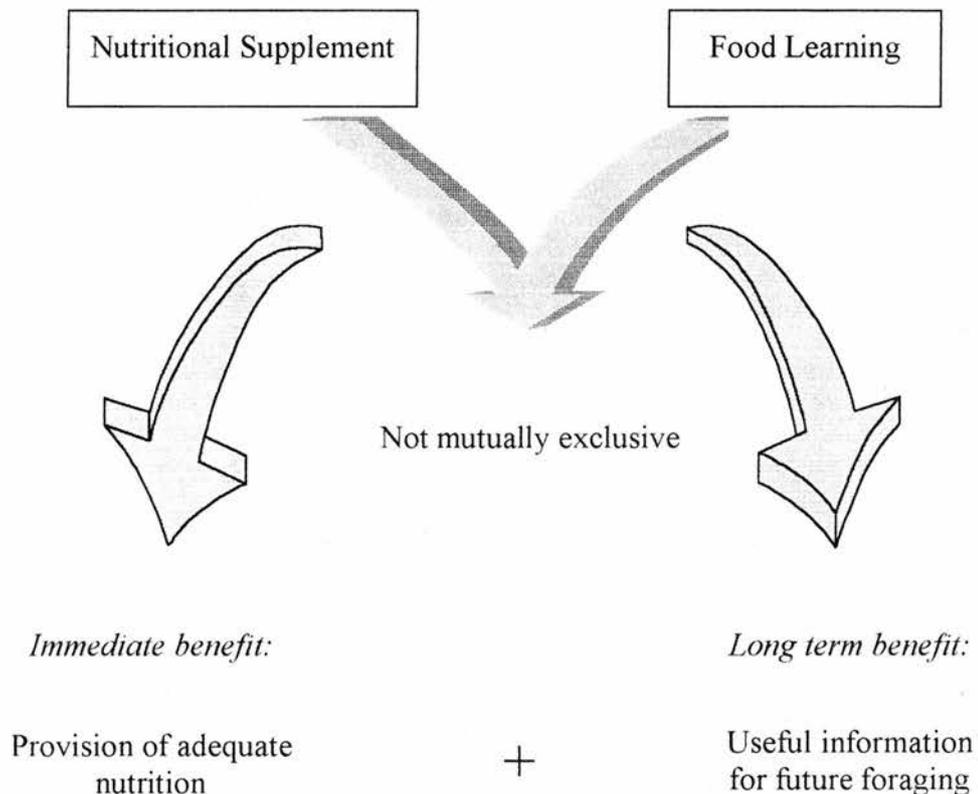
Lefebvre (1985) examined the first hypothesis by controlling for two developmental effects (gestation and age at sexual maturity) and one allometric effect (female body weight). By regressing these variables against age at weaning he tested whether chimpanzees and golden lion tamarins (*Leontopithecus rosalia*) were weaned earlier than 52 other, non-food sharing, primate species. The results were less certain for *Leontopithecus rosalia* than for *Pan troglodytes*. Golden lion tamarins were not weaned earlier than non-food sharing species as predicted by adult female weight or gestation length, but were weaned earlier according to regressions on age at sexual maturity. In light of these differing results Lefebvre (1985) concluded that body weight should be the preferred measure for these regressions in the case of *Leontopithecus rosalia*. He cites French (1983), who suggested that lactation has little efficacy in delaying fertility of the Callitrichids. Consequently, Lefebvre (1985) believed that developmental effects on weaning age

were negligible and that energetic costs, measured through the allometric effect of body weight, were the more important pressure. He therefore maintained that *Leontopithecus rosalia* is not weaned earlier than other non-food sharing species. In contrast, results were not at all ambiguous for chimpanzees. In all three regressions, chimpanzees fell well within the 95% confidence limits – they were not weaned earlier than the 52 other species. According to this study, then, the nutritional supplement hypothesis does not explain the occurrence of food sharing in chimpanzees. However, it seems likely that the provision of solid food and adequate nutrition must be important to an infant's development – perhaps affecting variables other than the ones tests by Lefebvre. And recent work by Frigaszy & Bard (1997) suggests that this may be true. Comparing chimpanzees and capuchin monkeys they suggested that food sharing may function as a prop that allows infant chimpanzees to continue to survive and grow during their extended period of immaturity and dependence.

In the past, nutritional supplement and food learning have been proposed as alternatives and treated as rival hypotheses (e.g. Nishida & Turner, 1996). However, I do not agree with such a distinction. The two hypotheses are not mutually exclusive and both probably reinforce one another reciprocally. The nutritional supplement hypothesis centres on an immediate benefit - the provision of adequate nutrition to the infant. As a result of this nutritional supplement the infant is supported in its prolonged period of dependence. This is necessary for it to accumulate information necessary to develop and perfect a range of skills, which is the long-term benefit of food learning - the infant may be acquiring useful information for future foraging. Hence, the two effects are intertwined and the hypotheses are compatible. Both hypotheses predict that mothers will minimise

maternal investment and ensure that the infant moves to a state of nutritional independence. Therefore, I suggest a new framework in which food sharing is considered as association of these two benefits, or the ‘concomitant advantages’ (see Figure 6.1).

**Figure 6.1:** Food sharing: the concomitant advantages.



Information that infants acquire through social interactions over food may improve the infant’s later foraging ability. However, in practise there are major problems of studying social learning in a field setting – we cannot rule out the possibility that improvements in foraging success were the result of individual learning through exploration and experience (see Chapter 1). Consequently, if there are any social learning effects resulting from mother-infant food sharing, their relative contribution will always be difficult to prove. However, the strength of

evidence for both types of benefit will be investigated, distinguishing at what developmental stage each is important in the transition to foraging independence.

If the assumption that food sharing is functionally important then this should be provable in terms of differential levels of sharing at different stages in development. Previous work seems to support the suggestion that food sharing could accelerate an infant's progression to foraging independence (Hiraiwa-Hasegawa, 1990c; Lefebvre, 1985; McGrew, 1975; Nishida & Turner, 1996; Silk, 1978). However, they have also failed to exclude all simpler explanations. Therefore it is important to test the null hypothesis that infants indiscriminately and haphazardly scrounge food from their mothers. If food sharing is spontaneous and random then the following predictions will be supported:

- Food sharing is correlated with the time that mothers spend feeding.
- Food sharing is correlated with the time that infants spend in close proximity to its mother.

If the short term benefit of food sharing is to decrease maternal investment by reducing the mother's lactation load and providing the infant with sufficient nutrients prior to foraging independently (McGrew 1975; Silk, 1978) then the following predictions will be supported:

- Mothers will share difficult foods which infants cannot obtain independently at higher rates than easy foods which infants can obtain independently.

- The mothers' rate of positive responses on a food item will be negatively correlated with the time it took mothers to procure and process that food.

As the infant grows its capacity to feed itself progressively improves and once it is able to sustain itself a mother should promote the weaning transition, driving the infant to fulfil its nutritional needs independently (Trivers, 1974). Specific predictions to be investigated are:

- As infants become older, mothers will increasingly reject solicitations for food from their infants, particularly solicitations for easy foods, but will be more tolerant of solicitations for difficult foods.
- In the face of this increasing resistance, infants will vary their level of persistence in attempting to obtain food from their mothers.
- As soon as an infant is successful in feeding independently on a food item it will cease to be shared.

Since the level of difficulty in obtaining an item is also an index of how much information needs to be acquired to successfully procure and process the item, these predictions also support the long term benefit of food sharing: that the mother is providing its infant with early experience and information about foods. Just as mothers restrict their period of nutritional investment to their offspring, they may be expected to restrict this period of 'information' investment.

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## 6.2 Methods

### 6.2.1 Definitions

**Food sharing:** (following Silk, 1978)

Any interaction between a mother and her infant that involves a series of attempts by the mother to donate food or by the infant to obtain food, that results in an infant manipulating or feeding on remains of its mother's food. For food sharing to occur the mother must be in physical contact with the food at the beginning of the interaction. If, as a result of any attempt within the food-sharing bout, food was transferred from mother to infant then the sharing bout was recorded as successful. In the case of successful food sharing bouts, it was noted whether the infant consumed the food. A food sharing bout was considered to be terminated if:

- (i) the donation or solicitation attempt was successful.
- (ii) the donation or solicitation attempt was changed in form (see the different types of donation and solicitation behaviours).
- (iii) the donation or solicitation attempt was discontinued for more than 30 seconds.

**Food retrieval:** (following Nishida & Turner, 1996)

The infant manipulated or fed on the remains of its mother's food without interacting in any manner with her.

**Infant solicitation:** (following Silk, 1978; Feistner & McGrew, 1989; Hiraiwa Hasegawa, 1990c).

This is any behaviour of the infant that was a request or appeal for food. Each type of solicitation gesture was counted as one bout, until the solicitation bout ended under the conditions above.

(i) **Passive solicitation.** During the solicitation attempt the infant made no physical contact with its mother's food. This included the following behaviours:

(a) The infant was within arm's reach of its mother and stared intently at her food with its head nearly touching (always less than approximately 20cm) its mother's food or mouth.

(b) The infant extended a begging (open) hand towards its mother.

(ii) **Active solicitation.** As part of the solicitation attempt the infant made physical contact with the food. This included the following behaviours:

(a) The infant placed its mouth over its mother's mouth.

(b) The infant took or snatched the food item from its mother.

**Maternal response:** (following Silk, 1978; Feistner & McGrew, 1989; Hiraiwa-Hasegawa, 1990c)

This was the mother's response to the infant's solicitation attempt. This was either:

(i) **Positive response:** The mother encouraged the solicitation attempt by donating ('actively giving') or offering the food item to the infant. This included the following behaviours:

- (a) The mother pushed the food towards the front of her mouth and held it there between her lips but did not visually inspect the food wadge.
  - (b) The mother opened the palm of her hand, offering the food within it to the infant and kept the palm open until the infant made some type of solicitation.
- (ii) Neutral response: The mother ignored the solicitation attempt, there was no type of encouragement or discouragement: the mother simply continued with her previous activity.
- (iii) Negative response: The mother resisted the solicitation attempt, she prevented the infant from obtaining the food. This included the following behaviours:
- (a) The mother turned completely away from the infant.
  - (b) The mother pulled the food out of reach of the infant.

## 6.22 Data Collection

Data on food sharing events were collected during 20 minute principal and subsidiary focal animal samples. The following data were recorded: type of infant solicitation, type of maternal response, and the result of the interaction. Data were recorded in a field notebook or in cases where food transfer events were rapid, data were recorded using a voice-activated dictaphone with an attached microphone. Data on mothers' and infants' proximity and feeding times were extracted from focal samples.

These behaviours were subtle and sometimes they were difficult to record. For example, sometimes vegetation partially obscured the animal at the critical moment so that only part of the food sharing interaction was observed. In these uncertain cases and others where my field assistant and I disagreed on the coding of the behaviour, the observation was noted as 'unreliable'. All these types of record were excluded from the subsequent analyses below.

### 6.2.3 Data Analysis

The solicitation and sharing of different food types could not merely be established using frequencies. A correction was needed to reflect the amount of opportunity that infants had to obtain foods. In all cases, solicitation and sharing rates were calculated using the mother's feeding time on the food item solicited or shared whilst the infant was within arm's reach of its mother. This is similar to Hiraiwa-Hasegawa (1990c), although she used mother's feeding time whilst the infant was within 5 metres. I believe within arm's reach is a more appropriate measure since within this distance the infant can properly observe its mother feeding and interact with her without needing to move nearer. The use of the mother's feeding time appears more suitable than Silk's (1978) method of using the infant's feeding time or Nishida and Turner's (1996) use of solicitation bouts per feeding bouts when calculating solicitation and sharing rates. Neither of these methods measures the duration of opportunity that infants have to interact with their mother over food.

Data on proximity and mothers' feeding times were extracted from instantaneous principal and subsidiary focal samples. The solicitation rate was calculated as the

number of solicitation bouts by the infant on a particular food item divided by its mother's feeding time for this food item whilst the infant was within arm's reach. This approximates to the infant's effort to solicit food per item according to opportunity. Similarly sharing rate was calculated as the ratio of the number of successful solicitation bouts by the infant on a particular food item divided by its mother's feeding time on this food item whilst the infant was within arm's reach.

The level of persistence of infants demonstrated whilst attempting to obtain food was measured in terms of the number of solicitation attempts following a previously unsuccessful solicitation attempt. This was calculated in a different way to Silk's (1978) 'persistence of solicitation', although it follows the same concept. Silk used the following: the ratio of number of attempts to solicit divided by the total number of bouts of solicitation observed. Here, I explore this concept more fully by examining the infant's behaviour following a solicitation attempt that failed. Following an unsuccessful solicitation attempt but within the same feeding bout of its mother the infant could either:

- (i) 'persist' and attempt again to solicit food from its mother.
- (ii) 'quit' and discontinue any attempt to solicit food from its mother.

This determines the degree of persistence, or effort, that infants maintain when experiencing a level of maternal resistance.

Foods were divided according to how easy they were for the infant to harvest and/or process on the basis of subjective observation judgements (for definitions see section 2.4.5.c). These were based on the following criteria: observations of infants'

handling foods, the fact that particular items required strength or dexterity to open (as in previous studies, e.g. Silk, 1978; Hiraiwa-Hasegawa, 1990c). In this study it was also possible to examine whether the subjective judgements about the infants' handling of foods reflected the true 'difficulty' of food items from mother's perspective, using a measure of her handling, or feeding intake rate. Within principal focal observations every bite or food item eaten was recorded (see section 4.3.5). Using these frequencies and feeding time, the actual feeding intake can be calculated as bites/items consumed per minute. These feeding intake rates provide an objective measure of processing difficulty from the mother's point of view. It was possible that the difficulty infants encountered with food items affected mothers' processing rates differently. For this reason it was important to examine maternal processing speed. In addition, this produces a quantitative, rather than qualitative, assessment. Mothers' feeding times and total consumption of different food items were calculated. Rates were calculated as bites/min or items/min depending on the size of the food item. Using the dry masses recorded for these food items, grams of dry mass consumed per minute were calculated for each food item.

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## 6.3 Results

A total of 193 infant solicitations for food were recorded and one case where a food transfer occurred with no infant solicitation. Infants that solicited food were aged between 6.5 and 41 months. In 151 of these cases a food transfer occurred – the remaining 43 solicitations were unsuccessful. In all cases where food was successfully transferred to the infant, the infant subsequently consumed the item.

### 6.3.1 Food sharing patterns

The number of food sharing bouts on a food item was not correlated with the mother's feeding time on that food item (Spearman Rank Correlation:  $R_s = 0.169$ , *ns*). Thus, infants did not receive food from their mothers as a function of how long she had been feeding. Neither were sharing rates a function of proximity tendencies. The mean sharing rate for each infant was not correlated with the mother's feeding time whilst the infant was within arm's reach (Spearman Rank Correlation  $R_s = -0.342$ , *ns*). Similarly, sharing rate was not correlated with the total time that the infant spent within arm's reach of its mother (Spearman Rank Correlation  $R_s = -0.036$ , *ns*). Mean party size was not correlated with solicitation or sharing rate (Spearman Rank Correlation solicitation rate:  $R_s = -0.33$ , *ns*; sharing rate:  $R_s = -0.17$ , *ns*).

### 6.3.2 Type of infant solicitation

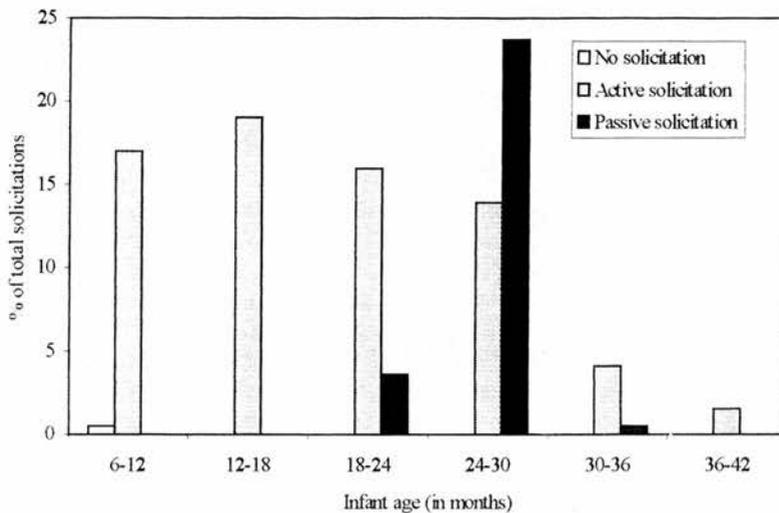
Infants did not always actively scrounge for food from their mothers. Although they did solicit foods more frequently by active means, i.e. by touching their mother's food, rather than by passive means (active: 139, passive: 54;  $\chi^2 = 37$ ,  $p < 0.001$ ). However, a two-way contingency chi-squared test showed that infants were not more successful actively soliciting food from their mother than they were when they passively solicited food ( $\chi^2 = 0.93$ , *ns*; Table 6.4). In fact there was no correlation between the proportion of active solicitations and the sharing rate (Spearman Rank Correlation  $R_s = -0.486$ , *ns*).

**Table 6.4:** Two-way contingency table for type and outcome of solicitations

	Active solicitation	Passive solicitation	Totals
Successful	111	39	150
Unsuccessful	28	15	43
Totals	139	54	193

In the first 18 months of life, infants did not passively solicit food at all. However, by 18-24 months, infants began to solicit food by passive means and by 24-30 months a greater proportion of solicitations were of this type than active attempts (see Figure 6.2).

**Figure 6.2:** Type of infant solicitation. The type of infant solicitation as a percentage of the total number of solicitations.



There was only one instance where an infant made no solicitation for food but a transfer still occurred. This incident was the only observed case of active sharing. Since this is a rare phenomenon, I have described this fully below (taken from field notes). The observations of my field assistant (ZTK) corresponded to my own.

*7<sup>th</sup> March, 1998. Block 5A.*

*09.04 Focal starts on RD [adult female] and RA [RD's female infant]. RD is feeding on ripe fruits of *Ficus sur* in a tree that overlooks the logging road. RD and RA are in good view. BO [RD's male juvenile] is out of view and not within 5m of*

*RD, but he is assumed to be present because he was briefly seen at 09.02. Focal on RD [principal focal subject] terminates at 09.24.*

*09.25 Focal starts on RA. RD feeding on fruits; RA is within arm's reach of RD and alternating between resting and independent play.*

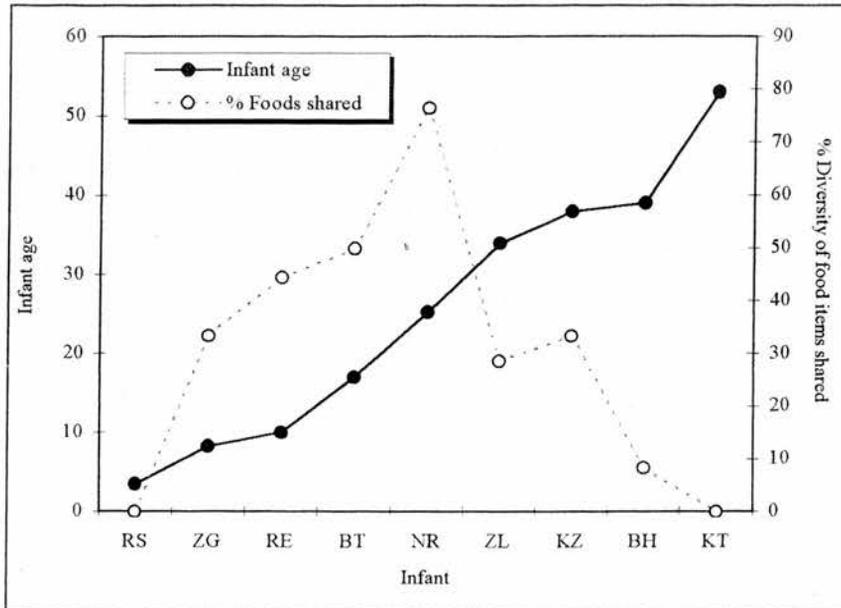
*09.37 RD is wadging ripe fruits of Ficus sur. RA is in physical contact with RD's right side. RA is playing independently with a branch; RA is in no way attending to RD. RD removes part of her wadge with her right hand (but, unusually, she does not remove the complete wadge, as is customary when discarding or repositioning a fig wadge). RD opens the palm of her right hand and with this arm made an active movement towards RA [this action constitutes 'offering' by definitions]. RA is still playing but within approx. 3 secs notices the food in RD's hand. RA places her hand under RD's, and then RA pulls RD's hand up to her own [RA's] mouth. RA then feeds on the wadge.*

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### **6.3.3 Diversity and amount of food shared**

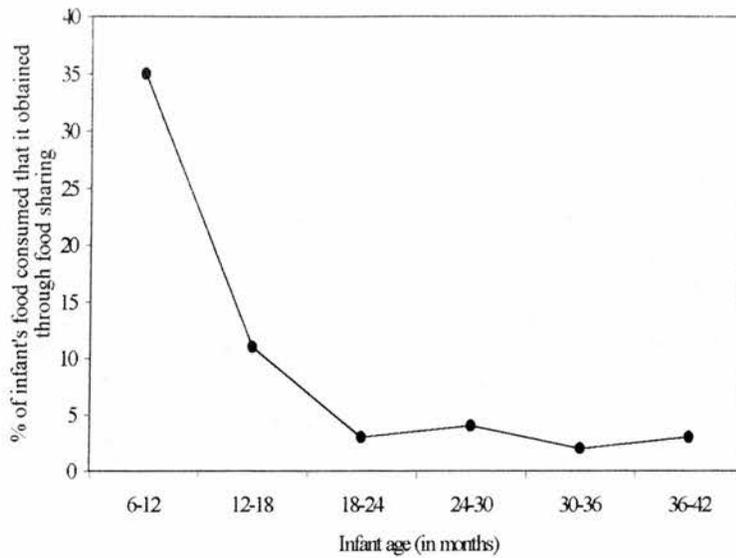
A high diversity – 52 % - of the food items that mothers fed on were solicited and shared at some point. The diversity of food items that mothers shared with their infants was plotted against age (see Figure 6.3). The diversity of food items that mothers shared with their infants varied with age, peaking in the infant's second year of life. Infants in their third and fourth years obtained a much smaller diversity of the food items that their mothers consumed.

**Figure 6.3:** The diversity of mothers' food items shared with their infants. To control for the effect of changes in proximity with age, this measure (open points: scale on the right) was calculated as the number of food items shared with the infant/total number of food items mother fed on whilst the infant was within arm's reach. Age of infant is shown by filled points.



The amount of food that infants obtained through mother-infant food sharing was also examined. Food sharing was particularly important in the infant's first year, providing 35% of the infant's nutritional intake. This decreased to 11% for infants aged 12-18 months of age and to relatively negligible levels in infants aged over 18 months (see Figure 6.4).

**Figure 6.4:** Amount of food infants obtained through food sharing as a proportion of the total food infants consumed

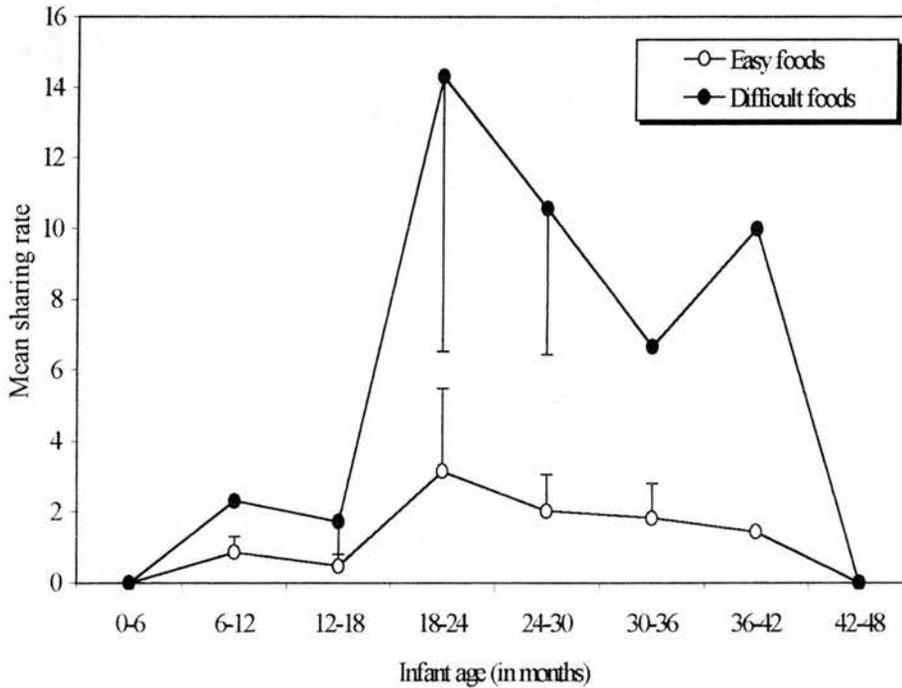


#### 6.3.4 Solicitation and sharing rates

Infants first started soliciting food from their mothers when they were about 6 months old. They continued to solicit and obtain food from their mothers into their fourth year of life. Food items were classified according to whether they were difficult or easy to procure and process. Difficult and easy food items were not shared equally: 83% of difficult food types eaten by mothers were shared, whereas only 35% of easy food types were shared: this was a significant difference ( $\chi^2 = 12.66, p < 0.01$ ; see also Figure 6.5). This difference could not be explained by mothers feeding for longer periods on difficult foods because although feeding times did differ significantly between difficult and easy foods, mothers actually fed for significantly longer periods on easy foods (Wilcoxon matched-pairs signed-ranks test  $Z = -2.366, p < 0.02$ ).

When the mean sharing rates across the 6-month age blocks were compared, difficult foods were shared significantly more than easy foods (Wilcoxon matched-pairs signed-ranks test  $Z = -2.201$ ,  $p < 0.05$ ; see Figure 6.5).

**Figure 6.5:** Mean sharing rates of easy and difficult foods.



Food items were shared particularly when infants were aged between 18 and 42 months of age (see Figure 6.5). The sharing rate of difficult foods increased dramatically in the second half of an infant's second year. In contrast, there were negligible differences in the rate of sharing of easy foods with infant age. Further, difficult foods continued to be shared at a higher rate, over a protracted period of time and later into an infant's life than easy foods.

When data for all target infants were pooled the mean sharing success was high for both easy and difficult foods (for easy foods: 75% SE=5, for difficult foods: 71% SE=10). Hence, mothers seemed to show a high level of tolerance towards the appeals for food from their infants. Further, there was no significant difference between the rates at which foods were shared and the rates at which they were solicited, for either easy or difficult foods (Wilcoxon matched-pairs signed-ranks test for easy foods:  $Z = -0.26$ , *ns*, for difficult foods:  $Z = -0.314$ , *ns*). In fact in both cases, for easy and difficult foods, there was a significant positive correlation between the rate of sharing and the rate of solicitation (Spearman Rank Correlation: for easy foods  $R_s = 0.943$ ,  $p < 0.05$ ; for difficult foods  $R_s = 0.812$ ,  $p < 0.05$ ). This indicated that firstly, most infant solicitations resulted in transfer of food. Secondly, that the higher rates of sharing of difficult foods was the result of a higher rate of solicitation for these foods by infants.

### 6.3.5 Maternal Response

It was possible to observe maternal response in 189 cases of the infant's solicitation (see Table 6.5). In the case of maternal response there was no need to correct for differences in "opportunity" for interaction. The occurrence of response for easy and difficult foods was investigated (see Table 6.5).

**Table 6.5:** Positive, neutral and negative response frequencies  
for easy and difficult foods

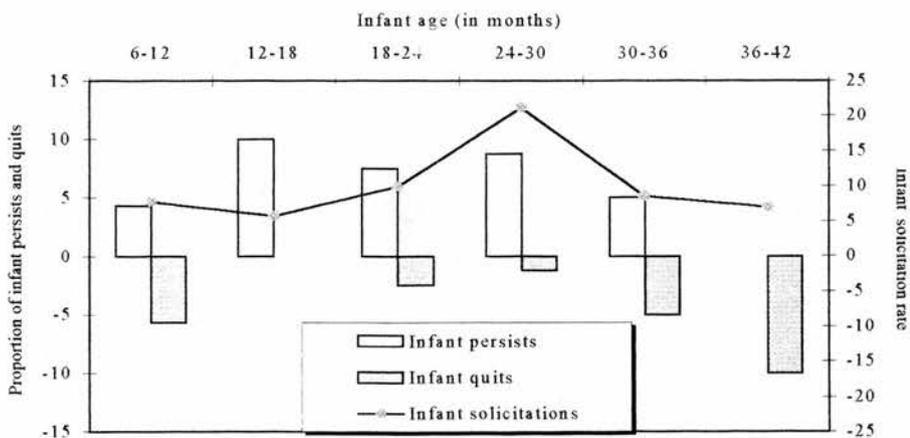
Type of food	Type of maternal response		
	Positive	Neutral	Negative
Easy food	36	33	12
Difficult food	41	66	1

Mothers did not start responding negatively to solicitations for difficult foods until an infant was in its third year. However, otherwise the proportion of positive and neutral responses for difficult foods followed much the same pattern as for easy foods (Table 6.5).

### 6.3.6 Perseverance of infant solicitation

There was no linear correlation between infant persistence and infant solicitation. For all food types, infant solicitation rates increased after 18 months, remained high but then fell after 30 months of age (see Figure 6.6).

**Figure 6.6:** Infant solicitation rates and infant perseverance following solicitation failure. Frequencies of 'persists' and 'quits' are summed within each six month infant age block and expressed as percentages. Since the number of unsuccessful solicitation attempts varied across age blocks, the proportion of 'persist' and 'quits' are used. 'Persists' are depicted as positive counts and 'quits' are depicted as negative counts.



Very young infants, aged 6–12 months, did not show a high level of perseverance, tending to suspend solicitation attempts following failure (see Figure 6.6). Infant perseverance was high between the age of 12 and 30 months but infants aged 36 months and above no longer displayed persistence following an unsuccessful solicitation. These older infants increasingly ‘quit’ and discontinued efforts to obtain food following a failed solicitation.

### **6.3.7 Maternal rates of processing and response to solicitation**

Mothers consumed easy foods at a higher dry mass intake rate than difficult foods (see section 4.3.2). In other words, the lower the dry mass intake rate, the harder the food item was to procure and process.

The response of mothers to solicitations for food items by infants was further examined. Mothers’ positive response rate was calculated for different foods by calculating the number of positive responses per unit time that the mother was feeding on that food item. This was then correlated with the feeding intake rates calculated above. There was a significant negative correlation between these two variables (Spearman’s Rank Correlation:  $R_s = -0.638$ ,  $p < 0.02$ ). This indicated that mothers’ positive responses to infants’ attempts to obtain food varied according to the time it took mothers to procure and process those food items. In other words, the easier the food was to process, the less mothers were willing to share. No such correlation was found when the same measure was correlated with neutral response rate or negative response rate.

### 6.3.8 Infant foraging success

In cases where the mother was observed feeding on the food type shared before a solicitation bout, infants had an opportunity to feed independently. There were four possibilities:

- Infants fed independently on the food item before the transfer and the transfer was successful.
- Infants fed independently on the food item before the transfer and the transfer was unsuccessful.
- Infants did not feed independently on the food item before the transfer and the transfer was successful.
- Infants did not feed independently on the food item before the transfer and the transfer was unsuccessful.

These conditions were randomly distributed ( $\chi^2 = 0.52, ns$ ). In other words, the likelihood of infants successfully obtaining food from their mother did not appear to be conditional on the infant being unable to feed on it independently.

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## 6.4 Discussion

The levels at which chimpanzee mothers actively encourage or discourage infants in their selection of food items does not appear likely to be influential in guiding a young chimpanzee's future foraging choices (see section 5.3). This suggests that active intervention is not important in the acquisition of feeding knowledge in chimpanzees. A more noteworthy candidate for study, providing a clear opportunity for social learning by infants, is the sharing of food between mother and infant. It is more widespread, occurring throughout wild chimpanzee populations wherever mothers and infants have been studied (Bossou: Inoue-Nakamura & Matsusawa, 1997; Gombe: McGrew, 1975, Silk, 1978; Kibale: Ghiglieri, 1984; Mahale: Hiraiwa-Hasegawa, 1990c, Nishida & Turner, 1996; Tai: Boesch & Boesch, in press).

In this study, chimpanzee mothers shared solid food with their offspring throughout the period of infancy. It is clear that in terms of the relative role of mothers and infants in information acquisition infants play the more active role (King, 1994). Mothers very rarely share food actively with their infants (only one case out of 194), this has also been the case in other studies of mother-infant food sharing (McGrew, 1975; Silk, 1978; Hiraiwa-Hasegawa, 1990c; Nishida & Turner, 1996) and adult-adult food sharing (Nishida, 1970). The studies that suggest a higher incidence of active sharing in adult-adult meat eating have been less scrupulous in their definition (e.g. Boesch & Boesch, 1989: see section 6.1). It is likely that active sharing is rare throughout the primate order (Feistner & McGrew, 1989).

However, mothers were highly tolerant of their infant's solicitations for food, as reported in previous studies (McGrew, 1975; Silk, 1978; Hiraiwa-Hasegawa, 1990c; Nishida & Turner, 1996; Boesch & Boesch, in press). Hence, mothers were considered to share food with their infants because it was volitional on the part of the mothers (Feistner & McGrew, 1989). Although they rarely offered food (with no discernible request from the infant), in the cases where infants solicited food mothers were making decisions whether to accept or refuse such a request for food. It is therefore considered that mothers 'share' their food with infants because the mother's behaviour is volitional, in that she was not intimidated into sharing the food and can in fact decide to withhold or accept the request for food.

The youngest infant observed to ingest plant food was approximately 6 months old and it is likely<sup>12</sup> that this was one of this infant's first experiences of solid food. In all cases, infants consumed food that they obtained from their mother, and it contributed substantially to their solid food intake: 35% in their first year and 11% in the first half of their second, indicating that mother-offspring food sharing is a significant behavioural strategy.

Previous studies have not always excluded less complicated explanations of infant solicitation patterns, such as infants simply solicit food whenever they are within arm's reach of their mother (e.g. Silk, 1978; Hiraiwa-Hasegawa, 1990c). Although Hiraiwa-Hasegawa (1990c) used a solicitation rate calculated against the

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<sup>12</sup> Clearly, complete subject histories will never be obtained through field studies. There is no certainty that the first observation of a behaviour was its first occurrence.

mother's feeding time whilst the infant was within 5m of the mother, this did not exclude the possibility that the more important proximity measure was the time the infant was within arm's reach of the mother (see section 6.2). The present study confirmed that the frequency of solicitation was not the result of certain infants spending more time close to their mothers. Nor was it contingent on the amount of time the infant's mother was feeding (similarly at Mahale: Nishida & Turner, 1996), nor did sharing or solicitation rates correlate with feeding competition, as indexed by party size. Hence, results of this study demonstrated that infants do not scrounge food indiscriminately.

Mothers were observed to tolerate and sometimes respond positively to their infant's solicitations for food and, (apart from the one exception of active sharing), infants were responsible for initiating all food sharing interactions. Infants more commonly made physical contact with their mother's food rather than passively 'begging'. However, although active solicitations occurred more frequently than passive forms of solicitation, active solicitations were not more successful. The hypothesis that infants solicit food randomly was rejected. Infants did not solicit all food types at a constant rate, they did not solicit foods more if they spent more time within arm's reach of their mother and they did not exclusively use the most effective strategy open to them: simply snatch food from their mother. Rather, infants sometimes passively solicited food by using begging gestures. Interestingly, active solicitations were used early in life but passive solicitations (begging for food) emerged later, only after the first 18 months of life. It is possible that infants need to learn the appropriate and species-typical begging gesture. Plooi (1984) stated that begging behaviour appears initially at 9-10 months, earlier than results indicate here. The differentiation of the two types of solicitation describes the

changing ontogeny and the increasingly competent use of communicative gestures within a goal-directed sequence of actions. These range from the clumsy active solicitation (grabbing or stealing) of food, which is the first to emerge, through to the classic begging gesture, which is used increasingly with age and is more frequently used by older infants than by younger infants. By their second year infants appear to have acquired the 'extended palm upwards with cupped hand' as a communicative gesture and a signal for food. Hence, infants also seem to be able to adjust their behaviour to obtain their objective. Similarly, orang-utans begin to use begging gestures at the age of two years (Bard, 1990). It could be argued that this shift in the type of signal used indicates the more appropriate method to obtain food and the development of a ritualised begging gesture, which is very similar to the chimpanzee typical extended hand palm-up greeting and appeasement behaviour patterns. Interestingly, in bonobo chimpanzees although the hand is frequently extended whilst begging, rarely is the palm-up cupped hand used, the hand is usually turned downwards and in a very small number of cases (2 out of 608) bonobo chimpanzees signalled for food by 'mimicking' eating food (Kuroda, 1984). Bard (1990) argued that the begging gestures of chimpanzees to obtain food is intentional behaviour since it is a goal-directed sequence of actions explicitly aimed at attaining food. It also involves 'response waiting', in that there is a delay between the action and the desired outcome, and for this reason it has been compared to the similar manner human infants use gestures to solicit objects from their mothers (Bard, 1990). When adult chimpanzees beg for meat they may not only make physical contact with the food or the possessor of the food (Goodall, 1986; personal observation) but, critically in consideration of intentional behaviour, they also alter their eye gaze between the possessor's eye and the food (Plooi, 1984; personal observation). This suggests that they understand the need to direct or manipulate the

possessor in order to meet their objective of obtaining food. Young infants do not alter their gaze between the mother and the target food in a manner that indicates such behavioural co-ordination and intentionality, however older infants and juveniles do (personal observation: Ngamba Island). This implies that before nutritional independence immature chimpanzees are capable of distinguishing their mother's role in attaining their goal and understanding the possibility of manipulating her as a social instrument or "social tool" (Bard, 1990).

In this study infants were not observed to 'retrieve' their mother's feeding remains. Nishida & Turner (1996) note that this most commonly occurs when mothers have been eating pith, which they harvest on the ground. No doubt it is because items are eaten terrestrially, that infants are able to feed on their mother's discarded food remains. Perhaps we should expect food retrieval under Nishida & Turner's (1996) definition to be a largely terrestrial phenomenon (and perhaps particularly important in less arboreal apes, e.g. mountain gorillas: see Watts, 1985). Unfortunately, in this study mother and infants were not sufficiently well habituated to allow good observation conditions on the ground and terrestrial feeding observations were rare (see section 2.4.1.c). Pith forms only a small proportion of the diet of Budongo chimpanzees (terrestrial herbaceous vegetation constitutes 4.6% of faecal samples, n=161: K. Fawcett, unpublished data). It is likely that infants at Budongo do retrieve their mother's feeding remains (and particularly terrestrial foods) and that the apparent contrast between Budongo and Mahale is an artefact of differences in habituation levels.

Food sharing provided a large proportion, (35%), of the infant's solid food nutritional intake in its first year, falling to a still significant 11% in its second year, and much lower levels thereafter. Therefore, the amount of solid food infants obtained from their mothers was substantial during their early years. The diversity of food items that mothers shared with their infants varied with age, peaking in the infant's second year of life. Infants in their third and fourth years obtained a much smaller diversity of food items compared to the full range of items that their mothers were feeding on. The diversity and quantity of foods shared was sufficient to support the first prediction: that food sharing is a modified maternal investment strategy, an alternative to the more energetically and reproductively costly lactation (McGrew, 1975; Silk, 1978).

The prediction that mothers would share foods infants could not process independently more frequently than those foods infants could process was supported. Infants particularly solicited, and received, difficult foods from their mothers, most often when they were aged 18-30 months. The difference between easy and difficult foods was evident not only in frequency but also ontogenetically: infants continued to solicit and obtain difficult foods at a higher rate over an extended developmental period. Such a pattern did not exist for easy foods. Other studies at Gombe and Mahale have found very similar patterns in the relationship between food sharing and the characteristics of food items and infant age (Silk, 1978; Hiraiwa-Hasegawa, 1990c; Nishida & Turner, 1996).

Infants appeared to distinguish between foods that they could acquire themselves and those that they could not. This indicates some early, rudimentary categorisation

of objects by infants on the basis of the perceptual or physical characteristics of the objects their mothers were feeding on. The focus on difficult foods cannot be attributed to differential reinforcement since mothers were not more likely to share difficult foods. The amount of time that their mothers were feeding on difficult items was controlled for. Therefore, infant chimpanzees, open to various options, spontaneously directed their attention towards these difficult objects, and did make such a distinction. It could be argued that simple foraging decisions (e.g. decisions about ingesting a ripe versus unripe fruit) are also examples of a natural ability to sort and classify objects. However, it is interesting that the ability to sort and classify the world emerges so early in chimpanzees and, further, that it is used in a number of different domains, most impressively in later developmental stages, in their selection of materials to be used as tool (Boesch & Boesch, 1990). In experiments chimpanzees are able to perceive relations of same/different between objects and pairs of objects, and to classify them by physically placing them in groups: 'categorical sorting' (Matsuzawa, 1990). Such an ability does not emerge in human infants until 3.5 years of age but the adult female chimpanzees consistently demonstrated categorical sorting (Matsuzawa, 1990).

The eldest infant in this study never solicited food and probably represents the upper age-limit to this behaviour. For more complicated tasks, such as using hammers and anvils to crack nuts in West Africa, young chimpanzees obtain food from their mothers for much longer periods (Boesch & Boesch, in press). Chimpanzees in the Tai forest begin to obtain *Coula* and *Panda* nuts from their mother in their first year. This sharing reaches a peak in the 4-5<sup>th</sup> year. It continues until the chimpanzee is 8 years old in the case of the softer and easier to crack *Coula* nuts. For the harder *Panda* nuts chimpanzees continue to receive nuts from their

mother into their 12<sup>th</sup> year, with chimpanzees not reaching adult efficiency at cracking these Panda nuts until they are at least 13 years old (Boesch & Boesch, in press).

The prediction that mothers are more tolerant of solicitations for difficult foods in comparison to easy foods was rejected. The pattern of infant solicitations closely corresponded to the pattern of sharing for both easy and difficult foods - in other words, when infants solicited food from their mothers, they generally succeeded in obtaining it. The higher sharing rate of difficult foods was not the result of a higher toleration of solicitations for these foods by mothers. Similar results have been found at Mahale (Hiraiwa-Hasegawa, 1990c; Nishida & Turner, 1996). Silk's (1978) results at Gombe diverge here, she concluded the opposite: that mothers were selective in their sharing disposition; that they were more willing to share difficult food items. Further, she suggested that mothers were minimising their lactation costs by intensifying their discrimination over food types with infant age - becoming less willing to share easy food items but remaining eager to share difficult food items. Since Silk's (1978) results conflicted not only with this study but also the two others of Hiraiwa-Hasegawa (1990c) and Nishida & Turner (1996) I further examined Silk's study for methodological differences that might explain this. Initially, I considered that Silk's use of infants' feeding times in the calculation of her solicitation and sharing rates might explain the difference. However, when I re-ran my analyses using infant feeding times to calculate solicitation and sharing rates my results and Silk's still did not coincide. Then, on closer inspection, it emerged that Silk had not used solicitation rates in this part of her analyses - instead, this conclusion had been based on the use of *proportions* of solicitations. She had compared the cumulative distributions of solicitation for easy and difficult foods and

found there was no significant difference. Then, when she compared the cumulative distributions of successful solicitations for easy and difficult foods, she found that there was a significant difference; from this she concluded that infants solicited indiscriminately, but it was the mothers that were sharing difficult foods selectively. However, I consider this result with some suspicion as it seems to be based on a rather convoluted method: surely a more direct approach to gain the same information would be to simply examine the success rates on easy and difficult foods. In her paper, Silk included a table of the 27 foods solicited in her study (19 easy and 8 difficult) in which she marked easy and difficult foods and included the percentage solicitation success for each food species. This allowed consideration of the number of food types and the difference in percentage success between easy and difficult foods. I calculated mean percentage success for easy food species as 24% (SE =7%) and for difficult food species as 36% (SE=12%). Hence, using this measure – which seemed intuitively rational - the difference in success was not significant between easy and difficult foods for Silk's data. I had previously averaged my percentage solicitation success over age blocks, so to follow the method that I had been required to adopt for Silk's data, I re-calculated my results for comparable averages in my study. Using this method (means across food species) the percentage solicitation success was 86% (SE=8%) for easy foods and 77% (SE=14%) for difficult foods. So, when success rates are examined the opposite result emerges: in Silk's study infants were not more successful in obtaining difficult foods and so mothers could not be sharing these food items selectively.

Another striking result produced by this comparison was that there was such a significant difference between overall percentage solicitation success (for both easy

and difficult foods) in my study (82%, SE=7) and that of Silk's study at Gombe (28%, SE=6). The other two studies at Mahale had high rates of success equivalent to my results for Budongo: Nishida & Turner (1996) = 73%; Hiraiwa-Hasegawa (1990c) = not stated but it appears to be 70-80% from her graph. I would suggest that a possible explanation for this lies in the fact that Silk's study occurred 20 years ago when provisioning levels would still have been high at Gombe. Silk states that "bananas were regularly provided" (p.131) and "bananas were solicited in 76% of the occasions they were fed to mother-infant pairs" (p.133). Such provisioning would have provided a super-abundant food source for mothers. In these circumstances we would expect neither mother nor infant to be under any particular nutritional stress and their motivation to forage on natural foods would have been reduced. In fact, we might expect that the cost to a mother of sharing a food item would be negligible, irrespective of whether the food item was easy or difficult to process. These two factors together may have led to a reduction in the solicitation rates on natural food items and might also explain the lower levels of sharing. The sharing of bananas would provide an energetic alternative to maternal lactation and have met the short-term nutritional requirements of infants. It is interesting then, that presumably mothers in this situation were under less energetic stress but nevertheless sharing rates were lower. Infants were less successful in their solicitations even when, under these circumstances of artificial provisioning, the cost of sharing to the mother would have been significantly less. According to the 'concomitant advantages' approach we might hypothesise that in this case the infants' nutritional requirements were being fulfilled by the shared bananas but the food sharing interactions involving natural plant foods continued because infants still needed to obtain information about these. The availability of alternative food resources is likely to be important in determining food sharing patterns. Indeed, it

would be interesting (although beyond these data) to examine food sharing in relation to general food availability and analyse the variation in sharing rates according to maternal nutritional condition. This could perhaps be tested alternatively by investigating correlates of relative maternal dominance rank.

Mothers did resist some solicitations for food. They responded negatively more frequently to solicitations for easy foods than difficult foods and earlier in the infant's life, in its first year; whereas mothers did not respond negatively to solicitations for difficult foods until the infant's third year. However, these differences were not statistically significant. In general, mothers were characterised by their high tolerance of infants' solicitations for food during the period of infancy.

Infants were very tenacious in continuing their solicitations. They repeated solicitation efforts even if their mother had rejected previous attempts. There was no linear correlation between the frequency with which an infant persisted with these attempts and its overall solicitation rate, but there were differences across infant age groups. The prediction that infants would vary their level of persistence, as a function of age, in attempting to obtain food from their mothers was supported. Infants persisted with attempts until they met with success during the first three years of life. Even though infants continued to solicit food into the fourth year of life, persistence was abandoned as a tactic by this time. In fact, if the graphs are compared the pattern of perseverance in many ways foreshadowed the pattern of solicitation by 6 months. It is possible that young infants may be more likely to persist with attempts because they may not have learnt to discriminate the

responsive signals of their mother, it may only be with age may that infants become attuned to subtle refusal communicative signals (Boesch & Boesch, in press).

The prediction that the rate of mothers' positive responses for solicitations for a food would be negatively correlated with the time it took mothers to procure and process that food, was supported. The longer a food item took to process the more willing mothers were to share it.

The relationship between food sharing and the infant's foraging success was investigated. In cases where the mother was observed feeding on the food type shared before a solicitation bout, infants had an opportunity to feed independently. The prediction that when an infant was capable of feeding independently on a food item it should cease to be shared was rejected. In these cases infants were just as successfully obtaining food from their mother even when they were capable of feeding independently on the item as when they were not. Hence, mothers shared foods with their infants irrespective of their infant's feeding competence, which lends further support to the notion that chimpanzee mothers are highly tolerant of their offspring's nutritional requirements. It also indicates that even when infants have mastered the foraging skills required, mothers continue to support their infant's progress by sharing food. Perhaps these later sharing events function to provide the final encouragement to motivate the infant to apply skills to other food types and reach full foraging independence.

In sum, chimpanzee mothers tolerate food scrounging by their infants because it minimises their reproductive and energetic costs. However, infants were responsible

for the higher rates of sharing of difficult food items. These difficult food items were difficult to process both for mothers and for infants. Through food sharing infants were able to acquire nutritional value from a food resource that they were not capable of processing by themselves. In addition, they may have been concentrating their attention where they had the most to learn: perhaps acquiring information not only to identify the food as being part of the adult diet but also how to obtain the correct part: the processing skills needed extract what is edible from the food item. So, the fact that solicitations were concentrated on difficult foods suggests that infants could be exploiting their mother's foraging expertise in a most effective manner. However, the relationship between food sharing and learning about foods may not be as explicit as is commonly assumed. In cases where infants are capable of processing and feeding on a food item independently we would predict that sharing of these food items should cease. However, this study found that infants were just as likely to successfully obtain food from their mother that they could obtain independently as when they could not.

Only in chimpanzees and the Callitrichids is food sharing a well-developed feature of infant development (see section 6.1). The higher incidence of 'offering' (active sharing) in the New World monkeys is interesting. It has been suggested that it is the result of ecological factors: young infants are not always in visual contact with possessors of food and an offering vocalisation is required to alert them to potential food (Feistner & Price, 1991). Clearly, no such ecological pressure for an offering vocalisation exists for chimpanzees since infants are in close proximity and visual contact with their mothers. So perhaps active sharing is not always a case of 'information donation' as King (1994) suggested. McGrew & Feistner (1992) examined these two groups - the habitual food sharing species - as models for the

role of food sharing in hominisation. From this comparison it seems that for chimpanzees and Callitrichids, food sharing has evolved for different reasons. These authors suggest that in the Callitrichids food sharing originated because of social determinants and has subsequently become embedded as part of the rich, co-operative social fabric of these monkeys. Perhaps the social determinant in this case was the unusually high reproductive demand on particular females within these species. In contrast, in chimpanzees McGrew & Feistner (1992) argue that food sharing is technologically based – perhaps, in this case originating in the procuring and processing of embedded food items. Parker and Gibson (1979) previously argued that food sharing was derived as a secondary adaptation to extractive foraging. I would suggest that the different reproductive pressures of these species need to be further examined. There appears to be a real difference in the significance of lactation to fertility between these two genera. The delay in return to fertility due to nursing young common to mammals (Nadler *et al.*, 1981), unusually, does not seem to affect Callitrichid primates. Contrary to earlier suggestions that the lack of effect of lactation on fertility only affected certain species of the *Callitricidae* family (Lunn & McNeilly, 1981), it now appears this is a feature intrinsic of marmosets and tamarins (French, 1983). Conversely, chimpanzees have very long inter-birth intervals (Tutin, 1994) and the effect of lactational amenorrhea on the interference with oestrus cycles is greater than in the *Callitrichidae*. It is likely that there will be differences in the relative importance of short term and long term benefits of food sharing in chimpanzees and the Callitrichids because in chimpanzees the mother is the sole provider, whereas in Callitrichids many individuals co-operate to invest time and resources in offspring. Consequently, further cross-species comparisons merit investigation.

# CHAPTER 7:

## DISCUSSION

We have tended to tackle the subject from a 'top-down' approach and made all kinds of assumptions about similarities and dissimilarities in strategies in the acquisition of knowledge with reference to ourselves.

*Box (1994)*

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Recent studies on social learning have tended to centre on identifying the cognitive mechanisms involved and so have been undertaken in laboratory settings where controlled testing conditions separate alternative social learning possibilities, such as imitation and stimulus enhancement, and individual processes, such as trial and error learning (Whiten & Ham, 1992). The impossibility of excluding all these processes when animals are studied in their natural habitats seems to have discouraged research in this area. Instead, attention has been restricted to the mechanistic perspective, which centres on establishing the highest levels of human-like ability great apes can attain, rather than performances that are typical, customary or functional. Experimenters introduce animals to novel tasks under artificial conditions where consideration of the animals being attentive or motivated both to complete the task and copy the model are questionable and the social environment that the animals were raised in clearly contributes to the results. Hauser's (1993)

was astute, when he noted: “we must be careful to distinguish between ability and performance...it takes considerable work to demonstrate the *lack* of an ability” (p. 524). This thesis has examined the development of foraging behaviour in wild chimpanzees from a functional perspective, investigating the mother-infant relationship as the contextual determinant of social learning. It is only by studying such natural tasks, in normal contexts with inherent ecological efficacy, that the origins and evolution of primate social learning can be understood.

There are inherent difficulties to studying behaviour in natural contexts, common to many field studies. The major limitation in this study was the level of habituation of mothers and their offspring who were shy and solitary. It was not possible to regularly follow subjects on the ground and secondary forest growth further impeded any observations that were possible on the ground. As a result, the majority of observations were made of mothers and their offspring feeding arboreally. Accordingly, the feeding choices for infants were not choices between species, rather they were choices about the part of the food species to be eaten given the tree the mother was in. In many respects any infant will be limited in the number of feeding choices available to it because the infant's proximity to its mother will limit the number of foraging choices. If the infant is near its mother, the likelihood that it will choose to feed on the same food type is increased although for juveniles who forage further from their mother this is less the case. It is accepted that if observations had been possible on the ground, infants in this study would probably have been shown to have a greater number of feeding options. However, this is not considered a major study limitation since chimpanzees primarily acquire their food arboreally.

Chimpanzee mothers are central, and almost exclusive to an infant's early social milieu (Goodall, 1967). Changes in the pattern of infants' social experiences and developing behavioural competence were charted. In their first year infants spent the majority of their time in physical contact with their mother and, hence, were continually in a passive manner exposed to sensory cues whilst their mothers were feeding. In their second year infants began to move out of contact with their mother but still within her arm's reach, and began to play and be groomed by her more often. Mothers focused their grooming on their infant but the amount of grooming an infant received from its mother did not vary across the years before weaning. Infants began to groom their mother in the second half of their second year and increasingly with age, presumably as grooming abilities improved. Juveniles focused their grooming on their mother and this approached reciprocal levels, grooming their mother almost as much as she groomed them. Younger infants engaged in more locomotory and acrobatic play than older infants, and there were large individual differences for both infants and juveniles in social play, which may reflect sex-differences, differences in play partner availability or differences in the sociability of mothers.

The feeding behaviour of young chimpanzees was investigated in relation to their mother's feeding choices. Infants began to feed independently in the second half of their first year, but not in large amounts and only on those foods that were easily obtainable, such as soft-shelled fruits. The diet of all subjects consisted predominantly of fruit. Infants consumed proportionally more ripe fruit and proportionally less unripe fruit when compared to their mothers, but juveniles ate similar proportions, suggesting that infants may be particularly sensitive to higher concentrations of tannins (Reynolds *et al.*, 1998).

Some foods consumed such as hard-shelled fruits and seeds encased in a pod, were designated 'difficult' because infants had not acquired the ability to handle these effectively: quantitative data demonstrated that even mothers consumed these foods at significantly lower rates per unit time. Infants started to feed on difficult foods later in life; physical constraints such as adequate strength, co-ordination, and dentition were likely to have prevented infants incorporating them into their dietary repertoire at a younger age. It was also possible that infants require more time to recognise these food items as suitable to eat because they are embedded (or 'hidden') within an inedible casing (Parker & Gibson, 1977, 1979) and sensory cues would not alone indicate their edibility.

By the end of their fourth year, infants were consuming all the foods their mothers ate but they were still significantly less efficient at processing these items than their older siblings and mothers, and consumed less dry mass per unit time. Infants did not start to use both hands to procure foods until their third year. Juveniles also used these actions less frequently than their mothers did. This may represent the long time needed to refine bimanual co-ordination but it may also be due to their smaller size, which may preclude the need to bimanually reach for food at the end of branches.

Commonly it is assumed that the early learning opportunities of being near the mother are important to infants. Such assumptions tend to be accepted uncritically. If learning from the mother is important then infants should maximise these contingencies by playing an active role in creating feeding-related encounters or interactions with the mother (King, 1994). The pattern of mother-infant spatial proximity, either as it is needed by the infant or tolerated by the mother, is the primary determinant for any social learning propensity

(Coussi-Korbel & Fragaszy, 1995). The extent to which infants co-ordinated their behaviour within the specific contexts of proximity and attention to their mother's feeding behaviour differed according to the age of the infant. Young infants (under the age of 2.5 years) selectively spent time near their mother when she was feeding whereas older infants did not. In addition, young infants visually attended at higher levels to their mother's feeding behaviour, were more likely to manipulate or 'play' with food items if their mother was feeding and were more likely to initiate their own independent feeding attempts if their own mother was feeding. These tendencies of young infants to watch their mother and synchronise their playful food manipulations and feeding attempts would no doubt increase the likelihood of acquiring relevant feeding information. However, although these tendencies were stronger early in development and degraded with time, there was no indication that these were particularly refined infant strategies to obtain information from their mother. The social influence of maternal feeding behaviour was general in its facilitatory effect in that it was not more evident with difficult foods. However, it was clearly effective: chimpanzee infants did not ingest items that their mother did not feed on and it is likely that mothers' feeding behaviour narrowed infants' focus to the salient variables. Clearly, if infants were more likely to play with food and start to feed independently when the mother was feeding and they were surrounded by food then this would minimise the likelihood of picking up unsuitable items. It was suggested that individual experience manually investigating, mouthing or tasting (without ingesting) potential food items might be more important as they represent opportunities to glean a fuller range of sensory cues. These cues would allow infants to discriminate not only foods from non-foods but also to assess the quality of individual items before ingestion, cues which would not have been available to infants if they only observed their

mother's feeding behaviour or spent time near her when she was foraging. These results also reflect the tendency of infants to sample novel foods (Watts, 1985; Frigaszy *et al.*, 1997a,b), which may explain why young chimpanzees are more likely to adopt new foods, feeding habits and behavioural innovations (Kummer and Goodall, 1985; Nishida *et al.*, 1984; Takasaki, 1983). Mothers did not direct or guide their infants: there were no observations of chimpanzee mothers actively intervening either to encourage or discourage infants feeding on particular items. Reports of such maternal intervention are in fact rare in the literature (Goodall, 1971; Hiraiwa-Hasegawa, 1990b; Nishida *et al.*, 1983). Evidently, such behaviour does not occur at levels that indicate mothers guide their infant's feeding choices. However, mothers did provide their infants with positive encouragement within the context of food sharing interactions.

The transfer of food from mother to infant is labelled 'sharing' because although mothers rarely offer food (i.e. donate food with no discernable request for food from the infant), the behaviour is volitional (Feistner & McGrew, 1989). Mothers are equally able to withhold food in response to these requests, as they are able to accept them. Chimpanzee mothers are in fact extremely tolerant of infant solicitations for food, consistently across populations wherever mothers and infants have been studied (Tai: Boesch, in press; Kibale: Ghiglieri, 1984; Gombe: McGrew, 1975; Silk, 1978; Mahale: Nishida & Turner, 1996; Hiraiwa-Hasegawa, 1990c). This is probably for two reasons. Firstly, sharing food reduces the burden of lactation for the mother by supplementing the infant's diet with solid food. Secondly, it may provide an opportunity for infants to acquire information that may then improve their competence in feeding themselves. These are two facets of the same phenomenon, which really describe the short and long

term benefits of food sharing. They are not competing hypotheses as previous authors have treated them (e.g. Nishida & Turner, 1996) and, therefore, it is not possible to draw a sharp line across these two effects. More likely they act together and reciprocally within the developmental continuum.

The quantity of food shared by mothers with their infants indicates that food sharing could be an effective component of maternal investment strategy. In addition, the timing, frequency, and type of food shared is consistent with food sharing being not only an important supplement to milk, but also an important means to introduce young infants to new foods. Although infants did not feed on difficult foods independently in significant quantities until their third year, they did obtain these difficult items much earlier, initially in their first year, from their mothers. Further, these difficult foods were shared at much higher rates than easy foods, and particularly when infants were aged between 18 and 30 months. Clearly, this could accelerate the infant discovering and learning about these foods, perhaps particularly useful in the case of these items since they are 'hidden' in that sensory cues will not indicate they are edible. Equally, it is clear that by obtaining items that they cannot open infants may simply be motivated to maximise their nutritional intake, not necessarily driven to obtain information but this occurs concurrently.

The period of development when food sharing was important was towards the end of the infant's first two years, a period when mere proximity would have determined learning conditions. Therefore, although infants do not increase their spatial affinity or demonstrate attentive observation towards their mother's feeding behaviour in a manner that persuasively indicated they create opportunities to acquire information, they did initiate

food-sharing interactions with their mother. These could serve the same purpose but in consideration of the infant's available time and attention resources, in a less expensive and more effective manner.

Contrary to earlier suggestions that mothers respond selectively to their infant (Silk, 1978), mothers were found to be less discerning than their infants, being equally tolerant of solicitations for easy and difficult foods. Re-analysis of Silk's (1978) data from Gombe on the solicitation success rates were very similar for easy and difficult foods. Hence, although the inherent tolerance of chimpanzee mothers in allowing their infants to take foods provides good learning contingencies, there are no data to support the notion that mothers modify their behaviour in a manner that would improve the prospect of infants acquiring information. In King's (1994) terminology: infants appear good 'information gatherers' but mothers are rarely 'information donators'. Clearly, if infants do learn something from these encounters, it is the infants themselves that are increasing the likelihood of useful information being obtained. Infants continue to scrounge and, more importantly, continue to receive food when they are capable of competently acquiring that food item themselves. There was some evidence that mothers became increasingly indifferent to infant's solicitations but there was little active rejection, which is consistent with weaning in chimpanzees being a gradual and typically non-aggressive process (Clark, 1977; Goodall, 1968). It is likely that scrounging is only an effective option as long as processing rates are poor, and as these improve the infant abandons scrounging as a strategy.

Infants are the active element within the food sharing phenomenon. Infants, rather than mothers, initiated sharing. The higher sharing rate of difficult foods was determined by infants focusing their solicitations on these particular foods. Infants did not scrounge indiscriminately as a function of the time they spend close to their mother nor as a function of the time that she was feeding or as a result of apparent feeding competition as indexed by a simple measure of mean party size. Moreover, it was not possible to attribute infants' selective solicitation for difficult foods to degrees of differential reinforcement by the mother, since mothers were not more likely to share difficult foods. Therefore, within the specific context of food sharing infant chimpanzees spontaneously directed their attention towards objects that they have the most difficulty with, a distinction they made even at a young age. The importance of the infant's role within these interactions is also relevant with respect to emergent infant abilities. Clearly with interactive phenomena the role that the mother and infant play affects the behaviour of the other and this will not be seen if each is considered alone. The infant's role within these interactions is more complex than simply 'scrounging' food. Infants are capable of delaying the tactic of directly taking food and, rather, will sometimes beg for food in an expectant manner. This implies that they might be able to adjust their behaviour from an immediate strategy to an expectant one in order to obtain their objective. Begging behaviour may be an early form of intentional communication (Bard, 1990) and a precursor to development of the species-typical gestures that adults use in the context of begging, greeting and appeasement. Infants became less persistent in their solicitations as they reached their fourth year. This may reflect a developing ability to discern contingencies between subtle responsive signals of their mother and the outcome of the event, with older and more experienced infants abandoning their solicitation attempts

earlier than younger infants. Clearly, food sharing is not unidirectional, which is something true of all social learning interactions, encounters and opportunities.

In conclusion, there has been a degree of urgency in identifying and demonstrating sophisticated learning and cognitive processes in chimpanzees and other great apes. It is important this does not overshadow the need for quantitative studies that investigate the functional dyadic context in which social learning occurs and the regulating or affective responses that support it. For a young, developing chimpanzee there are many learning opportunities over its long period of immaturity that progressively support its transition to eventual competent foraging. As infants grow older there is a continual interplay of physical, social, cognitive and environmental constraints, with these effects reinforcing one another reciprocally and determining what skills can be learnt at what age. For young infants starting to feed initially on solid food the most important of these factors is the development of physical attributes, particularly size, strength, adequate dentition and detoxification capabilities to deal with difficult to process and chemically defended food items. Mothers do not take an active role in supporting their infant's learning but infants do seem to increase their own learning contingencies. This is particularly evident in their propensity to solicit food from their mothers and within this context mothers respond positively and encourage their infants. Mothers, by sharing food, not only provide their infants with nutritional support and motivation to forage, but also facilitate their learning, allowing their infants experience with foods that they would otherwise be able to handle. Hence, mothers support learning within this dyadic context, possibly using infant demands to gauge the progress of their infant and to tailor their response accordingly.

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# APPENDIX 1:

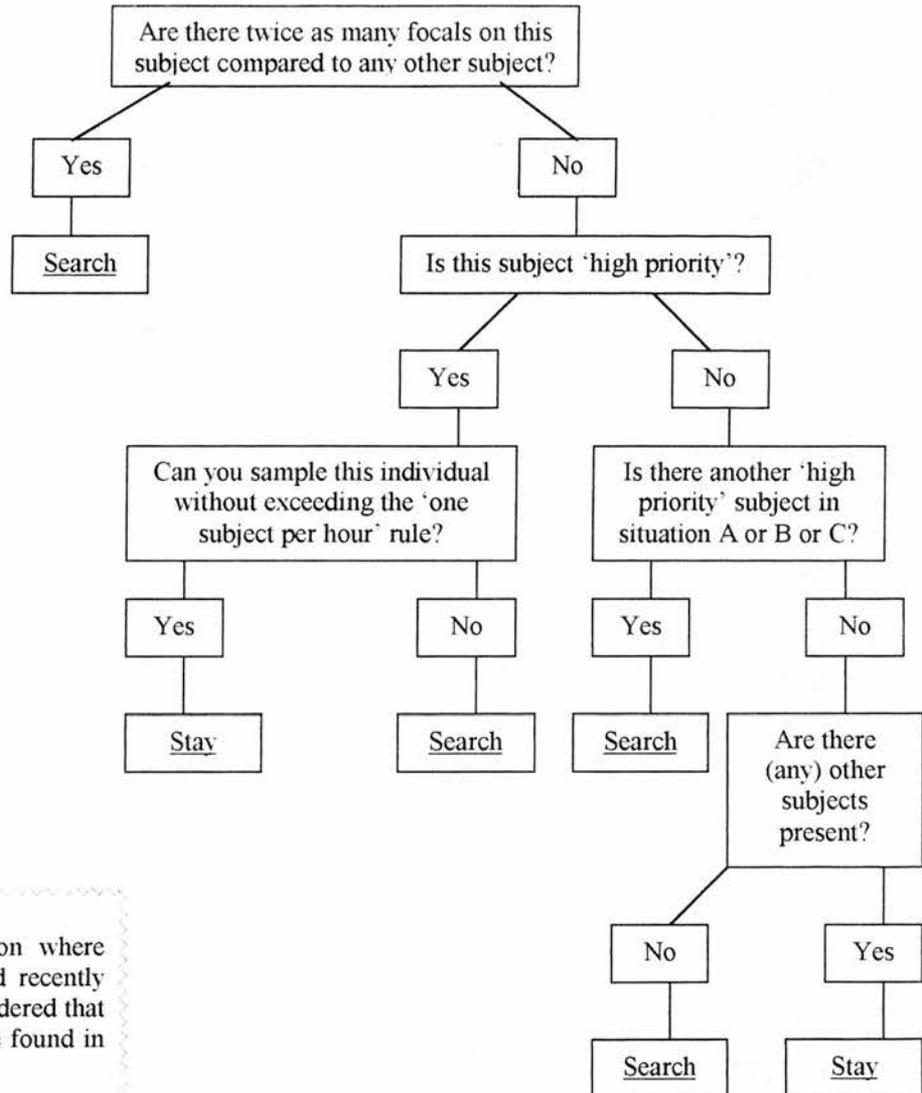
## Test of observer accuracy for proximity distances

My field assistant was principally responsible for estimating the proximity distance categories between mother and offspring. The results of 20 tests of his estimates are displayed below. There were two inaccurate estimates (in bold), both on the margin of the proximity category. Overall accuracy was 90%.

Test No.	Distance (in m)	Estimated distance (in m)
1	3.6	3-5
2	13.2	10-20
3	5.5	5-10
4	16.8	10-20
5	1	<1
6	20.5	>20
7	15.8	10-20
8	18.6	10-20
9	13.4	10-20
10	9	5-10
11	4.9	3-5
12	5.5	<b>3-5</b>
13	23.8	>20
14	3.15	<b>1-3</b>
15	9.3	5-10
16	14.1	10-20
17	33.7	>20
18	.65	<1
19	2.6	1-3
20	9.6	5-10

# APPENDIX 2:

## Sampling Decision



**Situation A:**

Refers to the situation where calls have been heard recently nearby, and it is considered that study subjects may be found in this direction.

**Situation B:**

Refers to the situation where there is a tree that is known to be in fruit, and it is suspected that study subjects may be found there.

**Situation C:**

Refers to the situation where another observer has seen a study subject in a nearby area and has radioed its location.

**SEARCH:** Leave these individuals and attempt to locate another subject.

**STAY:** Stay with these individuals and continue to sample the same subject until any factor in the sampling decision changes then, adjust accordingly.

## APPENDIX 3:

Total number of focal samples  
(in minutes) by individual

Focal Individual			Focal Individual, as:	
<i>Infant</i>	<i>Juvenile</i>	<i>Mother</i>	<i>Principal subject</i>	<i>Subsidiary subject</i>
RS			360	240
		RH	240	360
ZG			860	640
	GZ		400	
		ZM	640	1260
RA			660	540
	BO		360	
		RD	540	1020
BT			680	240
		BN	240	680
NR			1000	620
	MS		380	
		NM	620	1380
ZL			760	460
		ZN	460	760
KZ			1060	720
		KW	720	1060
BH			1000	620
		KL	620	1000
KT			520	420
		KU	420	520
	KD		400	340
		KG	340	400
Totals			12640	12880