

Primate Parenting

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INTRODUCTION

The conceptual and practical issues associated with parenting in primates, in general, and with maternal competence in chimpanzees in specific are addressed in this chapter. What does it take to be a good parent, if you are a primate? How can we characterize the ontogeny of maternal and paternal skills? Are there biological bases in primate parenting? What are the learning mechanisms involved in parenting in primates? It seems evident that there are specific behaviors that must be learned in order to be a competent parent, however the learning mechanisms remain unknown. It is unclear whether behavior patterns must be learned through actual practice or whether other mechanisms, such as observational learning, are equally effective. In addition, the influence of early experience on maternal capability remains an unknown factor. These central questions of parenting in primates have been asked for the past 30 years and still have not been satisfactorily answered (e.g., Rogers and Davenport, 1970).

Primates were studied in their natural habitat in the 1920s, 1930s, and 1940s in order to document the variety of primate species and to specify the habitat, group demographics, and gross aspects of behavior in each species (e.g., Bingham, 1932; Carpenter, 1964; Nissen, 1931, Zuckerman, 1932). In 1938, a monkey colony was established at Cayo Santiago with rhesus imported from India and the long-term study of Japanese macaques was begun (Dolhinow, 1972). Studies of the finer details of behavior during this time were conducted in the laboratory (e.g., [Harlow, 1958](#); Kluver,

1933; Kohler, 1925; Harlow Yerkes and Yerkes, 1929) or in the home as a laboratory (e.g., Jacobsen, Jacobsen, and Yoshioka, 1932; Kellogg and Kellogg, 1933; Kohts, 1935).

In the 1950s, there was a burst of long-term field studies and an equivalent burst of laboratory studies but few species were studied in depth. Basics about mother-infant relations and social systems were described in some species of macaques especially Japanese macaques (Itani, 1959) and rhesus (Altmann, 1962), baboons (DeVore, 1963; Hall, 1962; Rowell, 1966) and langurs (Jay, 1962). In the 1950s and 1960s Harlow and co-workers experimentally manipulated aspects of the mother-infant relation (Harlow, 1958; Kaufman and Rosenblum, 1969; Seay, Hansen, and Harlow, 1962) and Hinde and co-workers studied mother-infant relations in group-living captive rhesus (e.g., Hinde, 1969; Hinde and Spencer-Booth, 1967; Rowell, Hinde, and Spencer-Booth, 1964). These research efforts in connection with Ainsworth's (1967; Ainsworth and Bell, 1970) study of human mother-infant relations greatly effected Bowlby's (1969; 1973) theoretical works on attachment.

The 1960s was the beginning of long-term field work of great apes (Nishida, 1968; Reynolds, 1968; Schaller, 1963; van-Lawick-Goodall, 1968), prosimians (Jolly, 1966), and baboons (Kummer, 1967) and could be considered the beginning of the explosion of psychological, biological, anthropological, and evolutionary studies of primates that took place in the laboratory (e.g., Schrier, Harlow and Stollnitz, 1965), semi-natural settings (e.g., Altmann, 1962), and the natural habitat (S. Altmann, 1967; DeVore, 1965; Dolhinow, 1972; Jay, 1968; Morris, 1967). In addition, primate research centers

were established at Kyoto University (The Japan Monkey Center), the University of Wisconsin and Emory University (Yerkes Regional Primate Research Center: Parker, 1990).

The foundation of basic knowledge provided by these studies allowed specific issues to be addressed, such as the following: (1) what are the genetic and evolutionary bases of parental care (e.g., Trivers, 1974)?, (2) what functions are served by non-parents providing infant care (e.g., Hrdy, 1976; Lancaster, 1971; McKenna, 1979; Quiatt, 1979; Rowell, Hinde, and Spencer-Booth, 1964)? (3) why does infanticide occur (e.g., Hausfater and Hrdy, 1984; Hrdy, 1976; Nicolson, 1987; Quiatt, 1979), (4) how do disruptions/dysfunctions in parental care influence infants, e.g., child abuse (Nadler, 1980; Reite and Caine, 1983); (5) evolution of male - infant relations (Deag and Crook, 1971; Strum, 1984; Whitten, 1987), and (6) how do social systems influence patterns of parental care (e.g., Hinde and Spencer-Booth, 1967; Maestripieri, 1994).

These central issues have been further investigated, raising more specific questions. For instance, what are the major factors that influence the evolution of cooperative care? It was thought that males would provide care when paternity was certain, so monogamy was considered to be the best predictor of cooperative care. When types of care were compared across monogamous primates, some did have cooperative care but others did not (Wright, 1990). The ratio of infant(s) weight to mother's weight was also considered to be a predictor of cooperative care, but it was also found to be a poor candidate (Gursky, 2000). Cooperative care of infants is associated with increased vigilance and defence against predators (Caine, 1996;

Snowdon, 1996). A constant issue is how primate parenting relates to human parenting (Goodall, 1967; Higley and Suomi, 1986; Hinde, 1969; Hinde and Stevenson-Hinde, 1990; Nicolson, 1991; Rheingold, 1963).

This chapter is concerned with describing parenting behavior in primates. Chimpanzees are used as the basis for comparison with other primate species. Chimpanzees are our closest evolutionary relatives, sharing over 90 percent similarity in genetic material (King and Wilson, 1975), and provide important information relevant to human behavior. In addition parental prerequisites are proposed. As a result of research with chimpanzees, a proposal is made that there are optimal or sensitive periods during which different aspects of parental behavior are readily learned (e.g., Bornstein, 1989). Intervention strategies to maximize parental competence in chimpanzees are presented: optimal learning periods and ways to facilitate learning a full range of necessary behaviors are discussed.

The majority of research on primate parenting has been conducted in a relatively limited number of primate species. This chapter, as a product of our limited knowledge, focuses on the well-studied species listed in Table 1. Parenting behaviors in chimpanzees are described in detail and explicit comparisons are made in parenting behavior between chimpanzees and other primates. Social dynamics may also influence parenting styles (for example, see Maestriperi, 1994) and these are listed in Table 2, but due to lack of space are not discussed in detail here. In addition, issues pertaining to the development and ontogeny of adequate parental behaviors will be highlighted. This perspective provides insights on primate parenting because the focus

is on different parenting behaviors that are required for offspring of different ages.

Insert Table 1 about here

This chapter also presents data and specific hypothesis on parenting prerequisites in chimpanzees. The description that follows illustrates events that were instrumental in the formation of some of the ideas and research described in this chapter. Barbara, a 14-year old chimpanzee was pregnant for the second time. Would she be a competent mother and raise her infant in a species-typical manner? Barbara was born at the Yerkes Research Center of Emory University, and had been raised by her mother, Sonia, who was born in Africa. Sonia, a gentle and extremely competent adult female, had been a good mother to Barbara (Miller and Nadler, 1981). In 1987 when Barbara gave birth to her first infant, everyone's expectation was that she would be a 'good' mother because after all Barbara was mother-reared, housed with other adult chimpanzees (an indication that she has good social skills), and she exhibited sufficiently sophisticated sexual behavior to become pregnant through natural means. When her first baby, Winston, was born, however, Barbara did not pick him up. Barbara gave every indication of the best intentions toward Winston: She was disturbed by his crying and made herself available to him, she attentively leaned over him, stayed in close proximity to him, and leaned more solicitously whenever he cried. Barbara, however, had no maternal behaviors; she did not pick him up and did not cradle him. After a few hours, Winston was placed in the nursery because he could not have

survived without Barbara picking him up. Because Barbara was so solicitous but lacking in behavior, it was concluded that she did not know what to do with a baby.

A plan developed to provide a remedial intervention for Barbara. Conan, a 1-year-old chimpanzee infant, was temporarily moved to the great ape nursery at this very time in order for his mother to resume her menstrual cycle. The veterinary staff at the Yerkes Center decided to put Conan and Barbara together, hoping that both would benefit. Barbara was as solicitous as she had been toward Winston, her biological offspring, but Conan, a more capable 1-year-old, was quite different. Initially he avoided Barbara because she was a stranger. But finally after 2 to 3 days, Conan rushed into Barbara's arms accepting her as a substitute for his absent mother. In the next 3 to 5 months, Barbara was observed developing maternal behaviors, she was seen cradling Conan, allowing him to nurse, and gathering him up before she moved. Conan was allowed to remain with Barbara, his adopted mother, rather than disrupt him again with a return to his biological mother. Three years later, Barbara gave birth to her second baby, Kevin. No one was surprised that now Barbara exhibited the full range of appropriate species-typical maternal behaviors, she picked up Kevin and cradled him immediately. The experience involved in interacting with a motorically competent 1-year-old seemed to give Barbara the opportunity to learn how to pick up and cradle infants. It was clear that, in this case, Barbara's motivation to provide care was equal for Winston and for Conan. The difference in her maternal competence, however, before and after her hands-on experiences with Conan was striking and led to the specification of maternal competence in chimpanzees and necessary precursors (Bard,

1994-a).

This chapter contains two main parts, descriptions of species-typical parental behaviors and theoretical discussions of prerequisites for the expression of parental behavior. The section describing species-typical parental behavior is further divided by taxonomic divisions and by offspring age beginning with parental behaviors directed toward newborn chimpanzees, and ending with parental behaviors directed toward adolescent prosimians. Two small sections contain information on intuitive parenting and teaching in nonhuman primates. In the section on ontogeny of maternal behavior, the influence of different precursors of parental behavior is evaluated. The variables considered include early experience and observational learning. Discussions of the influence of these variables on general behavior has a long history (Whiten and Ham, 1992) as do discussions of their influence on parental behavior, in particular. A brief section describes a prospective study in chimpanzees to manipulate the amount of "hands-on" experience with infants and evaluate the subsequent effect on parental behaviors. The final section describes some of the ways in which primate parenting relates to human parenting.

PARENTING BEHAVIORS IN NONHUMAN PRIMATES

Different skills are required for parental care of infants of different ages (e.g., Tardif, Harrison, and Simek, 1993). The age of individuals within each period differs between the species on account of different rates of development. So, parenting behaviors are

discussed for newborns, infants, juveniles, and adolescents. The newborn period is defined as the initial period after birth during which the infant is unable to survive without parental support. Infancy is the period when the offspring is physically dependent on the mother's milk. The juvenile period is distinguished by longer times spent further away from the parent(s), and sometimes accompanying changes in coat color. Weaning marks the end of the juvenile period. The adolescent period begins at puberty and ends at the time when effective reproduction occurs (Walters, 1987). The skills necessary for parenting offspring at each of the developmental periods may have different developmental histories. Therefore, both the skills and their ontogeny are discussed within each age period separately. Parenting behaviors are additionally presented within sections by order (see Table 1). There are major differences between species in the skills required for maternal competence. For many species of monkey, the infants are motorically capable soon after birth. Maternal competence in many monkeys, therefore, involves only acceptance of the infant, i.e., allowing the infant to cling. For example, rhesus infants at birth are able to cling, climb on the mother's body, and suckle. In other words rhesus infants can survive as a result of their own behavior, as long as the mother does not actively reject them (i.e., pull them off her body and prevent them from clinging). In contrast, for chimpanzees as in humans, maternal competence requires active cradling and nurturing. Newborn chimpanzees are as helpless to survive without maternal support as are human newborns. Winston, Barbara's baby, could not move into her arms; Barbara needed to take the active role and to pick him up – but this was one of the behavioral skills that she lacked. Maternal

competence in chimpanzees therefore requires the mother to take positive action including picking up the helpless newborn. Competence in all species is defined broadly as the ability to raise offspring to adulthood.

This section of the chapter concentrates on parenting during infancy for a number of reasons. Primarily, parenting responsibilities are greatest during this period when offspring are least capable of coping on their own. The second reason is that there are already good reviews on juveniles (i.e., Pereira and Fairbanks, 1993) and adolescents (Bernstein, Ruehlmann, Judge, Lindquist, and Weed 1991; Caine, 1986), although there remains little known about parenting juveniles and adolescents. Adolescence is typically the time when emigration occurs and offspring may permanently leave the family group. In most primate species, it is the sons who leave and the daughters who stay in close proximity with their mothers. Although parental status within the group may be crucial to the long-term outcome for an adolescent, the observable parent-offspring interactions are minimal.

Parenting Newborn Chimpanzees and Apes

The newborn period is defined as the initial period after birth during which the infant is unable to survive without parental support. For some species there is really no clearly definable neonatal period subsequent to the minutes after birth, for others the period last through the first 30 days as is true for human newborns (e.g., Brazelton, 1984).

This section will discuss those special parental skills applied to newborns, distinct from the parental behaviors to infants. The term infants refer to nonhuman primate infants: Human infants are distinguished explicitly.

Existing field studies of free-living chimpanzees do not richly describe newborn chimpanzee behavior because the very small neonate is difficult to detect on the body of the mother who must be observed amid the trees and grasses of the chimpanzee's African habitats (Plooij, 1984). The chimpanzee newborn and mother are in constant ventral-ventral contact during the first 30 days of life (van Lawick-Goodall, 1968). Newborn chimpanzees are as helpless to survive without maternal support as are human newborns. Newborn chimpanzees and humans have a strong grasping reflex (Bard, Hopkins, and Fort, 1990) but it is insufficient to support the infant for more than a few seconds at a time. Unlike most primates, chimpanzees are unable to support their own weight independently for at least the first 2 months of life (Bard, Platzman, Lester, and Suomi, 1992; Goodall, 1968; Plooij, 1984; Rijt-Plooij and Plooij, 1987). Mothers provide the majority of physical support during this time although she seldom helps the neonate to suckle. Feedings are short in duration and irregularly spaced (Brown and Pieper, 1973; Dienske and Vreeswijk, 1987; Plooij, 1984).

Detailed observations of newborn chimpanzees with their mothers are possible in the laboratory setting, such as at the Yerkes Research Center of Emory University. These observations reveal that sleep is the predominant infant state throughout the first 30 days of life, about 50 percent of observation time (Bard, Platzman, and Coffman, 1989). The newborn is alert and quiet for considerable periods, especially on the first

day of life and increasingly through the first month an average of 25 percent of the time. Active alert states are apparent but account for less than 10 percent of observation time during the first month of life. Newborn chimpanzees do cry and fuss but it is rarely and for short periods of time (Bard, 2000). Nuzzling, rooting, and nursing account for approximately 20 percent of the infant's time during the first month. In addition, EEG sleep patterns are evident in chimpanzee newborns, and are similar to those of human newborns (Balsamo, Bradley, Bradley, Pegram, and Rhodes, 1972).

The vast majority of maternal behavior is simply cradling newborn infants, providing the support they need to remain in physical contact (over 80 percent of the time; Bard, 1994-a: Figure 1). Other activities, in addition to cradling, occurred on average of 10 minutes per hour. These additional activities include grooming the infant (6 percent), playing with the infant and eliciting some smiles (3 percent), examining the infant (2.5 percent), assessing the behavioral and physical state of the newborn (2 percent), and encouraging the infant's motor development with physical exercises (1 percent).

Insert Figure 1 about here

Gaze is an important aspect of primate behavior. On average, chimpanzee mothers spend 12 minutes an hour looking at their newborn infants (Bard, 1994-a). Half of that time is spent looking at the infants' face during activities of assessing, examining, playing, and grooming. Newborn infants also gaze at the face of their mother (Goodall, 1986, p. 86). Numerous instances of mutual gaze occur between mother and infant, 10

times in an hour on the average. Although not explicitly investigated, it seems that chimpanzee mothers encourage brief mutual glances in striking contrast to the extended mutual gaze encouraged by human mothers (e.g., Trevarthen, 1979; Tronick, Als, and Adamson, 1979).

The social structures of orangutans and gorillas differ from that of chimpanzees and one might expect differences in parenting. Orangutans are the most solitary of the great apes and gorilla groups consist of a dominant male silverback and 5 to 7 unrelated females (i.e., harem). Newborn orangutans and gorillas appear more capable motorically compared with chimpanzees (Figure 2). Orangutan mothers do not travel far or quickly, and they rest frequently with newborns (Galdikas, 1982). Maternal support of the infant may be minimal even on the first day of life and the placenta may or may not be eaten (Fossey, 1979; Galdikas, 1982). Gorilla mothers with newborns are given preferential proximity to the father, the silverback male. Newborn gorillas can cling unsupported by mother for up to 3 minutes (Fossey, 1979). The social group is important for the maintenance of maternal competence in gorilla, perhaps heightening protective responses (Nadler, 1983). New gorilla mothers isolated from the group typically exhibit abusive behavior (Joines, 1977; Nadler, 1983).

Insert Figure 2 about here

The lesser apes, gibbons and siamangs are monogamous and territorial. In fact, as expected the males engage in paternal care, but mothers provide exclusive care to

newborn lesser apes. Gibbon mothers provide cradling support to newborns and reposition the infants to a safer spot on the mother's body prior to leaping between trees (Carpenter, 1964).

Parenting Infant Chimpanzees and Apes

Infancy is the period when the offspring is physically dependent on the mother's milk and could be differentiated into an early time, during which no independent locomotion occurs and a time during which there is some independent locomotion but the infant remains close to the parent(s) during the day and night. Great apes (chimpanzees, orangutans, bonobos and gorillas) remain in an infancy period for 4-6 years. Goodall classifies infancy in chimpanzees as the period from birth to the time of weaning (and cessation of travel on the mother's body), which occurs at approximately 5 years of age (e.g., Clark, 1977; Goodall, 1968). The early infancy period is characterized by almost constant physical contact. The first break in contact is typically initiated by the 3-or 4-month-old laboratory infant (Miller and Nadler, 1981; van Lawick-Goodall, 1968). By 3 months the amount of maternal restraint of infant movement has increased fivefold (Bard, 1994-a), indicating both how active the infant is and that the mother is responsible for maintaining the proximity to the infant.

In the first three months, chimpanzee mothers (with good maternal competence) engage their infants in a variety of interactions (Bard, 1994-a; Goodall, 1968; Plooj,

1984). There are many instances of encouragement or exercising of skills in infants during this time. Motor development is stimulated through maternal maneuvers such as standing infants while holding their hands. Mothers repeatedly and alternatively stimulate their infants to hold their weight with legs and then with arms. Encouraging of early crawling is accomplished in a similar way. Because mother-infant contact is rarely broken in these early months, these stimulating exercises are typically performed on mother's body. "Sooner or later every mother encourages and variously aids her baby to learn to creep, stand erect, climb, and finally to walk and run" (Yerkes and Tomilin, 1935, p. 333).

Early mother-infant communication in chimpanzees is often accomplished with touch (Plooij, 1979) and accompanied by vision and audition. Mothers monitor their infant's behavioral state by stretching and moving infants' toes, fingers, arms, and legs and sometimes just by looking at them. During play, infant smiles are sometimes "marked" as critical features by the mother with an emphasized touch (e.g., Adamson and Bakeman, 1984). When the infant smiles in response to a tickle in the neck or groin, the mother may place her index finger on the infant's lower gums and exaggerate the smile by pushing gently on the lower gums.

Mothers appear to be sensitive to infants' eye gaze and will shift their own gaze away whenever mutual eye gaze is attained (Bard, 1994-a). Chimpanzee mothers spend considerable amounts of their time gazing at their young infants, and gazing at the infant's face. There are numerous instances of mutual gaze every hour within the infant's first months of life. The role played by maternal eye gaze and mutual eye gaze

in chimpanzees is still uncertain and may be different from human mother-infant pairs where mutual eye gaze is the foundation for interpersonal communication (Tronick et al., 1979) and interaction (Trevarthen, 1979). In Old World monkeys, mutual eye gaze is exceedingly rare and prolonged gaze by an individual monkey constitutes a threat. In chimpanzees, mothers are very attentive to infants, even to the extent of monitoring behavioral states as subtle as sleep, and cessation of nursing. Chimpanzee infants gaze at their mothers' faces. Very young infant chimpanzees appear to have a greater visual acuity at 30 cm than 15 cm, but see quite comparably to human infants at 15 cm (Bard, Street, McCrary, and Booth, 1995: Figure 1). Moreover, neonatal chimpanzees reared with human adults engage in extended eye-to-eye contact (Bard, 1998-b; Bard et al., 1992). Previous reports indicate very limited episodes of mutual gaze in mother-infant great apes (e.g., Plooi, 1979; Papousek, Papousek, Suomi, and Rahn, 1991; Rijt-Plooi and Plooi, 1987). Early social environments seem to influence the expression of behavior as early as 30 days of life (Bard, 1994-b; Bard et al., 1992). It appears that chimpanzee mothers regulate the duration of mutual gazes by looking away within seconds of achieving mutual eye contact. Thus, it may be that one of the early behaviors that is "culturally" regulated in chimpanzees is eye gaze (e.g., Bard and Gardner, 1996: Figure 3).

Insert Figure 3 about here

From 5 to 7 months, the infant begins to ride on the mother's back. Typically it is

not until 1 ½ years of age that infant chimpanzees reliably respond to the mother's communicative signals to "climb aboard" (van Lawick-Goodall, 1968). But, one mother was explicitly observed to teach her young infant to climb on her back when she displayed a hunched posture while looking over the shoulder which constitutes the communicative signal (Rijt-Plooij and Plooij, 1987). From 5 or 6 months, the mother places the infant on her back or reposition the infant from ventral to dorsal position. Independent quadrupedal steps and climbing appear as early as 4 months of age (Rijt-Plooij and Plooij, 1987). Some argue that mothers act aggressively toward the infant in order to attain dorsal riding and breaks in contact, but careful reading suggests that typical maternal behavior is determined rather than aggressive (Rijt-Plooij and Plooij, 1987). Chimpanzee mothers provide both physical support and encouragement for these motor developments (Bard, 1994-a; Goodall, 1967; Yerkes and Tomilin, 1933).

From 8 months, infants and mothers are comfortable out of physical contact and within arm's reach, but infants whimper when mothers move too far away (Rijt-Plooij and Plooij, 1987). It is perhaps no different from increased attachment and separation anxiety that surrounds the period during 7 to 9 months when developing cognitive processing allows both human and chimpanzee infants to distinguish novel from familiar (Ainsworth and Bell, 1988; Bard and Gardner, 1996; Bowlby, 1969; Bowlby, 1973; Fritz and Fritz, 1985; Plooij, 1984; Rijt-Plooij and Plooij, 1987). A reasonable conclusion from Rijt-Plooij's descriptive data is that between 8 and 11 months the infant becomes responsible for maintaining contact and proximity with the mother in contrast to the earlier time when the mother proximity with the infant. Around 11 months of age, there

appears to be an infantile regression and ventral contact is again predominant. But from 12 months to 18 months infants return to being comfortable within mothers arm's reach and as they get older they spend increasing amounts of time more distant from the mother.

Social skills such as greeting social partners and using communicative signals to initiate play or grooming, develop first in interaction with the mother then are used in interaction with older siblings and peers. In the second month of life, infant chimpanzees respond to mothers' tickles with smiles and very quiet laughter (Bard, 1998-b; Plooij, 1979). In the third month, infants reach, with a smile, to initiate tickle games with the mother and sometimes with older siblings (Goodall, 1968; Plooij, 1979).

In the second half year of life, infants initiate social interactions with others by approaching them with vocal greetings. Mothers monitor infants' interactions with others and immediately rush to pick them up at the first signs of infants becoming distressed.

Infants learn a great deal of social communicative signals in the first two years of life. Communicative signals constitute all the ways that social partners negotiate social interactions. Some might label these communicative signals the natural "language" of chimpanzees. The sharing of food is a negotiated event that involves communicative signals (Figure 4). It can serve as one example of this type of social skill development.

Food sharing is a phenomenon which occurs in chimpanzees (Goodall, 1986) and orangutans (Bard, 1992). Mothers typically allow young infants, around 4 or 5 months, to take some food from her mouth. Chimpanzee infants use communicative gestures to

request food between 9 and 12 months (Plooij, 1984). These food begging communicative gestures also allow individuals, when they are older, to obtain some meat from adult males. It appears that chimpanzee mothers selectively share only the more difficult to process or difficult to obtain foods as the infant matures (Silk, 1978, 1979).

Insert Figure 4 about here

From 2 to 5 years there is much to be learned about food, food processing, traveling, and hunting. Chimpanzee mothers monitor what infants eat and prevent them from manipulating or eating undesirable objects. Mothers serve as models for older infants to learn termite fishing (Goodall, 1986), tool manufacture (Wright, 1972), plant foraging (McGrew, 1974, 1977), food processing (Lefebvre, 1985) and locomotory behaviors (Bard, 1993, 1995). There is an increasing amount of evidence that Great Ape mothers actively instruct their infants under some circumstances. Boesch (1991) argues convincingly that chimpanzee mothers "take an active part in the apprenticeship of their female offspring" (Boesch and Boesch, 1981, p. 592) to crack nuts with a hammer tool. Chimpanzee mothers facilitate arboreal locomotory behavior by "bridging" gaps between trees allowing the young infant to cross the gap on her body and allowing older infants to cross the gap on branches that are she holds close together (Bard, 1995-b; Goodall, 1986). It is likely that adult male chimpanzees play a teaching role in the apprenticeship of male offspring in cooperative hunting (Boesch

and Boesch, 1989, 2000).

The subtle communication between mother and infant is documented in "meshing". Rijt-Plooij and Plooij (1987) discuss meshing only in the locomotor context and define it as maternal anticipation of and coordination with the infant's contact behavior. Meshing occurs from 8 to 24 months but monthly levels rise and fall in correspondence with the infants' responsibility for contact maintenance. "It is the mother's role to (force) teach the infant how to use newly emerged abilities it might not, or not fully, have used otherwise" (Rijt-Plooij and Plooij, 1987, p. 72).

Clark (1977, p. 235) describes the two-year gradual weaning process in 2 to 4 year-old chimpanzees as a period when infants may "display many elements of depression". It begins with mothers preventing access to the breast by holding the infant away, pushing the infant away, or physically blocking access with an arm or knee pressed firmly against their own chest. Mothers often distract the infant with play or grooming when they attempt to suckle, and mothers may move away from the infant as the infant approaches to suckle. It was extremely rare for any mother to exhibit aggressive behavior in relation to weaning her infant. In response to these tactics infants whimper and become physically more intrusive in their attempt to access the nipple. As the infant grows older and weaning is more strictly enforced, temper tantrums ensue. But as weaning progresses elements of depressive response are seen including decrease in play, loss of appetite, huddled posture and resumption of infantile behavior with the mother including ventral riding, and increased contact (Yoshida, Norikoshi, and Kitahara, 1991).

All 4- to 5-year-old infants exhibit distress when the mother's milk is no longer available and within months make no further attempts to suckle. Clark (1977) notes that all mothers appear "remarkably tolerant and gentle with the infants during the weaning period" (p. 252) and increased their attentiveness to the infant through grooming and waiting for them in traveling. Infants, however, appear depressed through the period of the birth of the younger siblings. Their depression is exhibited in lethargic movements, lack of positive emotions, and sometimes decreased appetite and moderate weight loss.

Orangutan infants, less than 2 years are less frequently out of contact with the mother compared with chimpanzee infants (Bard, 1993, 1995-b). Mothers may tolerate relatively close proximity with other mothers in order to allow their infants to play. Fewer peers are available for socialization in orangutans compared with chimpanzees during the entire infancy period up to 5 years (Bard, personal observation). Orangutan infants are weaned between 4 and 8 years of age (Bard, 1993; Galdikas, 1979).

The gorilla infant in early infancy is motorically more advanced than chimpanzees, chewing food items in the first 2 months of life, and clinging to the mother's hair without support by 2 months, and reaching for objects earlier. Mothers spend time grooming the infant and begin to rebuff suckling attempts before the infants' first birthday. Gorilla mothers encourage the development of infant locomotor skills in a manner similar to that of chimpanzees (Whiten, 1999). By 2 years of age infants travel primarily independently but they retain the white tail tuff, that indicates an infant through part of the third year (Fossey, 1979).

Infancy in the lesser apes lasts 2 to 2.5 years (Leighton, 1987). When the gibbon mother rests her 6-week-old infant begins to move a little distance from her. Infant gibbons in the first weeks of life may eat some solid food and engage in locomotor play (Carpenter, 1964). One of the most striking behaviors exhibited by gibbon parents is their vocal duet, songs are given morning and evening. "Infants often squeal during a mother's great call" (Leighton, 1987, p. 140). As older infants travel independently, they sometimes are unable to cross gaps between trees, and they "cry" until the mother retrieves them (Carpenter, 1964). In the second year of life, fathers carry gibbon and siamang infants and groom them. Paternal care can be as high as 78 percent of the day (Whitten, 1987); the infant returns to the mother to nurse and to sleep at night (Alberts, 1987).

Gorilla infants and their fathers play frequently in notably contrast to chimpanzees (Figure 5). In addition, gorilla fathers carry some young infants (Tilford and Nadler, 1978). Some gorilla infants spend more time near or interacting with their father than with their mother (Fossey, 1979, 1983; Harcourt, 1979). "Gorilla males often groom, cuddle, and nest with their 3- and 4-year old offspring" (Whitten, 1987, p. 346). The father also monitors play between infants and stops it before it becomes too rough (Fossey, 1979). Gorilla fathers appear through these early interactions to form a particularly close relationship with at least one male infant who will remain in the father's group (Harcourt and Stewart, 1981; Tilford and Nadler, 1978). Chimpanzee males are remarkably tolerant when infants attempt to interfere with mating and males may reassure uneasy infants with a touch. The tolerance of infancy appears to continue as

long as the infant retains the "tail tuft", long white hairs at the base of the spine (Goodall, 1986). Chimpanzee males in captivity do engage in play with infants showing there is a capability (Bingham, 1927; Taub and Redican, 1984). The difference between gorilla and chimpanzee fathers may be that paternity in chimpanzees is usually not known either by observers or apparently by the chimpanzees (Gagneux, Woodruff, and Boesch, 1997; Goodall, 1986), but in gorilla harems paternity is certain. Male orangutans rarely engage in interactions with infants.

Insert Figure 5 about here

Parenting Juvenile Chimpanzees and Apes

The juvenile period is distinguished by longer times spent further away from the parent(s), and sometimes accompanying changes in coat color. In chimpanzees the end of infancy is indicated by disappearance of the white tail tuft. Attention turns from mothers to peers in the juvenile period (e.g., Horvat and Kraemer, 1981). Maternal responsibilities in terms of providing milk and transportation diminish while responsibility for increasing offspring independence increase. It is when offspring reach this period of semi-independence that mothers facilitate learning of travel techniques (Goodall, 1986), of food processing (McGrew, 1977; including tool use: Boesch, 1991), and of

socialization. Puberty marks the end of the juvenile period.

Juvenile chimpanzees are weaned but remain in close association with their mothers. Mothers groom juvenile daughters and sons, but daughters more often groom family members compared with sons (Prevschoft, Chives, Brockelman, and Creel, 1984). Juvenile sons and daughters play, groom, and carry young infants who may or may not be siblings (Nishida, 1983). All juveniles exhibit submissive behaviors to adult males, for example presenting their hindquarters and pant grunting. Occasionally juveniles display and attack adolescent females, but this only occurs when the mother joins to support her son or daughter (Pusey, 1990).

Juvenile lesser apes (2-4 years of age) begin to receive aggressive behaviors from their parents: typically mothers harass daughters and fathers harass sons (Preuschoft, Chivers, Brockelman, and Creel, 1984). Fights ensue most often over access to food (Leighton, 1987). Juvenile lesser apes may join in singing the duet with their parents. The song tends to be sex-appropriate but imperfect (Leighton, 1987).

Parenting Adolescent Chimpanzees and Apes

The beginning of adolescence signaled in females with small sexual swellings, occurs around 9 years of age in wild chimpanzees (Nishida, 1988) and orangutans (Galdikas, 1979) and 5 1/2 years in the laboratory (Sarah Phythyon, personal communication, 1993). Menarche and full sexual swellings occur when a chimpanzee is 11 to 12 years

of age in the wild and 8 to 10 years in the laboratory. The adolescent period includes the time when offspring travel independently throughout days and nights, sometimes engaging in sexual activity and reproductive behavior, but the individual is neither fully adult socially nor physically. Adolescence lasts from the age of 9 to 14 years in wild female chimpanzees (Nishida, 1988), until 15 years in male chimpanzees (Nishida, 1988) and until 21 years in male orangutans (Galdikas, 1979). The adolescent period begins at puberty and ends at the time when effective reproduction occurs (Walters, 1987). Some physical changes that characterize the adult status include coat color (e.g., silver colored hair on the backs in the dominant male gorilla), secondary sexual characteristics (e.g., cheek flanges in male orangutans), and full growth (e.g., canines, testes, and general body size).

At adolescence, there are striking differences between chimpanzee daughters' and sons' behavior in whom they groom, and with whom they spend their time. Sons are more often in the company of adult males than daughters. Mothers provide support to their daughters in agonistic encounters whereas sons solicit and receive support from older brothers. The behavior of adolescent males is molded by adult males who touch to quiet adolescent males during boundary patrols (Pusey, 1990) and guide adolescent males in assuming complimentary and cooperative roles while hunting colobus monkeys (Boesch and Boesch, 1989; 2000). It is during mid-adolescence, when females exhibit adult-sized, sexual swellings that daughters leave their mother, join a new group, and are solicited and protected by adult males (Pusey, 1990).

During adolescence in lesser apes, fighting occurs over breeding access and

adolescents are eventually evicted from the family. Male adolescent gibbons appear to be inhibited from singing with their parents but females emit great calls simultaneously with their mother. Fathers and adolescent sons form a coalition in territorial defense against intruders. Fathers may facilitate the process of their sons establishing their own territory, either by joining the sons to usurp neighbors' territory or by expanding the home territory and then leaving the son in the new area (Leighton, 1987). Young adult male gibbons sing solo apparently to attract unmated females, but unmated females rarely sing alone (Leighton, 1987).

Parenting Newborn Old World Monkeys

Macaques (e.g., rhesus, cynomologus, pigtailed and bonneted) have a strong crawling and grasping reflex that may actually aid in the birth process (Rosenblum, 1971; Tinklepaugh and Hartman, 1932). Their "strong righting reflexes and negative geotropism...function to produce the proper orientation" (Rosenblum, 1971, p. 324). Mothers must provide a supportive base during the expelling of the newborn especially important when the mother is in an arboreal environment, or else, the infant may not initially get a grasp of the mother's hair (Rosenblum, 1971; Timmersman, 1992).

Little attention is paid to the newborn. The placenta is eaten during the initial birthing period. This period is followed by a period of intense grooming of the infant. Mothers may gaze at their newborn infants and infants may gaze at their mother's face

(Higley and Suomi, 1986). Newborn macaques, through reflexive behaviors, suckle without maternal aid. Nipple contact is maintained over 80 percent of the time during the first month of life (Higley and Suomi, 1986) in striking contrast to the 20 percent nipple contact of chimpanzees.

Paternal behaviors toward newborns varies by species but generally ranges in the indifferent category. Mothers with newborns may stay in close proximity to adult males in baboons (Papio anubis: Hrdy, 1976). One-week-old Barbary macaques are carried by adult males as well as by juvenile and subadult males (Deag and Crook, 1971), and there is a report of the dominant male holding an infant 4 times on the day it was born (Burton, 1972, cited in Hrdy, 1976).

Parenting Old World Monkey Infants

Most macaques remain in infancy for only 1 to 1 1/2 years. Baboon infants have black hair and pink skin in contrast to the light hair and black skin of adults and have a new sibling when 1 1/2 to 2 years of age, so are weaned at 1 to 1 1/2 years of age (Altmann, 1980; Strum, 1987). Macaque infants mature quickly and begin to crawl/walk in the first days after birth. Mothers monitor the infant and remain ready to retrieve and protect the infant. Some mothers of some species, however, encourage infant locomotion (in pigtailed, Bolwig, 1980; Hinde and Simpson, 1975; Ransom and Rowell, 1972: see Teaching section below). Macaque infants typically engage in independent excursions in the third and fourth weeks of life. The mother provides a "secure base" from which

the infant travels (Harlow and Harlow, 1965). "Mothers now become psychologically more than physically important for their infants" (Higley and Suomi, 1986, p. 160). However, during this time mothers are providing kinesthetic and vestibular stimulation through grooming and physical contact while traveling, and contingent responsive stimulation in their social interactions. Mothers respond to infant cries and seem to respond selectively or at least differentially in positive, negative, or neutral manner to all infant social communicative signals. It is this type of selective and contingent social responsiveness that mothers in particular provide to infants that peers do not. However, it is rare that macaque mothers engage in extended play with their infants (e.g., Suomi, 1979). Play in macaques is primarily a peer activity.

Parental behavior in Old World monkeys varies considerably among species. Mothers stay close to adult males in baboon species and male langurs may respond to infants in distress with protection and rescue (Hrdy, 1976). Young mangabeys spend most of their time with an adult male rather than their mothers. Intensive caretaking by males is found in one species of Old World Monkeys, the Barbary macaque. Adult males "groom, nuzzle, and mouth infants, lick and smell them, manipulate their genitalia, and teeth chatter at them" (Whitten, 1987; p. 345), engaging in interactions analogous to those of mothers (Taub, 1984-b). Males may temporarily foster an infant or permanently adopt an orphaned infant anubis baboon (DeVore, 1963), Japanese macaque (Itani, 1959) or hamadryas baboon (Kummer, 1967). In fact, Kummer reports that motherless infant hamadryas are invariably adopted by young adult males. But males in each of these species, and in langurs and vervets, also use infants as an

"agnostic buffer" which puts the infant at risk for injury or death. Males carry an infant to or near another male: the presence of the infant inhibits aggression and the males interact in a less tense environment. Cases of infanticide in langurs and rhesus by adult males typically involve non fathers, and appear to be cases whereby the adult male is maximizing his inclusive fitness (Trivers, 1974) whereas cases of infant care, play and other affiliative interactions are by dominant males who are likely fathers (Hrdy, 1976). Infants are used by adult males as agonistic buffers regardless of genetic relatedness (Whitten, 1987).

Maternal "style" is the term used to differentiate both species differences and individual differences in maternal behaviors toward older infants that reflect the balance between permissive and restrictive rearing (e.g., Hinde and Simpson, 1975). Maternal style in early infancy is reflected by how contact and proximity are regulated and how much contact the infant is allowed with others. In rhesus and pigtail macaques, and baboon species, none may touch the newborn infant for many weeks. In contrast, colobus and langur mothers may allow others to carry away their newborns (Bennett, 1988; Fimbel, 1992). Bonnet macaque mothers allow their infants to interact in a limited fashion with others in the social group but not immediately after birth. It is common, however, to allow older siblings limited access to infants. Mothers exhibit consistent rejection rates with each of their offspring and across the development of each offspring. Moreover, there is consistency in maternal style across generations. So it appears conclusive that maternal style is a characteristic of the mother and not the mother-infant bond, in rhesus (Berman, 1990) and vervet monkeys (Fairbanks, 1989).

Maternal "style" is also apparent at weaning. Frequency of rejection and punishment have been documented to be a stable maternal characteristic in rhesus monkeys (Berman, 1990). Rejection and punishment as a weaning style clearly differentiate species; rhesus have high rejection rates compared with bonnets for instance (Rosenblum, 1971). By the end of the first year of life, weaning is complete in old world monkeys. Baboon mothers hit, push, grab, and bite at infants. Individual differences between mothers occur, but by the time that infants are 5 months of age they have experienced maternal aggression at least once (Altmann, 1980). Weaning occurs between 4 and 6 months. Weaning begins somewhat later in Hanuman langurs and different responses noted from male and female offspring, but all mothers are harsh, punitive, or indifferent (Rajpurohit and Mahnot, 1991).

Baboon mothers encourage Independent locomotor behavior when infants are 7 months of age. The mother may descend from the sleeping trees without carrying the infant. Infants "protest" with whimpers. Sometimes mothers return halfway up the tree still requiring that the infant descend part of the way independently. Mothers always monitor the tree, even if they do not facilitate any of the travel, until the infant travels down. Typically, the infant immediately runs to the mother and nurses. By the end of one month of these "lessons", the 8- or 9-month-old infants descend from the sleeping tree independently.

Competing theories have suggested either that punishment/rejection facilitates, if not causes, independence (e.g., Hansen, 1966; Hinde and Spencer-Booth, 1967), or that high levels of punishment/rejection cause increased dependence and delays in the

attainment of independence (Kaufman and Rosenblum, 1969; Rosenblum and Harlow, 1963). In experiments on cross-fostered rhesus monkeys, Suomi (1987) evaluated the independent contributions of inherited reactivity, foster caregiver reactivity, and foster caregiver style on infant reactivity. Foster caregiving "style" is a better index of infants' behavioral reactivity than inherited temperament, or caregiver temperament, under stable environmental conditions. However, when presented with environmental challenges, such as a brief separation from the caregiver, infants' reactivity were best predicted by inherited reactivity. When initially returned to the foster mother, then the caregivers' reactivity best predicted the infants' behavior (Suomi, 1987).

Parenting Juvenile Old World Monkeys

In rhesus macaques, baboons, and Japanese macaques, the age of menarche is 5 1/2 years of age on the average but can be influenced by hierarchical dominance status (Pereira and Fairbanks, 1993). Male testes descend in baboons around 5 1/2 years of age (Altmann, Altmann, Hausfater, and McCuskey, 1977). Infants and juvenile baboons are given the preferential center location during group travel.

Mother macaques allow juvenile daughters to handle infant siblings and juvenile sons to play with infant siblings. Mothers also allow unrelated juvenile females access to infants. Sometimes mothers are intimidated by juveniles of high-ranking matriline and their infants are kidnapped (Hrdy, 1976; Maestriperi, 1993). In agonistic encounters the entire matriline will support their kin. Juveniles begin to acquire ranks

similar to their mothers and exercise dominance toward all females that are subordinate to their mother.

In *Hamadryas* baboons, adult males form "special relationships" with juvenile females. These begin as friendships but grow to be consortships. Juvenile males may have strong affiliative bonds with an adult male or with male peers, which develop into coalitions later in life (Kummer, 1967; Walters, 1987).

Parenting Adolescent Old World Monkeys

There is a great deal of variance in the age of adolescence in Old World Monkeys. In baboons full adult size is reached in females around 7 years of age and full secondary sexual characteristics are developed by 10 years in males (Altmann et al., 1977). In vervets, breeding is seen at 3 years, but females are not adult in size until 4 years and males not before 5 years (Fairbanks, 1990). Rhesus monkeys are in early adolescence between 2.5 and 4.5 years (Bernstein, Judge, and Ruehlmann, 1993) but may remain in adolescence for 4 years or more years (Bernstein et al., 1991).

In rhesus, the males leave the birth group during adolescence. Few specifics on parenting known to account for the large differences between male and female behavior. Female rhesus spend significantly more time grooming and males spend more time with male peers. The result of these differences in behavior is a loosening of the sons' bonds with mother and sisters and a strengthening of the daughters' bonds with mother and sisters. The role played by the mother during the process is

unspecified. "Male macaques and vervets frequently emigrate in the company of brothers or natal group peers" (Walters, 1987, p. 365). In hamadryas baboons, the alpha male acts aggressively toward subadult males eventually evicting them from the natal group (Caine, 1986). It is the daughters in red colobus groups, however, that migrate as adolescents (Caine, 1986).

Parenting Newborn New World Monkeys

New World monkeys are arboreal and forest dwelling. Care of infants is different for the species who are pair-bonded (e.g., Marmosets, tamarins, titi monkeys) and for the species who live in large social groups (e.g., squirrel monkeys, howler monkeys, and capuchins).

Squirrel monkey newborns, and capuchins can move independently from the ventral position used in nursing, to the dorsal position used in travel. Early field studies of newborn howlers documented that mothers regularly restrained and pulled the infants as they continually climbed up the mother's ventrum (Carpenter, 1964). Although newborn New World Monkeys can support their weight with their tails, it appears that newborns are uncoordinated with their tails (Carpenter, 1964; Fragaszy and Bard, 1997). From the day of birth, squirrel monkey infants respond visually and vocally to the communication of others. Adult females and juveniles are allowed to touch newborn squirrel monkeys but many mothers avoid adult males or prevent them from touching the newborns (Hopf, 1967). Adults vocalize "caregiver calls" to newborns, and

newborns vocalize responsively (Biben, 1994). These vocal exchanges occur when infants and adults are engaged in mutual gaze. It is noteworthy that these communicative exchanges are not between infant and mother but rather with other adult members of the group.

Marmosets, tamarins, and titi monkeys are monogamous species. Marmoset and tamarins typically give birth to twins (80 percent); triplets are as common as single births. The amount of maternal care relative to paternal care varies among the species as does the amount of care by non-parents, however, in all these species there are substantial amounts of infant care by individuals other than the mother (Goldizen, 1987). Systematic research indicates that helpers of specific age, gender, and experience levels participate with care of infants of different ages (e.g., Price, 1992). Mothers typically provide infant care exclusively in the neonatal period. Infants ride on the mother's back. In titi monkeys, the mother and father work as a team from birth. From the first week of life, however, the father carries the infant more than 70 percent of the time (Mason and Mendoza, 1998). For marmosets and tamarins, multiple births are the norm. Specialized behavior has developed to cope with twin births (fraternal twinning is typical: Tardif, Carson, and Gangaware, 1992), specifically "helpers" to carry the infants which includes fathers. Helpers become an important factor during infancy but after the newborn period. Behavior to newborns, however, appears to be similar to that in Old World Monkeys. Mothers are primarily responsible for carrying and totally responsible for feeding the newborns (e.g., Box, 1977; Rothe, Darms, Koenig, Radespiel, and Juenemann, 1993; Wamboldt, Gelhard, and Insel, 1988).

Infants can be actively rejected by mothers who have insufficient prior experience (e.g., Johnson, Petto, and Sehgal, 1991; Tardif, Richter, and Carson, 1984), and these mothers show some fear and avoidance of the newborn presumably due to the lack of prior experience (Pryce, Abbott, Hodges, and Martin, 1988). Although deaths of newborns occur due to lack of sustenance, most early deaths appear to be due to falls (i.e., skull fractures found in autopsies of newborn squirrel monkeys: Hopf, 1981). Tamarin, marmoset, squirrel monkey, and capuchin mothers actively reject an infant by rubbing the infant off their body. It appears for these species that maternal cradling of newborns does not occur. In fact, the New World monkey infant even at birth has sufficient strength and motor maturity to support their own weight and to maneuver to the nipple. However, the survival rate of infants born to first time tamarin mothers is quite low (i.e., 10 percent, Snowdon, 1996). This appears to be due to the first time tamarin mother doing most of the carrying of her twins: experienced mothers typically carry their infants only 50 percent of the time during their first week of life.

Parenting Infant New World monkeys

The infancy period in New World Monkeys is relatively short (approximately 5 months). Squirrel monkeys are weaned within the first 3 months of life (Biben, 1994) as are capuchins (Wamboldt et al., 1988). Marmoset and tamarins, however, appear to be weaned around 6 months of age. Both adult and adolescent squirrel monkey females carry and play with infants (Robinson and Janson, 1987). Mothers groom their infants

regularly. Cebus infants, 2-months-old or older, are occasionally left with the dominant male who either huddles with them or is tolerant of their play (Robinson and Janson, 1987). Food is shared with infants through an exchange of infant vocalization and tolerated taking.

Many view the commonalities in infant care patterns within the cooperatively breeding species of New World Monkeys but “variation and flexibility emerged as major themes” when considering parenting in cooperatively breeding species such as tamarins, marmosets, and tit monkeys (Snowdon, 1996, p. 682). In some monogamous species, mothers have primary responsibility for infant care at birth. The infant is able to crawl ventrally to nurse and otherwise rides on the mother's back. In some monogamous species, fathers have primary responsibility for the infant from shortly after birth. In titi and night monkeys, fathers carry the infant up to 90 percent of the time and the infant forms a strong attachment to the father (Wright, 1990). In these species, the mother only holds the infants for nursing. Mothers rarely groom their infants. Infants transfer to other carriers for the majority of their time. Initially, the infant's transfer is facilitated by the helper by adopting a different posture, “including extension of the arms toward the infant and direction of the infant's crawling motions” (Tardif et al., 1992, p. 156). Both male and female non-parents act as helpers with equal frequency in cotton-top tamarins, but which gender helps may be constrained by age. Females carry more than males as subadults, but as adults, males carry more than female non-parents. Very young infants are more often carried by adults compared with subadults, but subadults carry more than juveniles (Yamamoto, Box,

Albuquerque, and Arruda, 1996). There is evidence that in some species (red-bellied tamarins) younger, less experienced helpers are not allowed access to very young infants (Pryce et al., 1988). Weaning is accomplished by the 8th month of life, when mothers were observed to act aggressively to infants who attempted to nurse (Snowdon, 1996).

The squirrel monkey pattern of mutual gaze and responsive vocalizing which occurs between newborns and reproductively active females becomes a characteristic pattern between the squirrel monkey infant and mother when the infant begins to leave mother in independent forays in the third or fourth week of life (Biben, 1994). Infant position, riding on the mothers' back, influences the infant's ability to engage in eye contact with the mother. Constant physical contact in the early days of life also makes it unlikely that contact-resuming vocalizations will be directed at the mother. Perhaps these vocal exchanges or dialogues serve socialization purposes, acquainting infants with the sounds of group members (Biben, 1994).

A noticeable aspect of paternal care in tamarins, Cebus apella and Ateles is food sharing, which is tolerated taking by infants. Some males, in some species, are reported to initiate food taking with specific vocalizations (Brown and Mack, 1978) but primarily it is the infant who begs. Older siblings also participate in sharing food with infants. As is the case for chimpanzees the type of shared foods are those that the infants find difficult to process or difficult to obtain (Whitten, 1987).

Fathers will defend infants against intruders and rescue them, at some risk to their own welfare. Typically parental caretaking of this sort is given only to very young

infants, i.e., until infants can locomote independently (Whitten, 1987). Titi and night monkeys fathers, however, are reported to guard their infants for their first full year of life (Wright, 1990). Adult male howler monkeys may carry and play with infants for short periods of time (Vogt, 1984).

Parenting Juvenile New World Monkeys

In tamarins, marmosets, and squirrel monkeys, the juvenile period begins around 5 months and ends at puberty, around 14 months of age (Tardif et al., 1992). In some callitrichids, the presence of the mother inhibits their daughters sexual development (Walters, 1987). In cotton top tamarins, juveniles, 6 ½ to 15 months of age, react with stress to the birth of new infants. Parents and juveniles were seen to be more often in conflict. Initially, it was thought that this conflict was due to competition for parental resources (that is conflict between the juveniles and the infants). But, when the parents were not carrying the new infants there was no conflict, so it was clear that the conflict was due to competition for the infants. When juveniles were allowed to carry the infants, about 4-6 weeks after they were born, then all conflicts ceased.

Parenting Adolescent New World Monkeys

Adolescents play less than juveniles do and when the newest set of twins is born then adolescent behaviors becomes more adult-like (Caine, 1986). Adolescent sons and

daughters help with infant care by grooming and caring for younger siblings. For marmosets and tamarins, adolescence appears to end at approximately 3 years (Santos et al., 1997). Prior to achieving adult stature, however, both males and females leave the family. In New World monkeys, squirrel monkeys for example, primiparous females give birth around 3 years of age (Hopf, 1981), but males are not fully mature before 5 (Biben, 1992). Adolescent squirrel monkeys continue to play, but play takes on sexual elements (Caine, 1986). It appears that adult females actively reject adolescent males who are forced to the periphery of the group (Caine, 1986).

Parenting Newborn Prosimians

Some prosimian newborns cling and are carried ventrally (without support) by mothers.

In some species transport of infants is by mouth and infants are left unattended in nests or left "parked", meaning grasping on tree branches (Higley and Suomi, 1986; Klopfer and Boskoff, 1979). In these prosimian species, mothers may leave their infants unattended for up to 12 hours. Mothers may scent mark the infants for identification, an indicator that mothers do not visually identify their infants as individuals (Niemitz, 1979). Prosimians are the most quickly maturing of primate species and reach sexual maturity by 1 year of age.

Parenting Infant Prosimians

Infant prosimians ride dorsally on the mother. This is accomplished by 2 weeks of age in Lemur catta and by 4 weeks in Lemur fulvus. In Varecia variegata, however, infants engage in independent excursions away from the mother by 3 weeks of age (Klopfer and Boskoff, 1979). Mothers groom their infants frequently. In contrast to monkeys, but like chimpanzees, prosimian mothers may play for extended periods of time with their infants (Charles-Dominique, 1977; Niemitz, 1979). Prosimians, which are the most evolutionarily distant from humans, are weaned by 2, 3 or 4 months depending on the species (Jolly, 1985; Klopfer and Boskoff, 1979).

Prosimian fathers tend not to participate at all in infant care (Vogt, 1984). Male Lemur catta involvement tends to be limited to occasional grooming or sniffing of the infant, but if the mother is removed from the group the amount of time that the infant spends in contact with the male increases (Vogt, 1984).

Parenting Juvenile and Adolescent Prosimians

Very little is known about parental influence on older prosimian offspring. Dispersal by sons appears to be voluntary. Immature male bushbabies may leave by following an adult male when he travels through the mother's home range. Daughters remain close to their mothers; even as adults, daughters sleep close to mother at night (Charles-Dominique, 1977).

INTUITIVE PARENTING IN PRIMATES

The concept of intuitive parenting is considered in order to summarize the behaviors involved in parenting across primate species. Intuitive parenting consists of a psychobiological preadaptedness to stimulate infants' integrative development (Papousek and Papousek, 1987). The behaviors are neither reflexive nor based on rational thought but they appear to require prior experience with infants.

Chimpanzee mothers act responsively, contingently, and nurture development in their infants. Of special significance are the intuitive parenting behaviors utilized to support development in motor behaviors and in communicative behaviors (Bard, 1996, 1994-a; Rijt-Plooij and Plooij, 1987). Those behaviors that support motor development have been called 'exercising' (Yerkes and Tomilin, 1935) and occur for up to 20 percent of the time while the mother is engaged with her young infant (Bard, 1994-a). Similar observations have been made in a gorilla mother (Whiten, 1999). Orangutan mothers appear to 'scaffold' crossing gaps between trees by staying in the gap longer than usual. When the infant is very young, the mother waits for the infant to move from clinging to her body to crossing the gap and as the infant gets older, the mother waits for infant to cross on the branches that she holds (Bard, 1995-b).

The lesser apes, gibbons, and siamangs, also facilitate infants' motor development by providing scaffolding to travel between trees. Fathers, in particular, are frequently noted to help their older offspring become well socialized and to help sons establish new independent home territories (Leighton, 1987).

Among Old World Monkeys there are scattered reports of facilitation in motor development consisting basically of the encouragement of early walking. Some rhesus mothers and pigtail mothers engage in elaborate “games” (Hinde and Simpson, 1975), when the mother leaves a short distance, turns back to look at the infant and gives a retrieval signal (either a facial expression, vocalization expression, or whole body posture that indicates the infant should approach the mother). The mother may move away again before the infant fully approaches, as long as the infant does not show signs of distress in which case the mother immediately returns. There is strong evidence that such intuitive parenting serves to enhance the locomotor development of the infant (significantly but only by 4 days: Maestriperri, 1995). There are striking individual differences, even among old world monkey mothers, in sensitivity to infants' needs. When infants are sick, for example, mothers increase contact time and carry them more frequently (Nicolson, 1991). Comparisons of maternal parenting style across Old World Monkey species and across different environments illustrate the influence of foraging demands (in terms of predictability and availability of food; Rosenblum and Pully, 1984), of social rank (low ranking mothers tend to be more restrictive of infants than high ranking mothers and species with strict dominance hierarchies tend to be more restrictive than species with looser or little dominance; Nicolson, 1991), and maternal temperament (reactive versus laid back: Suomi, 1987). Evolutionary benefits are said to be the basis of intuitive parenting of locomotor skills in monkey, including early cessation of infant carrying, early weaning, and thus, increased the likelihood of a shorter interval to the next birth (Maestriperri, 1995).

New World Monkeys exhibit components of intuitive parenting consisting of vocal exchanges accompanied by eye gaze (Biben, 1994) and the sharing of food also accompanied by vocalizations and eye gaze (Starin, 1978). It is important to note that group members of family members are frequent exhibitors of intuitive parenting in New World Monkeys. Typically there is no indication that mothers facilitate their infants' motor development. In special circumstances, however, when infants are artificially handicapped (e.g., temporary taping of infants' arms) mothers compensate for the infants' inability to hold on (Rumbaugh, 1965).

Prosimian mothers (non-Lemur) spend relatively little time with their young infants as they are solitary foragers and leave their infants in a nest of tree branch except for feedings. Lemurs, however, are group living and adult females in addition to mothers provide care to infants.

TEACHING IN NONHUMAN PRIMATES

Teaching has re-emerged as a controversial topic and is considered here as distinct from intuitive parenting. As much of infant learning was once labeled 'imitation', much of parental behavior was once labeled 'teaching'. So, it is not surprising to find that there are major debates about the definition: What constitutes teaching in nonhuman primate parents? At one extreme are those who argue that 'teaching' should be reserved for those instances in which the instructor (usually the mother) 'intends' that the other learn, as is the case with some human instruction (e.g., Tomasello and Call,

1997). However, since much of the teaching even in human parents occurs without full conscious awareness (in teaching early socialization of eye gaze patterns, for instance), this definition seems unnecessarily limiting. Another view is that 'teaching' should be used to reflect those instances in which performance is enhanced by the purposeful (in the sense of being goal-directed) efforts of an instructor (Caro and Hauser, 1992). More specifically, teaching is evident whenever the instructor modifies their behavior in a manner that is sensitive and responsive to the performance of the learner. In this latter sense, 'scaffolding' (a term used to mean maternal support of infant development: Wood, Bruner and Ross, 1976) can be evidence of teaching. That is, 'teaching' occurs when the instructor helps to structure the environment, structure the activity, or otherwise acts to help the infant, in a way that allows them together to accomplish a task that the infant could not perform alone.

Boesch and Boesch-Acherman (2000) distinguish 3 different types of pedagogy with reference to the acquisition of nut-cracking skills: Stimulation, Facilitation, and Teaching. Stimulation appears to be an aspect of scaffolding that involves setting the environment conditions for the infant to practice the behavior on their own. Facilitation involves more active intervention by the mother, such as giving the offspring her own good quality tool, while she uses the poor quality tool that her offspring had tried unsuccessfully to use. The mother had to work harder to crack nuts with the poorer tool but the offspring was more successful. Since facilitation was often a teaching strategy used with older offspring, 4 to 5 year-olds and stimulation was the strategy most often used for younger 3 year-olds, there seems to be clear evidence that the mother adjusts

her strategy to the competence of her offspring. Boesch (1991) argues that active teaching of specific actions is seen when the offspring experience 'technical problems' and mothers adjust the pupils grip on the tool, or adjusts the position of a nut on the anvil in a slow, exaggerated, and deliberate way to emphasize the technical solution.

A similar sort of developmental analysis could be applying to orangutan mothers teaching their offspring to bridge the gap between two trees (Bard, 1993,1995-b). Two types of stimulation occur. Initially, the mother pauses in the middle of crossing a gap and waits for the infant to stop clinging and to walk across to the next tree. When the infant is walking independently, the mother crosses a gap ahead of the infant but waits in the middle so that the infant can cross on her body or on the branches that she holds. Orangutan mothers facilitate learning when they cross ahead but wait to release the tree branches until the offspring is in position to catch the tree on the backswing. Active teaching of this arboreal behavior was difficult to identify with certainty in orangutans (Bard, 1995-b).

THE ONTOGENY OF MATERNAL COMPETENCE

In chimpanzees, maternal competence includes providing supportive care (i.e., cradling, grooming), enjoying interactions (i.e., playing), being responsive (i.e., soothing, assessing, inspecting), and nurturing development (i.e., exercising: Bard, 1994-a; Rogers and Davenport, 1970; Yerkes, 1943). Chimpanzee mothers with marginal skills exhibit some of these behaviors, but there appears to be some mismatching of

emotional signals between infants and marginal mothers (Bard, 1994-a). The mismatch may include insensitivity to infant crying, treating newborns as if they were much older infants, and either a lack of enjoyment or a lack of gentleness. The overall impression given by chimpanzees with marginal maternal competence is that they are out of tune with their infants. Infant cues of discomfort tend to be disregarded by mothers with marginal skills. Caregiving is applied with the mother's personal agenda, rather than that of the infant.

A review of the literature on great apes makes clear that there is probably not a single factor responsible for all cases of inadequate parenting in primates. In addition, parenting behaviors which are important for the care of newborns are very different from those which are important for care of juveniles. The following section delineates prerequisite variables in understanding primate parenting and reviews remedial interventions. This section on ontogeny of maternal competence focuses on the learning mechanisms by which individual chimpanzees acquire behaviors that accompany maternal competence. Early experience, observational learning, and direct learning are discussed in turn.

Primate Parental Prerequisites

There is a great interest in providing remediation of some sort for cases of inadequate parenting in primates. Initially a lack of knowledge of natural conditions and later various constraints of captive conditions, resulted in adult primates with insufficient or

inadequate parenting behaviors. For example, initial efforts at captive breeding of tamarins and marmosets consisted of removing fathers and older siblings from the cage when mothers gave birth to twins. Without the presence of helpers, many infants died. Older siblings, denied opportunities to interact with infants, were subsequently less efficient in parental behaviors as adults.

Maternal competence in chimpanzees is not instinctual. Although hormones may influence some aspects of maternal behavior, hormones do not determine maternal competence (Coe, 1990; Maestripieri, 1998). Early experience (i.e., whether an individual was raised with her biological mother) is not sufficient in itself to promote maternal competence. Some individual chimpanzees raised with their mothers show maternal competence and some do not, therefore there must be additional factors involved. Observational learning (i.e., watching another individual provide adequate care for her offspring) may provide familiarization with infants, but again is not a sufficient condition in itself to promote maternal competence in chimpanzees. The crucial factor may be individual learning through direct "hands-on" interaction with an infant, a younger individual. A behavioral intervention was designed to maximize maternal competence, in which natural learning conditions were approximated, giving juvenile chimpanzees monitored and limited exposure to younger infants (Bard, 1996). This discussion is focused on the evolutionary and comparative foundations of maternal behavior and maternal competence.

Early Experience

This section presents support for the conclusion that early experience is not sufficient in itself to promote maternal competence in chimpanzees. Although early experience may influence a number of variables, such as maternal attitudes in humans (Fleming, 1990), familiarity with infants in rhesus monkeys (Dienske, van Vreeswijk, and Kongis, 1980), coping style in chimpanzees (Fritz and Fritz, 1985), security of attachment in chimpanzees and humans (Goodall, 1986), or other variables that relate to temperamental responsiveness (Fairbanks, 1996; Rijt-Plooij and Plooij, 1987), including cognitive style in problem-solving (Capitanio and Mason, 2000)--- early experience (i.e., being mother-reared) in itself does not result in maternal competence.

We have thought that adult competence in chimpanzees was practically assured as long as infants were raised with their mother. In fact, when mother-rearing includes social groups of mixed ages and genders with family membership approximating that found in the wild, then adult competence appears to be the rule (Goodall, 1968, 1986). "A female who has had a prolonged and positive relationship in infancy with her own mother, contact with peers, and an opportunity to handle or observe infants is very likely to become a good mother herself" (Nicolson, 1991, p. 41). When mother-rearing does not include the addition of social groups, such as in conditions with limited space or limited social relations (e.g., when mothers and infants may remain together for 1 or 2 years, or when the only other social companions are adults), then maternal competence is not a likely result (Fritz, 1989; Goosen, Schrama, Birnkhof, Schank, and van Hoek, 1988; Seal and Flesness, 1986). From this information alone, we can conclude that

maternal competencies in chimpanzees are not instinctual (Rogers and Davenport, 1970).

The most basic primate parental behavior necessary but not in itself sufficient for survival of the newborn is physical contact. Physical contact, either in the form of allowing the infant to cling (as in rhesus monkeys) or in the form of maternal active cradling (as in chimpanzees), is required for nursing, protection from predators, and thermoregulation. Harlow's (1958) studies demonstrated the preference of monkeys for surrogate mothers who provide "contact comfort" rather than those who provided food as a secure base. Additional information from rhesus monkeys illuminated the requirement that newborns be something familiar. This was necessary in order for isolation-reared mothers to acquire maternal behaviors. Experience with infants prior to becoming a mother is essential in order for female macaques to find neonates attractive (Sackett and Ruppenthal, 1974). Isolation-reared Japanese macaques are frightened of newborns. When the infant is born, they move away and threaten the neonate (Negayana, Negayana, and Kondo, 1986). Dienske, et al. (1980) demonstrated that one of the most important initial responses of rhesus monkeys to new infants is tolerating physical contact. If new mothers had never before seen a newborn infant, they forcibly removed the clinging infant, hence the origin of the term rejection. If provided with opportunities to observe adequate mothers, even from a distance and through plexiglass barriers, then new rhesus mothers were less likely physically to reject the newborn. Additionally, if infants spent at least two days with the mother then the mother's behavior was significantly improved for the second infant (Ruppenthal, Harlow,

Eisele, Harlow, and Suomi, 1962). Note that in Java macaques, however, only extensive peer contact is required for adequate maternal behavior (Kemps, Timmermans, and Vossen, 1989); however, differences were found in maternal behavior of rhesus monkeys as a function of early rearing (Champoux, Byrne, Delizio, and Suomi, 1992).

The picture is more complicated in chimpanzees even with respect to newborn behavior. Chimpanzee newborns cannot cling independently at birth. If chimpanzee mothers are frightened of their newborns, they simply do not pick them up. In fact, chimpanzee mothers must engage in active nurturing behaviors: New mothers must pick up the infant and then must provide cradling support for 2 to 3 months, a much longer period of time than is the case with monkey infants. Baboon mothers provide support to their newborns for the first day or two of life (Altmann, 1980; Strum, 1987), but rhesus infants can survive if the mother does not actively reject. In contrast, chimpanzee infants cannot survive if the mother does not actively accept them.

In order for any primate infant to survive past the first days of life, sustenance must be provided. This is another area in which mothers must have competent behavior. In almost all primate species (prosimians, New World Monkeys, Old World Monkeys, and great apes) infants have sufficient reflexive behavior to suckle provided that the mother does not actively interfere. Mothers can interfere with infants' attempts to suckle by preventing them from attaining proximity to the nipple and by actively disengaging them from the nipple. Although these behaviors are species-typical maternal patterns, they are used appropriately at the time that the infant is weaned (e.g., Nicolson, 1987) and

they are not adaptive when they occur at birth.

Tactile experience with an infant may also be required for learning the normal holding or carrying postures. This is true for rhesus (Dienske et al., 1980) and callitrichids (especially for male and sibling helpers: Tardif et al., 1992). In callitrichids, holding is less important than appropriate behaviors to facilitate the transfer of the infant from the mother's body to the helpers. Previous knowledge of both body postures and handling by the individual who will carry the infant aids the transfer process.

When extensive observations indicate that an adult female chimpanzee does not provide adequate care to her offspring, then that infant must be reared under alternative conditions to ensure the survival of the infant. At the Yerkes Research Center of Emory University in the 1970s, nursery-reared chimpanzees began to be raised in same-age peer groups as an alternative to either isolation-rearing or rearing with exclusive human contact. Initial social groups began as early as 30 days of age and were rarely delayed beyond 4 months of age. Nursery-reared chimpanzees were not isolation-reared, and each individual was given extensive contact both with conspecifics and human caregivers. Chimpanzees left the nursery when they were approximately 4 to 6 years old and most were placed in mixed-age and mixed-gender social groups on the Great Ape Wing. This policy provides chimpanzees with social experiences that lead in adulthood to most chimpanzees displaying relatively normal behavioral repertoires. Most chimpanzees raised under these conditions interact appropriately in social situations, including reproduction. Male and female nursery-reared chimpanzees exhibit appropriate mating behavior and the females become pregnant. Despite

concerted efforts of researchers and veterinarians, however, many chimpanzee mothers do not exhibit sufficient maternal behavior to raise their own offspring through the first year of life.

An analysis was conducted on the historical records at the Yerkes Center to assess whether there was a relation between an individual herself experiencing adequate maternal care and her subsequent maternal competence. The rearing history of each female at the Yerkes Main Center who has given birth to an infant from January 1, 1987 through January 1, 1992 was collated. The historical records of 30 female chimpanzees allowed them to be classified into one of two early experience categories: mother-reared (which included those females who were probably wild-born) and nursery-reared. The maternal competence of each female was then classified as either "poor" (i.e., their infants were nursery-reared) or "good" (i.e., mother-reared). Poor is defined as not cradling the infant; good is defined as cradling and providing sufficient care for the infant to remain with the mother. A third classification "marginal" was required for the mothers who picked up and cradled their infants and allowed them initially to nurse but did not provide sufficient care for the infant to remain with her for three months. Only one infant was counted for each mother so as not to bias the count: mothers whose infants are reared in the nursery gave birth to more infants than mothers who have good maternal competence. Some mothers gave birth to more than one infant during this period. Typically, each of the infants could be classified in the same category. For those mothers whose maternal competence status changed, the better rating was used for analysis.

The results revealed that there was no relation between the early experience (i.e., rearing history) of an individual and her subsequent maternal competence ($\chi^2=1.43$, ns). Fourteen mothers were themselves mother-reared and 16 mothers were nursery-reared. Fifteen infants stayed with their mother immediately after birth and 15 were placed in the nursery, but almost twice as many infants were in the nursery at 3 months of age than were with their mothers (18 versus 12). Mothers with "marginal" maternal competence account for this difference. They picked up their infants, carried them, and allowed them to nurse but did not provide adequate care longer than several weeks. There were no differences in the results of the statistical analysis if marginal mothers were counted as good or as poor mothers. For marginal mothers, it appeared that additional factors contributed to inadequate care of their offspring, such as low rank within the group, or a lack of adult grooming partners. If conditions could be optimized for these mothers, perhaps they could all provide adequate care.

Thus, the mother's rearing history, her early experience, does not predict the rearing status of her infant. There was an equal distribution of maternal competence in individuals who were nursery-reared and mother-reared although approximately half of the mothers exhibited some maternal behaviors. An individual will not necessarily exhibit maternal competence just because that individual was mother-reared. Therefore, one must look elsewhere for those variables that are sufficient for the expression of maternal competence. Among the candidate variables, discussed in the following sections, are observational learning of maternal behaviors and, most importantly, direct hands-on experience with a younger infant.

Observational Learning and Imitation

It is widely believed that chimpanzees can learn behavior patterns through the observation of others and, furthermore, can imitate the observed behaviors of others. The extent to which observational learning accounts for the development of new skills continues to be a highly debated issue (e.g., Bard and Russell, 1999; Custance and Bard, 1994; Russon and Galdikas, 1993; Tomasello, Davis-Dasilva, Camak, and Bard, 1987; Visalberghi and Fragaszy, 1990; Whiten and Ham, 1992). Experiments indicate that 4-year-old nursery-reared chimpanzees can imitate arbitrary actions (Custance, Whiten, and Bard, 1995), can imitate actions on a foraging task (Whiten, Custance, Gomez, Teixidor, and Bard, 1996) and 3-year-old chimpanzees' performance on a tool task was enhanced by the presence of a model (Bard, Fragaszy, and Visalberghi, 1995). Yet, there remains surprisingly little published evidence of imitative copying of actions on objects by any great ape (Tomasello and Call, 1997).

The historical records of chimpanzees and available social companions do not provide sufficiently clear information to evaluate the singular role of observation (i.e., in the absence of direct learning opportunities) in the development of maternal competence. Research with rhesus monkeys suggests that observation of competent mothers by juveniles facilitates maternal competence (Dienske et al., 1980). Familiarization with neonates is undoubtedly an important prerequisite for the expression of maternal competence and may be obtained through observation without

direct contact (Rogers and Davenport, 1970). The fact that some multiparous chimpanzees continue to exhibit "poor" maternal behavior and some chimpanzee mothers show a decrement in performance with subsequent infants (Struthers, Bloomsmith, and Alford, 1990) are strong arguments against the singular variable of familiarity through observation. The conclusion, therefore, is that observation of maternal competence by another individual is not a sufficient condition for the expression of maternal competence in chimpanzees.

Direct "Hands-on" Learning

Although observation may indeed facilitate the learning process, the thesis of this section is that the crucial variable in acquiring appropriate maternal skills is direct "hands-on" interaction with an infant. It is suggested that each individual must learn maternal behaviors individually through their own interactions with infants. One of the most fundamental skills that is lacking in chimpanzee mothers with poor maternal competence is picking up the baby. Although some new mothers are actively avoidant and fearful of the newborn, even the most interested of chimpanzee mothers cannot successfully rear her infant if she does not pick up and cradle the infant for the first months of life.

At the most fundamental level, a chimpanzee mother must pick up her newborn and support the infant against her until the infant is strong enough to accomplish this independently, usually 2 to 3 months of age (Miller and Nadler, 1981). In addition,

basic maternal competence includes allowing the infant to suckle. In the captive setting, these behaviors will insure infant survival, barring illness or injury. Responsive caregiving and contingent responding are additional characteristics of chimpanzee mothers with "good" maternal competence (Rogers and Davenport, 1970; Yerkes, 1943).

In wild chimpanzee groups, juvenile and adolescent females show keen interest in their younger siblings (Goodall, 1968, 1986). Unrelated subadult females, as well as older female siblings, acquire access to infants by enticement, invitation, or grooming the mother prior to taking the infant from her arms (Nishida, 1983). When the infant cries or screams, then the mother always retrieves it. Therefore, when the juvenile or adolescent wants to handle the infant for extended periods, she must learn to handle the infant in a manner that does not create infant distress. Such interactions with infants by juveniles, adolescent, or nulliparous females has been called allomothering (Nishida, 1983), play-mothering (Lancaster, 1971), and aunting (Rowell et al., 1964) and has been given privileged status as a strategy employed by mothers to reduce parental investment (e.g., Fairbanks, 1990; Hrdy, 1976; Trivers, 1974).

Long-term naturalistic observations of both monkeys and apes provide strong documentation that allomothering serves as direct "hands-on" practice of maternal behaviors. This is the learning-to-mother hypothesis of allomothering. Specifically, the learning-to-mother thesis is supported by fieldwork with chimpanzees (Nishida, 1983), by studies of both captive (Fairbanks, 1990) and free-ranging (Lancaster, 1971) vervet monkeys and patas monkeys (e.g., Chism, 1986), and by more theoretical

considerations. One study compared species characteristics and found those species with higher firstborn mortality are those with limited direct opportunities to handle young infants (Nicolson, 1991). Further research with human beings indicates that the infants of adolescent rather than adult mothers are at greater risk for neglect and abuse (Field, Widmayer, Stringer, and Ignatoff, 1980).

The learning to mother hypothesis does not explain all allocarer interactions with infants. For instance, female-female competition is suggested to be at the root of the harassment of macaque infants by others (Maestriperi, 1994). In bonnet macaques, there was no difference in infant handling between young and old females, and allocarers who handled infants more often did not have enhanced reproductive success compared with those who handled infants less (Silk, 1999). In wild capuchins, infant handling appears to be a mechanism by which allocarers assess their current relationship with mothers: if the mother is willing to allow the allocarer to handle the infant then the relationship between allocarer and the mother is good (Manson, 1999). It is important to assess separately the costs and benefits to each member of the infant-mother-allocarer triad: there are likely to be different functions served for each member and these are likely to vary across primates (Paul, 1999; Ross and MacLarnon, 2000).

Young female chimpanzees do appear to learn mothering behaviors through interactions with younger individuals. Evidence from the field indicates that, of all age/sex classes, subadult female chimpanzees engage in the most hugging and transport of young infants. Mothers differentially allow access of infants to their own daughters but even touching of infants less than 2 months old is rarely tolerated

(Nishida, 1983). Multi-generational observations of vervet monkeys demonstrate that juveniles who spend more time carrying infants have increased survivorship of first offspring compared with juveniles who spend less time engaged in allomothering (Fairbanks, 1990).

Direct learning by each individual is suggested to be a necessary variable for the expression of maternal competence in chimpanzees. Experimental support of this proposition is limited to interventions involving resocialization experiences (Nankivell, Fritz, Nash, and Fritz, 1988) and specific interventions designed to maximize the likelihood of direct interaction with younger individuals (e.g., Hannah and Brotman, 1990). These studies and a prospective longitudinal study (Bard, 1996) are discussed in the following section.

INTERVENTION STRATEGIES TO IMPROVE PARENTAL COMPETENCE

Often it is the case that remedial interventions by humans are required to facilitate species-typical behavior of individuals, such as a chimpanzee who has had insufficient social experiences (e.g., Fritz, 1986, 1989), or opportunities exist to design programs to provide remedial intervention (e.g., Keiter, Reichard, and Simmons, 1983; Mehren and Rapley, 1979). There are many examples of remedial training (e.g., Fritz, 1986) but the emphasis of this section is on preventive intervention, i.e. intervention provided before an individual reaches adulthood, and intervention strategies which relate to improving maternal competence. Interventions should be designed to provide many avenues for

the development of species-typical skills.

Resocialization

Remedial procedures have been successfully implemented to maximize the likelihood of maternal competence in adult females through resocialization with conspecifics of individuals prior to adulthood. One of the reports of successful intervention with a hand-reared chimpanzee involved 6 years of extensive resocialization involving contact with at least 6 infants; the result was a chimpanzee female with good maternal competence (Nankivell et al., 1988). Many other successful projects have provided remedial experiences to some or many adult chimpanzees, usually already pregnant or already with a newborn to maximize maternal skills.

It is time-intensive and potentially very dangerous for humans to provide experiences to maximize maternal skills to an adult chimpanzee (but see Fouts, Hirsch, and Fouts, 1982; Fritz, 1986). Often the success of the project depends on the adult female having a particular temperamental style (e.g., very responsive to human interactions). One extremely successful project (Hannah and Brotman, 1990) provided first-time pregnant chimpanzee females with opportunities to interact with infants. Although all females were pregnant, all were still quite young (i.e., most were less than 10 years old) and would be considered subadult (Goodall, 1986; Davis, Fouts, and Hannum, 1981). Nine out of ten females given exposure to infants successfully reared their infants whereas none of the eight females without exposure to infants was

successful. The results appear to support conclusively the importance of previous handling of infants for the expression of good maternal competence in chimpanzees.

There is much evidence that under "normal" circumstances (i.e., chimpanzees raised in family groups with older and younger siblings and offspring of other individuals), the learning of basic maternal skills, such as picking up, holding, and providing support to infants, occurs when individuals are juveniles or adolescents (Goodall, 1986 see above section, Nishida, 1983). In nature, the offspring may be 5 to 8 years old when this occurs. In the laboratory setting, where maturation is more rapid and females routinely give birth at 8 to 10 years of age, it seems appropriate to give exposure when individuals are 3 to 5 years old.

Foster Care

Two fostering projects at the Yerkes Center were conducted, one with a group of 1-year-old nursery-reared chimpanzees, the other with a group of 2-year-old nursery-reared chimpanzees. With a gradual introduction process the individuals of the groups, now young adults, successfully interact with adult males and with adult females, some of who have offspring of similar age as the nursery-reared individuals. It is not the case, however, that any adult female has "adopted" any nursery-reared subject. In the future, this project may provide prospective evidence of whether observational learning and exposure to adults is sufficient to promote maternal competence. It is possible that these nursery-reared infants will develop to be more socially competent adults than will

non-fostered nursery-reared chimpanzees because of exposure to older individuals. It is possible that the fostered individuals will not exhibit enhanced maternal competence because of a lack of exposure to individuals younger than themselves. An alternative possibility is that, because of the long-term nature of the fostering situation, the infants eventually will develop affiliative bonds with the adult females and with their subsequent infants. As the fostered infants grow, it is hoped that the affiliative bonds will grow, the fostered individuals will be allowed to allomother, and obtain direct hands-on experience with individuals younger than themselves.

Another fostering alternative is to give a nursery infant to a lactating female who is without an infant. Potential foster mothers at the Yerkes Center, however, are exceedingly rare. If a female is a good mother then she generally is caring for her own biological offspring. If she does not have good maternal competence, then she would not be a good candidate to be a foster mother for a newborn. Occasionally, opportunities arise and successful fostering is accomplished (e.g., Van Wulfften Pathe and Van Hooff, 1975). In the wild, juveniles have been adopted by adolescent and adult males, as well as females (Thierry and Anderson, 1986).

Intervention Designed to Enhance Maternal Competence in Chimpanzees

Behavioral and developmental research on both nursery-reared chimpanzees and mother-reared chimpanzees has been conducted at the Yerkes Center (for example, Bard, 1991, 1994-a, 1994-b, 1998-a, 1998-b, 2000; Bard and Gardner, 1996; Bard et

al., 1992; Hopkins and Bard, 1993, 2000; Lin, Bard, and Anderson, 1992; Russell, Bard and Adamson, 1997). Major goals of the National Chimpanzee Breeding and Research Program were to produce behaviorally normal chimpanzees and to produce a self-sustaining population of chimpanzees (Seal and Flesness, 1986). With the rapidly increasing population of laboratory chimpanzees, management policies that foster the expression of the full range of adult competencies, including social, reproductive, and especially, maternal competence, are vital. If self-sustaining populations of laboratory chimpanzees are desired, the urgency for employing corrective interventions remains great.

A direct "hands-on" protocol was designed for use in the Great Ape Nursery of the Yerkes Center. This behavioral intervention was designed to enhance maternal competence by providing a juvenile chimpanzee with hands-on experience with a younger infant. The first nursery-reared female that participated in this study was Katrina. Previous to this experience, the juvenile had only direct experience with peers (individuals of the same age as herself), visual exposure to younger infants, and experience with many adult human caregivers and researchers. Two adult human females were available to mediate and protect each individual. We introduced Katrina when she was 3-years-old, into a large outdoor area in which Duff, a one-year-old was already comfortable. Upon introduction, although very excited, the 3-year-old gently hugged the 1-year-old and lay on her back to gently pull the infant higher on her chest. Although this juvenile might have been one of those individuals who are nursery-reared but exhibit good maternal competence, we are confident that now with the direct hands-

on experience she will exhibit "good" maternal competence. As we continue this project in the years ahead and give every juvenile nursery-reared chimpanzee experience with younger infants, we maximize the likelihood that every adult female will prove competent with their own offspring (Bard, 1996). The potential explication of the proximate causes of behavioral inadequacies in maternal, reproductive, and social competence makes long-term research such as this extremely valuable.

HOW DOES PRIMATE PARENTING RELATE TO HUMAN PARENTING?

One explicit rationale for the study of parenting in primates is to learn more about the evolutionary basis of parenting in the human primate. Primate mother-infant studies have been especially useful in the development of Attachment Theory, for example, where the "parental caregiving system is seen as reciprocal to an infant's attachment system" (Hinde and Hinde, 1990, p. 62). This brief section presents primate models of human parenting and primate models of dysfunctions in parenting. The aim is to better understand both what "works" in primate parenting, things that might be adopted to improve human parenting (Goodall, 1967; Higley & Suomi, 1986; Hinde, 1969; Hinde & Stevenson-Hinde, 1990; Nicolson, 1991; Rheingold, 1963; Yogman, 1990), and models of primate parenting that might provide insight to resolving problematic issues in human parenting.

Primate models of human parenting

A biosocial model of motherhood, incorporating primate and nonprimate research incorporates many variables thought to be important in determining 'good' parenting, including genetically based temperament, attachment (quality of attachment in infancy through to working models of attachment in adulthood), environmental responsiveness (e.g., to stress), neurobiological responsiveness, and extent of social support (Pryce, 1995). The model has been criticized, however, because it is not useful for predicting maternal competence, does not differentiate maternal neglect from maternal abuse (Maestriperi, 1999), and is based on research with nonprimate species. Nonhuman primates serve as a better model: "the rich behavioral and emotional repertoires and cognitive capabilities of monkeys and apes provide opportunities for modeling aspects of human stress response patterns that are simply not feasible with rodents." (Suomi & Levine, 1998, p. 627).

There is a danger in drawing explicit comparisons between a particular primate species and a particular human society. Perhaps every facet of human parenting can be found to occur in some other primate species, yet clearly no one other primate species exhibits a complete repertoire of human parenting. It is perhaps more helpful to abstract principles from primate studies of parenting and to utilize these principles to better understand human parenting (Hinde, 1987). One principle might be the importance of physical contact in the developing mother-infant relationship (e.g., Harlow's work providing the evidence that contact comfort is an important primary need). Another principal is that attachment with the mother provides protection from

danger. The evolutionary basis of attachment can account for some of young children's fears, for example of being alone at night (Hinde, 1987). Another principle, derived from Hrdy's (1976) research in support of Trivers' (1974) theory, is that the optimal mothering style for the mother may not equate to the optimal mothering style for the infant. There are selective pressures that support infanticide, infant neglect, and non-maternal care given certain social, environmental, and individual conditions. There may not be a single optimal maternal style.

One of the principles of parenting that can be derived from the studies of abuse and separation is that early stress can have long-lasting consequences. Stress experienced early in life may induce changes in emotional reactions to stress, and these changed responses may last a lifetime (Suomi and Levine, 1998). Emotional behavior, mediated by the limbic system, results in emotional reactions that are easily transferred to other individuals and to the next generation (e.g., phobic reactions: Mineka et al., 1984). It is important to note that the magnitude of disturbance in adults is clearly related to the magnitude of the stress response in infancy. Therefore one could argue that it is not the experience itself, be it abuse or separation-induced stress, but the individual's experience of the event that significantly predicts the degree of effect later in life.

As we develop new primate models of human parenting, it will be important to integrate findings about the emotional components of parenting. There is substantial information about the role of the limbic system in emotional behavior but little work utilizing our sophistication in localizing brain activity (e.g., fMRI and PET) to better understand its role in maternal behavior (Coe, 1990; Suomi & Levine, 1998).

Krasnegor & Bridges (1990) advocate that we look more closely at how the brain changes in response to parenting behavior, how parenting once established is maintained, and how reproductive and parenting experiences might cause long-term changes in both the neurochemical and neuroanatomical substrates of parenting. Emotional attitudes toward infants could be considered a theme to explain some causes of abuse and some causes of neglect (for example, emotions are definitely involved in phobic reactions to newborns).

Evolution may have acted, in part, on the reinforcing aspect of bonding with infants. The opioid system is an under explored aspect of parenting. For example, sucrose appears to act via an opioid pathway to produce sustained calming in newborn human infants. By 4 weeks of age, however, sucrose must be paired with eye contact in order to continue to be effective in calming crying babies (Zeifman, Delaney, and Blass, 1996). There has been a great deal of research on the effects of stress and fear, but we have not spent equivalent energy in investigating the effects of positive emotions and attachments (Panksepp, 1986). Providing positive emotional responsiveness to infant chimpanzees, for as little as 4 hours per day, had dramatic effects on cooperation, social responsiveness, and on emotional expressiveness (increasing positive affect). In contrast, early stress had equally dramatic effects but on different systems --- early stress caused deficits in attention span, goal-directed efforts, and on emotional expressiveness (increasing fearful responses: Bard and Gardner, 1996). Beta-endorphins are important in primate social relationships and may be implicated in both the initiation and maintenance of maternal behavior (e.g., Keverne, 1992). Coe (1990,

p. 179) challenges us to “develop holistic psychobiological models” of parenting.

Modeling dysfunctional human parenting

Major disruptions in the environment can cause maternal dysfunction. Lack of species-typical social support, for example, impacts maternal competence. In rhesus, mothers with ‘good’ competence when raising infants within the social group, will abuse their infants when forced to raise them in small cages without social companions (Reite, 1996). Similarly, captive gorillas will show poor maternal care of newborns if alone, but will improve dramatically when at least the male is allowed to live with them (Nadler, 1980). Early separations from the mother can have both immediate and long-lasting effects. When infant rhesus monkeys are separated from their mother under experimental conditions, they can become hyperaggressive adults and not provide adequate care for their infants (e.g., Harlow, 1958). In pigtailed, separations lasting only 10 days in infancy can result in juveniles and adolescents being deficient in developing close friendships and social networks (Reite, 1996). In rhesus, early separations in infancy can compromise adult immunological responses (e.g., to SIV challenges, Capitanio and Lerche, 1991).

Maestripieri and Carroll (2000) argue that the naturally occurring variation in maternal competence in macaques and mangabeys can serve as a model of child abuse in humans, as long as clear distinctions are made between abuse and neglect. Abuse has clear consequences for the infant, ranging from distress to injury and death.

Even distress which may be the mildest consequence of maternal abuse, however, can have long lasting effects (Maestriperi & Carroll, 2000). Neglect is slightly harder to define than abuse but is evident when infants are abandoned. Risk factors for neglect of monkey infants include 1) maternal age, 2) lack of experience, 3) infant age, and 4) poor health. Poor maternal health or poor infant health can cause neglect of infants. Many argue that abandoning infants under conditions of poor health is an adaptive strategy (e.g., Fairbanks, 2000). Mothers are more likely to neglect their first offspring compared with subsequent births. Mothers with little or no prior infant handling experience are more likely to neglect their offspring. Finally, newborns are at highest risk for neglect.

The risk factors for abuse in monkeys, in contrast to neglect, do not include parity, infant age, infant sex, or prior experience: “the primary risk factor for infant abuse appears to be genetic relatedness to another abusive individual” (Maestriperi & Carroll, 2000, p. 249). In fact, abusive monkey mothers have a distinctive temperamental profile that includes high anxiety, high aggressiveness to other adults, high protectiveness to infant, and a high vulnerability to stress. Abusive monkey mothers, either rhesus, pigtail, or mangabeys, abuse most of their infants. The mechanism of cross-generation transmission of abuse is not yet clear. There is some evidence that abuse is likely to be caused by both direct experience and observational learning (Berman, 1990; Fairbanks, 1989). Evidence of a genetic basis for impulsiveness and anxiety has led both Fairbanks (2001) and Maestriperi & Carroll (2000) to suggest that some temperamental factors associated with maternal style may be inherited.

Maternal abuse has consequences for the infant. Abused infants cry more, both as a direct consequence of abuse and they cry more even when they are not being abused. Abuse increases the infant's tendency to cling to the mother, which may paradoxically cause more abuse. Abused infants are developmentally delayed in initiating play with peers, and they play less (Maestriperi, 1998; Reite, 1987).

What are the advantages of "good" parenting?

Reflections on maternal behavior across primates and across environments has caused serious reconsideration of 'Mother Nature' (e.g., Hrdy, 1995; 2000), and the 'Nurture Assumptions' (Fairbanks, 2000). There is not a maternal instinct for warm and caring attention to infants; that is, there is not an instinct to provide care to infants that is always responsive to their needs. Mothers tend to provide care in balance with meeting their own reproductive needs: 'good' mothers are ones that "adjust and withhold parental care according to rules that promote the mother's reproductive success, thus providing support for parental investment theory and contrary to the 'ideal mother' assumption" (Fairbanks, 2000, p. 23). However, when maternal conditions are poor, or when the infant's probability of survival is low, then it can be advantageous to the mother to weigh her own survival against that of her infant. Therefore to cease investing any further energy into a current offspring in order to increase the mother's chances of survival to raise more (or healthier) offspring later, is an expected outcome (Hrdy, 1995). For some species, a 'good' mother is one that allows others to provide

most of the care. For those species that typically produce twins, for example, it appears that a “cooperative breeding system is critical for offspring survivorship” (Wright, 1990, p. 96).

What are the consequences for the old world monkey infant of being raised by mothers with different “maternal styles”? In general, protectiveness is thought to protect infants from potential dangers, including harassment from others (Maestripieri, 1994). Infants and juveniles of more protective mothers are more cautious in response to novelty (Fairbanks, 1996). Although these infants do have less risk from predation, they appear to be less able to cope with stressors, such as the loss of the mother (Hinde, 1987). Maternal style can include differences in abuse or rough handling, typically reflected in ‘rejection rates’. Rejecting mothers have infants that show more enterprise (if they survive): the infants develop independence at an earlier age and are more resourceful (Fairbanks, 1996). Infants of rejecting mothers are more stressed, however, as they vocalize more and have more temper tantrums. Rejecting mothers, however, have adolescents that are rated as more bold (for males only $r=.55$: Fairbanks, 1996). For daughters, it appears that the mothers’ maternal style is the best predictor of her own maternal style with her offspring (Berman, 1990: Fairbanks, 1996).

Infant temperament and the maternal style experienced early in life interact in the attainment of dominance status, which is a measure of social success. High-reactive rhesus monkey infants reared with nurturant mothers attain high status in an adolescent peer group whereas high-reactive rhesus monkey infants reared with punitive mothers are lowest in dominance status (Scanlan, 1986). Schneider (1984) found that high-

reactive nursery-reared rhesus infants and low-reactive mother-reared infants score highest on cognitive assessments when tested as juveniles even though there were no overall group differences based on rearing or on reactivity. In chimpanzees of the Tai Forest, there appears to be differential maternal investment in sons and daughters, based in part on maternal dominance rank. Mothers of high rank have a longer period of time between the birth of a son and the next offspring – which does decrease the mortality of sons of high ranking mothers, whereas mother chimpanzees of low rank tend to invest more in their daughters (Boesch and Boesch-Achermann, 2000).

Moreover, through their continuing support, mother chimpanzees of high status aid their sons in achieving high dominance status as well (Boesch and Boesch-Achermann, 2000).

Parenting can vary with ecological variables. In macaques and vervets, there is some variation in maternal style that is dependant on the environmental conditions. When the infant is at great risk, either from social aggression, from the introduction of a new male, or because the mother is of low status, then mothers tend to be more protective. Mothers also increase their protectiveness if they have lost a previous infant. In general, however, the degree of protectiveness is inversely related to interbirth intervals, so that less protectiveness correlates with increased fertility. If the mother is in 'good' condition, that is there is lots of food and she is healthy, then she will increase the rejection of her infant. Increasing rejection causes the infant to wean earlier, the mother begins estrus earlier, and can have more offspring. In food rich conditions, the infants mature more quickly and achieve independence earlier. In food

rich conditions, rejection is not related to infant mortality. But when mother in poor or marginal condition, then increased rejection is related to increased infant mortality (Fairbanks, 1996). Changing the foraging demands on mothers even in the laboratory, has an effect on mother-infant relations (Andrews & Rosenblum, 1994). Moreover, those infants that experienced changes in maternal responsiveness as a function of changing environmental demands were more reactive to stress as adolescents (Rosenblum et al., 1994). The magnitude of the effect of environmental variables on maternal style or on infant outcome, however, is small in Old World monkeys (Fairbanks, 1996). The effect of changing environmental conditions is likely to vary by species.

CONCLUSIONS

There is no single 'primate pattern' of parenting. Diversity, variability, and flexibility are among the most important characteristics of primate parenting. There is obviously a strong genetic basis for maternal behavior, but an equally strong influence of experience. It would be a mistake to expect any single variable to have an exclusive determination for parenting: "Maternal behavior is obviously so important to the survival of a species that it has been 'overdetermined' – that is, driven by multiple behavioral and physiological systems " (Coe, 1990, p.178).

Maternal competence in primates can be simply defined as rearing an infant and incompetence defined as an infant requiring nursery rearing. Maternal competence in

chimpanzees, expressed in interaction even with very young infants, reflects sensitive responsivity during which the mother engages in contingent behavior and encourages development of infant capacities (Bard, 1994-a). These behaviors parallel those observed in intuitive parenting in humans (Papousek and Papousek, 1987). Necessary conditions for the emergence of adult competence in chimpanzees appear to be interaction with conspecifics of both same and different age classes. It appears that early experiences facilitate the development of cognitive, social, and reproductive competencies. These conditions, however, are not sufficient for the emergence of maternal competence in chimpanzees. Although early mother-rearing provides many benefits, it is not a sufficient condition for the expression of maternal competence. The most important early experience for chimpanzees appears to be giving care to a younger individual, that is direct hands-on exposure rather than receiving competent maternal care.

For chimpanzees, the role of early experience in maternal competence in adulthood is becoming more clear. For chimpanzees, being reared with your mother provides a myriad of benefits. No argument is being offered that the experiences of early infancy are not critically important for cognitive, motor, emotional, and communicative development in chimpanzees. However, these experiences do not provide all the necessary experiences to promote maternal competence. Longitudinal research and remedial intervention strategies provide strong support for the thesis that direct hands-on experience with infants is required in order for chimpanzees to demonstrate maternal competence in adulthood.

There may be differences among primate species in terms of the necessary and sufficient conditions to demonstrate maternal competence in adulthood. In many primate species, maternal competence is neither instinctual (Rogers and Davenport, 1972) nor hormonally determined (Coe, 1990). It is clear that in rhesus monkeys, even abusive motherless ones, repeated exposure to infants results in improvements in maternal behavior (Ruppenthal et al., 1976). In rhesus monkeys, observation of another female exhibiting maternal care even without direct exposure is sufficient to promote maternal behavior (Dienske et al., 1980). Allomothering for rhesus juveniles has the advantage of increasing the survival of firstborn infants but no effect for survival for subsequent offspring (Berman, 1990). Maternal competence in rhesus monkeys requires passive acceptance without active rejection. In chimpanzees, however, there are many examples of females who have given birth to more than ten infants and show no diminution of terror at the sight of their newborns. These are also examples of females who are very attentive to their newborns but do not have the sufficient skills to pick up and cradle their newborns. Maternal competence in chimpanzees requires active and positive behaviors.

There is not a single theoretical account, barring evolutionary theory, that can explain the diversity of parenting patterns in primates. Moreover, there is not a single theoretical account that explains or predicts the diversity of patterns of infant interactions with individuals other than the mother (Caine, 1993; Chism, 2000; Maestriperi, 1994; Manson, 1999; Paul, 1999; Ross & MacLarnon, 2000; Silk, 1999; Snowdon, 1996; Wright, 1990). It is likely that there will not be a single theoretical

account that explains the ontogeny of maternal competence in primates, since there is a similar pattern of diversity in maternal behavior across species. For some species, such as tamarins, mothers must learn to let others help in infant care. Rhesus mothers must learn to let infants cling. Chimpanzee mothers must learn to provide support for the infant, physically, emotionally, and communicatively.

The optimal or sensitive period of maximizing maternal competence appears to be the juvenile period rather than infancy. In fact, it appears in rats that parental behavior may be induced in juveniles merely by exposure to infants. The juvenile period "may represent a universally important time for the development of parental behavior" (Brunelli and Hofer, 1990, p. 373). The parenting behaviors that are frequently observed during the juvenile period often have a playful character, thus providing support for use of the term "play-mothering" and support for the idea that "play" has an extremely important developmental function (e.g., Bruner, 1972).

Parenting in primates is diverse. Some Prosimian mothers park their infants in nests, carry them in their mouth, and let them nurse and otherwise do not engage with their infants. In contrast, chimpanzee mothers provide cradling support and spend up to 15 minutes in an hour interacting socially, communicatively, or didactically with their infants. Some New World monkey fathers play an important role in parenting infants, as do gorilla fathers. Consideration of the influence of monogamy or living in a harem group illuminates the manner in which social organization contributes to the behavioral expression of parenting. Cognitive influences on parenting, especially evident in the Great Apes, typically provide for flexibility and richness in parenting behaviors, making

great ape parenting more similar to human parenting than that of other primates. The evolutionary risks, however, include greater dysfunction in parental behavior when learning environments are altered. The continuing influence of parents on older offspring, especially adolescents, requires more focused study. The manner in which independence is achieved is an important consideration. Evidence of the teaching of complex locomotor behaviors, tool use, hunting, and subtle food searching patterns suggest that primate parents continue to influence offspring throughout development. As we develop new primate models of parenting, it will be important to consider emotional components of parenting with an emphasis on the positive aspects of bonding and attachment, and on investigation of the mechanisms underlying the reinforcing qualities of parenting. There is much that remains to be learned.

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FIGURE CAPTIONS

Figure 1: Mother chimpanzees, such as Vivienne, provide cradling support to their newborns. Keith, at 20 days of age, is quiet and alert and able to focus on the photographer K. A. Bard who is 10 feet away.

Figure 2: Orangutan newborns, in contrast to chimpanzees, are capable of clinging without maternal support, at least for minutes at a time. Photograph by K. A. Bard.

Figure 3: Mother-newborn chimpanzees engage in mutual gaze, ten times an hour on the average. This picture illustrates the typical situation when the infant is 3 months of age. The mother tickles the infant while en face, but the infant keeps her eyes tightly closed. Photograph by J.A. Schneider.

Figure 4: Among the great apes, gorilla fathers are unique in the amount of time they spend interacting with infants. This silverback, with a big smile, allows the youngster to pull on his hair and bite his hand. Photograph by F. Kiernan.

Figure 5: Juvenile chimpanzees practice social skills. In this photograph, food is exchanged between juvenile and infant chimpanzees when appropriate communicative signals are used. Photograph by J.A. Schneider.

Table 1: PRIMATE TAXONOMY (with familiar species listed)

PROSIMIANS

Suborder: Strepsirhini**Superfamily:** Lemuroidea (Malagasy lemurs)Lemur catta, ring-tailed lemurs**Superfamily:** LorioideaLoris tardigradus, slender loris; Galago senegalensis, Lesser bushbaby**Suborder:** Haplorhini**Superfamily:** TarsiioideaTarsius bancanus; Borneo tarsier, Tarsius spectrum, Spectral tarsier

NEW WORLD MONKEYS

Superfamily: Ceboidea**Family:** Callitrichidae (tamarins and marmosets)Callithrix jacchus, common marmoset ; Saquinus oedipus, cottontop tamarin**Family:** Cebidae (Cebid monkeys)Cebus apella, tufted capuchin; Callicebus moloch; Titi monkey; Saimiri sciureus, squirrel monkey; Alouatta palliata mantled howler monkey; Ateles paniscus, Black spider monkey

OLD WORLD MONKEYS

Superfamily: Cercopithecoidea**Subfamily:** CercopithecinaeMacaca mulatta, Rhesus macaque; Cercocebus torquatus sooty mangabey; Papio hamadryas, Hamadryas baboon; Erythrocebus patas Patas monkey**Subfamily:** ColobinaePresbytius entellus, Hanuman langur; Nasalis larvatus, Proboscis monkey; Cercopithecus aethiops, Vervet monkey; Colobus badius, Red colobus monkey

APES AND HUMANS

Superfamily: Hominoidea

Hylobates lar, Gibbon; Pongo pygmaeus, Orangutan; Pan troglodytes, Chimpanzee; Pan paniscus, Bonobo or pygmy chimpanzee; Gorilla gorilla, Gorilla; Homo sapiens, Human

(abstracted from Jolly, 1985; Napier & Napier, 1967)

Table 2

	Group Structure	Breeding	Migration	Raising of Young
PROSIMIANS				
Ring-tailed lemur	Matrilineal Multi-Male			Mother
Slender loris	Solitary			Mother
Bushbaby	Matrilineal	Polygynous	Male	Twins: nested carried in mouth by mothers
Tarsier	Solitary	Pairs:polygynous		
NEW WORLD MONKEYS				
Marmoset	Monogamous family	Pairs	Male & Female	Twins: Mother & Father and older siblings
Tamarin	Monogamous family	Pairs	Male & Female	Mothers, Fathers, Siblings + Helpers
Tufted capuchin	Multi-female Multi-male	One-male	Male	Mothers (allomothers)
Squirrel monkey	Multi-male Multi-female	Polygynous	Male	Mothers (+ allomothers)
Howler monkey	Multi-male	Polygynous	Female	Mother
Spider monkey	Multi-male Multi-female	Polygynous		Mother
OLD WORLD MONKEY				
Barbary macaque	Multi-male	Polygynous		Mothers (fathers play etc.)
Rhesus macaque	Matrilineal		Male	Mothers
Hamadryas baboon	Harem	One-male	Female	Mothers
Hanuman langur	Matrilineal	Multi-male	Male	Mothers + allomothers

Vervet monkey	Multi-male		Male	Mothers + allomothers
Red colobus	Multi-female Patrilineal	Multi-males One Male	Female	Mothers
APES				
Gibbon/Siamang	Monogamous, Family	Pairs	Male & Female	Mother, Father
Orangutan	Solitary matrilineal	One-male	Male	Mother
Gorilla	Harem	One-male	Female	Mother - (Father plays)
Chimpanzee	Multi-male Multi-female	Polygamous	Female	Mother

Polygynous - one female + Many males

Polygamous - either sex multiple mates