

Mother–Infant Interactions in Western Lowland Gorillas (*Gorilla gorilla gorilla*): Spatial Relationships, Communication, and Opportunities for Social Learning

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This study investigated mother–infant interactions in lowland gorillas (*Gorilla gorilla gorilla*) with particular focus on the relative role of mothers and infants in creating situations that are potentially conducive to infant social learning. Eleven gorilla mother–infant dyads were focally observed in weekly 1-hr sessions for 12 months. Spatial relationships were affected by age as well as by ambient temperature. Although the youngest infant was encouraged by its mother to walk and climb, mothers showed little or no encouragement in other contexts. In contrast, infants were quite interested in their mothers' activities, on some occasions repeated their mother's behavior, and actively encouraged their mothers to share food, play, or follow them. These findings suggest that gorilla infants are more active than their mothers in creating situations that are potentially conducive to the acquisition of knowledge or skills.

Over the last 3 decades, the study of mother–infant relationships in primates has concentrated on understanding the proximate determinants and adaptive function of interindividual differences in maternal behavior, with particular emphasis on the regulation of contact and proximity between mother and infant (Fairbanks, 1996). Most of this research has been conducted with Old World monkeys, notably macaques, baboons, and vervet monkeys, because of the ease with which large populations of these primates can be studied for long periods of time. Recently, a growing interest in primate communication and cognition has stimulated attention to the exchange of signals and the transmission of information between mothers and infants through social learning processes (Evans & Tomasello, 1986; Maestriperieri, 1995a; Maestriperieri & Call, 1996; Rendall, Cheney, & Seyfarth, 2000; Tomasello & Call, 1997). One of the questions addressed by this research was

whether mothers take an active role in the social learning processes of their infants (e.g., through elementary forms of teaching) or whether infants acquire information from their mothers and other adults without any assistance (King, 1991, 1994; Maestriperieri, 1995c). Despite the interest in these questions, there have been only a few studies of mother–infant communication and cognition, some of which were conducted with very small sample sizes or reported observations of a qualitative nature.

Maternal encouragement of early infant locomotion has been observed in both Old World monkeys and the great apes (Maestriperieri, 1995b, 1996), but the observations of this phenomenon in the great apes are mostly qualitative (e.g., chimpanzees, Nicolson, 1977; van de Rijt-Plooij & Plooij, 1987; Yerkes & Tomilin, 1935; gorillas, Hess, 1973; Whiten, 1999). Some qualitative observations of maternal encouragement or discouragement of infant behavior have also been made in the context of food sharing and processing, tool use, or social communication, particularly in the great apes. Although passive food sharing between mother and infant is not uncommon in the great apes (McGrew & Feistner, 1992; Silk, 1979; Watts, 1985), observations of mothers that actively offered food to their infants or provided assistance in food processing are very rare (e.g., Boesch, 1991; Schaller, 1963). Observations of mothers taking nonfood items away from their infants, however, have been made in both gorillas (Fossey, 1979; Schaller, 1963; Watts, 1985) and chimpanzees (Goodall, 1973; Nishida, 1987). Clear cases in which mothers encouraged their infants to use tools or guided their infants' actions were only rarely observed by Boesch (1991) in the context of nut cracking. Some researchers have suggested that primate mothers occasionally encourage their infants to interact with particular group members (e.g., de Waal, 1990), but these observations can be interpreted in different ways.

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Finally, there are some hints that mothers, or other adult conspecifics, may take an active role in facilitating infants' learning of signals. For example, Caro and Hauser (1992) suggested that vervet monkey infants may learn the use of appropriate antipredator alarm calls, in part, through adult encouragement or punishment. In summary, these observations suggest that nonhuman primates, and notably the great apes, have the potential to display something similar to instruction but that instruction is rare and limited to specific contexts.

Obviously, maternal encouragement or discouragement is not strictly necessary for infants to learn new skills or new information about their physical and social environment. In fact, infants may acquire new skills and a great deal of knowledge through individual learning or social learning processes that do not require active instruction (e.g., social facilitation, emulation, or imitation). All primate infants are probably careful observers of adult behavior, and there is some evidence that they often take an active role in acquiring information from adults or in requesting adults' participation in their activities (King, 1994). For example, baboon infants often cofeed with adults and closely inspect what the adults are eating (Hall, 1963; King, 1994), chimpanzee and orangutan infants actively solicit food from their mothers with eye gaze and begging gestures (Bard, 1992; Hiraiwa-Hasegawa, 1990), and great ape infants occasionally attempt to use adults as an agent to achieve goals concerning objects or other conspecifics (Bard, 1992; Gomez, 1990; Plooi, 1979).

King (1994) has hypothesized that a significant shift occurred in primate evolution in the relative role played by adults and infants in the social learning processes of infants. In King's view, infant monkeys, and to some extent also infant great apes, acquire information from adults, particularly from their mothers, mostly with social learning processes that do not involve active instruction or teaching. In humans, however, much social learning among children is guided and directed by adults. Although it is quite obvious that active instruction is more prominent among human than nonhuman primates, the relative role of primate mothers and infants in the transfer of information across generations has not been investigated. Thus, it is not clear whether the evolutionary shift toward adult-guided learning processes took place after the pongid-hominid split, or whether a tendency toward this shift can be detected in the primates that are phylogenetically closest to us, that is, the great apes.

In the present study, we investigated mother-infant interactions in a relatively large number of lowland gorillas with two main goals. First, we intended to expand our knowledge of mother-infant relationships in this species, which is currently based on very few studies with small sample sizes (e.g., $N = 3$, Hoff, Nadler, & Maple, 1981a, 1981b, 1983; $N = 1$, Hess, 1973; Kingsley, 1977; Nadler, 1974; Whiten, 1999). Specifically, we assessed whether some of the social and demographic factors that are known to affect variation in mother-infant relationships in Old World monkeys (e.g., the mother's age, the mother's parity and dominance rank, or the infant's sex) also play a similar role in lowland gorillas. Second, we aimed to conduct a preliminary investigation of the relative role of mother and infant in their communicative exchanges and in the infant's acquisition of knowledge about the environment. Our specific goal was not to attempt to document the occurrence of maternal instruction or to assess the specific nature of the infant's learning processes (i.e., individual vs. various types of social learning), if any. Rather, our goal was to assess the relative role of mothers and infants in creating situations and opportunities that are potentially conducive to infant social learning, regardless of whether or not such learning actually occurs.

Method

Subjects and Housing

Study subjects were 11 lowland gorilla (*Gorilla gorilla gorilla*) mother-infant dyads. Six dyads were housed at Zoo Atlanta (ZA) in Atlanta, Georgia, and 5 dyads were housed at Lincoln Park Zoo (LPZ) in Chicago, Illinois. All of the infants were mother reared, although 2 infants at LPZ and 1 at ZA were raised by a surrogate mother. Table 1 presents information on some social and demographic characteristics of mothers and infants. Preliminary analyses showed that the surrogate-reared infants did not differ significantly from the mother-reared infants in any of the behavioral measures considered in this study. Dominance rank was assessed on the basis of ad libitum observations of aggression and avoidance conducted before and during the study period. Observations of aggression and avoidance done and received were entered into a matrix in which cells contained the number of interactions between every possible dyad of gorillas. The dominance hierarchy within the group was then obtained by ordering the gorillas so as to minimize inconsistencies in the directionality of aggression and avoidance.

Table 1
Characteristics of Subjects

Location	Infant	Infant's sex	Infant's age (months)	Mother's age (years)	Mother's parity	Mother's rank
LPZ	Rollie	F	38	34	P	High
LPZ	Mumbali	F	24	34	P	High
LPZ	Jelani	M	35	13	N	Low
LPZ	Madini	F	42	11	N	Low
LPZ	Bengati	M	18	10	N	High
ZA	Olympia	F	42	11	N	Low
ZA	Charlie	M	42	35	N	High
ZA	Sukari	F	19	37	P	High
ZA	Kidogo	M	20	24	P	High
ZA	Jasiri	M	18	37	P	Low
ZA	Lulu	F	2	15	P	Low

Note. LPZ = Lincoln Park Zoo; F = female; P = parous; M = male; N = nulliparous; ZA = Zoo Atlanta.

The ZA mother–infant dyads lived in two social groups housed in outdoor, naturalistic enclosures. One group was composed of 1 adult male silverback, 3 adult females, and 2 infants (for the purposes of this study, gorillas ranging in age from 0 to 5 years were considered infants). The other group was composed of 1 adult male silverback, 4 adult females, 2 subadults, and 4 infants. During the course of this study, the silverback of the latter group died, and the group remained with only the 4 adult females, the 2 subadults, and the 4 infants. The exhibits contained grass substrate as well as trees, bushes, and rock outcroppings. Gorillas were fed four meals a day: a morning and evening feeding of monkey chow and a morning and afternoon feeding of fruits and vegetables. The LPZ mother–infant dyads lived in a social group composed of 1 adult male silverback, 5 adult females, and 5 infants. The group was housed indoors in two adjacent rooms with a combined area of approximately 1,000 ft² (~305 m²). The rooms contained a variety of climbing structures, including ropes, nets, and “metal trees,” and ranged in height from 20 to 27 ft (6 to 8 m). Fresh hay was the primary substrate, and skylights provided fresh air and sunlight in favorable weather conditions. Gorillas were fed twice daily by scattering chow, fruit, and vegetables throughout the exhibit.

Procedure

Each mother–infant dyad was observed once a week for 60 min during 12 months, beginning in January 2000. After reliability tests showed at least a 90% agreement between the observers, data were collected by different observers in Atlanta and Chicago. Observations were made between 0900 and 1700, and the order in which the gorillas were observed was randomized. Data were collected with a check sheet and a tape recorder. The instantaneous sampling method with 60-s intervals was used to record whether the infant was on the mother’s nipple, in bodily contact with the mother, or within arm’s reach proximity to the mother without contact. The focal sampling technique was used to record the following behaviors:

Mother inspects: Mother visually or manually inspects the infant’s body without grooming.

Mother restrains: Mother prevents the infant from leaving using physical restraint (e.g., by pulling the infant by the arm or leg or by holding the infant firmly in her arms).

Mother rejects: Mother prevents the infant from making contact or suckling by holding the infant at a distance with her arm, by blocking her chest with her arm, or by avoiding the infant.

Mother–infant play: Mother initiates social play (e.g., tickling, wrestling, or chasing) with the infant. A new bout of play was scored after a 10-s pause in the behavior.

Mother–infant grooming: Mother grooms the infant. A new bout of grooming was scored after a 10-s pause in the behavior.

Mother–infant aggression: Mother attacks the infant (e.g., by threatening, hitting, or biting).

Mother–infant support: Mother threatens, attacks, or chases another gorilla to protect the infant.

Maternal Scaffolding of Infant Behavior and Infant-Initiated Interactions

Maternal attempts to encourage or discourage infant behavior in the context of locomotion, food sharing and processing, object manipulation, and communication and social interaction were recorded ad libitum during focal observation sessions (see Appendix for definitions). To investigate

whether infants actively engaged their mothers in communicative interactions and/or took an active role in creating potential opportunities for social learning, we recorded any attempts by the infant to encourage the mother to follow and move to another location and to obtain food. Finally, we recorded any events in which the infant observed and repeated some aspects of the mother’s behavior within 10 s after the occurrence of the mother’s behavior (see Appendix for definitions and examples). We referred to this aspect of the infant’s behavior as *repeating*, without any implications as to the type of social learning processes potentially involved (e.g., social facilitation, emulation, or imitation). Thus, repeating is a purely descriptive term that indicates temporal contiguity between behaviors performed by the mother and similar behaviors performed by the infant.

Data Analyses

Possible significant differences in infant sex, mother’s parity, and mother’s dominance rank between the LPZ and the ZA gorillas were analyzed with chi-square tests. Infant’s and mother’s ages were compared with Student’s *t* tests. Behavioral measures were also compared between the two locations with *t* tests for unpaired samples. Correlations were assessed with the Pearson product–moment correlation coefficient. Data on maternal scaffolding and infant-initiated interactions in relation to context and infant age were analyzed with factorial analyses of variance, *t* tests, and Pearson product–moment correlation coefficients.

Results

The 6 ZA mother–infant dyads did not differ significantly from the 5 LPZ dyads in terms of infant sex, $\chi^2(1, N = 11) = 0.11$; infant age, $t(9) = 0.93, ns$; mother’s age, $t(8) = -1.28, ns$; parity, $\chi^2(1, N = 10) = 1.67$; or dominance rank, $\chi^2(1, N = 10) = 0.11$. A female infant at ZA (Lulu) was much younger than all the other infants (see Table 1). The dyad with Lulu was a clear outlier in several measures of mother–infant interactions including time spent in contact and proximity or maternal restraining. The dyad with Lulu was therefore excluded from the data analyses assessing the sources of variability in mother–infant interactions.

The ZA mothers and infants spent a higher percentage of time in contact ($M = 26.16, SEM = 5.73$) than the LPZ dyads ($M = 3.32, SEM = 0.62$), $t(8) = -3.96, p < .05$ (see Figure 1A). This finding may have been due to differences in temperature between the ZA outdoor enclosure and the LPZ indoor enclosure. In fact, Figure 1A shows that the differences in percentage of time in contact between the two locations were minimal in the summer months and maximal in the winter months, in conjunction with high and low temperatures at ZA, respectively (the temporal changes in mother–infant contact were similar in the two ZA groups). Figure 1B shows that the 2-year-olds and 4-year-olds in the two locations spent similar amounts of time in contact with their mothers without appreciable developmental changes within the 12-month study period. There were no significant differences between ZA and LPZ dyads for measures of percentage of time spent on the nipple, percentage of time spent in proximity, maternal inspection of the newborn, maternal restraining, maternal rejection, maternal grooming, maternal support, or maternal play. Because of the significant difference between the ZA and the LPZ dyads in the percentage of time in contact, this measure was no longer considered in subsequent data analyses.

The percentage of time spent in proximity by mother and infant was negatively correlated with infant age, $r(8) = -.70, p < .05$

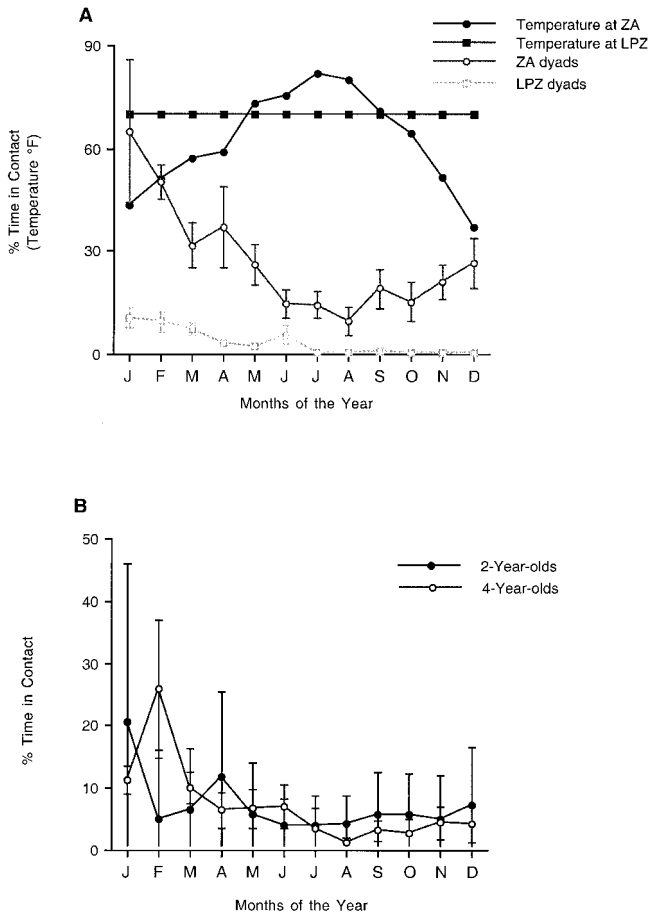


Figure 1. A: Mean (\pm SEM) percentage of time spent in contact with the mother by the 5 mother–infant dyads at Zoo Atlanta (ZA) and the 5 dyads at Lincoln Park Zoo (LPZ) during the 12-month study period (the ZA dyad with the youngest infant is excluded). Figure 1A also shows the average temperature (in degrees Fahrenheit) per month in the outdoor enclosure at ZA and in the indoor enclosure at LPZ. B: Mean (\pm SEM) percentage of time spent in contact with the mother by the five 2-year-olds and the five 4-year-olds during the 12-month study period, irrespective of location.

(see Figure 2A). The percentage of time spent in proximity was also significantly positively correlated with the mother's age, $r(8) = .59, p < .05$ (see Figure 2B). Thus, older mothers with younger infants spent more time in proximity than younger mothers with older infants. The infant's and the mother's ages were not significantly correlated. Although parous mothers were generally older than nulliparous mothers (parous, $M = 29.4, SEM = 4.34$; nulliparous, $M = 16.0, SEM = 4.77$), $t(8) = -2.08, p = .07$, there were no significant differences in percentage of time in proximity in relation to parity. Thus, the correlation between mother's age and proximity was unlikely to be mediated by parity.

The mother's dominance rank did not significantly affect any mother–infant interactions. Male infants were restrained by their mothers more than female infants were (males, $M = 0.11, SEM = 0.04$; females, $M = 0.006, SEM = 0.006$), $t(8) = 2.83, p < .05$. Maternal behaviors such as inspection, grooming, or support were relatively infrequent, and individual differences in these

behaviors were not correlated with any of the characteristics of mothers and infants considered in this study.

In summary, these results suggest that maintenance of contact between mother and infant is important in the 1st year of life, whereas spatial relationships between mothers and their 2- or 4-year-old offspring mostly take the form of proximity without contact. Time spent in proximity decreases steadily with infant's age, but the mother's age is also an important source of variation because older mothers spend more time in proximity with their infants than younger mothers. Infant sex accounted for only some variability in the frequency of maternal restraining, with male infants being restrained more by their mothers than female infants were.

Table 2 reports the observed occurrences of maternal encouragement and discouragement of infant behavior as well as some infant-initiated interactions recorded in this study. The dyad with the youngest infant, Lulu, was included in these analyses because the goal of these analyses was to document the occurrence of relatively rare behaviors, along with their context of occurrence, at any infant age and irrespective of individual differences in behavioral tendencies.

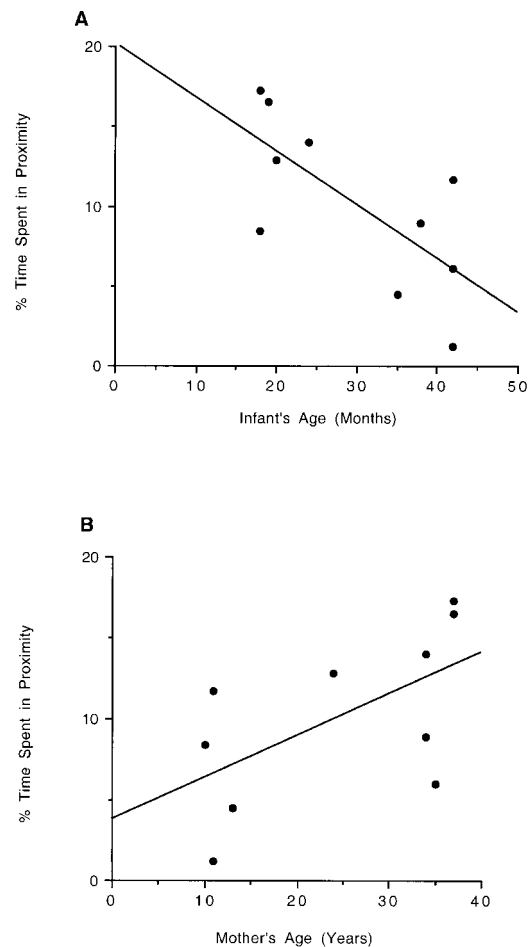


Figure 2. A: Scattergram of percentage of time spent in proximity and of the infant's age. B: Scattergram of percentage of time spent in proximity and of the mother's age.

Table 2
*Observed Cases of Maternal Encouragement/Discouragement
 and Other Infant-Initiated Interactions*

Behavior	Yearling	2-year-olds		4-year-olds	
		<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
Mother encourages					
Locomotion	3	0.8	0.5		
Food sharing		0.2	0.2		
Object manipulation					
Communication/social					
Mother discourages					
Locomotion	2				
Object manipulation	3			0.8	0.5
Communication/social	2	0.8	0.6	0.2	0.2
Infant solicits					
Following		0.4	3.4	3.4	2.9
Food	11	5.6	2.4	2.2	0.6
Mother tolerates					
Food sharing	9	4.8	1.8	0.6	0.1
No food sharing	2	1.0	0.3	0.2	0.2
Infant repeats					
Maternal feeding	1	0.6	0.4	0.8	0.4
Maternal object manipulation	1	0.9	0.5	0.2	0.2

Note. Empty cells indicate there were no occurrences for these behaviors.

Although Table 2 presents the scores for Lulu separately from those for the other infants, for the purposes of data analysis, the scores for Lulu and for those of the 2-year-olds were lumped together and compared with those of the 4-year-olds.

Clear cases of maternal encouragement of infant behavior were rarely observed. Mothers were never observed to hand objects to their infants or to encourage interaction with the objects. Mothers were never observed to encourage or discourage the use of facial expressions or other signals and were never observed to encourage social interactions between their infants and other gorillas. There was only one observed case of active food sharing, that is, a case in which a mother actively offered food to her 2-year-old infant. Overall, there was a significant main effect of infant age on maternal encouragement, $F(1, 27) = 5.95, p < .05$, and a main effect of context, $F(3, 27) = 3.25, p < .05$. Thus, younger infants were more encouraged than older infants, and encouragement was more frequent in the context of locomotion than in the other contexts. The mother of the youngest infant, Lulu, was observed to encourage her locomotion with gestures or body postures more than any other mother.

Maternal discouragement of infant locomotion, object manipulation, or social interactions with particular gorillas was rarely observed. Most cases were observed with Lulu, although differences between the 6 younger infants and the 5 older infants were not statistically significant. Differences in the number of discouragement episodes observed in the three contexts were not significant. This was true regardless of whether or not cases of discouragement of infant locomotion scored as maternal restraining were included in the analysis.

Infants actively solicited food sharing from their mothers or encouraged their mothers to follow them with eye gaze or tactile interactions (e.g., by pulling their mothers by their arm or hand). There were no main effects of age (younger vs. older infants) on

infant solicitations, and there was no significant difference between types of solicitation (food vs. following). However, there was a significant interaction between these variables, $F(1, 9) = 6.02, p < .05$, indicating that requests for food were more frequent among younger infants, whereas requests to follow were more common among older infants (see Table 2). Mothers were significantly more likely to allow than not to allow their infants to share food, $F(1, 9) = 9.67, p = .01$, and more likely to do so for younger than for older infants, $F(1, 9) = 6.84, p < .05$. Finally, infants were observed to repeat their mother's behavior in the context of both feeding and object manipulation. There were no significant differences between the frequency of the behavior in the two contexts, and no significant interaction between the context and the infant's age.

The parity of the mother or the sex of the infant did not significantly affect any of the above variables, although there was a tendency for male infants to repeat their mother's feeding behavior more frequently than female infants, $t(9) = 2.11, p = .06$. The mother's age was significantly correlated only with their intolerance for food sharing, $r(8) = -.55, p = .05$, with younger mothers being more intolerant than older mothers.

In summary, these results suggest that although mothers of very young infants may actively encourage their locomotor skills or discourage other behaviors, mothers of older infants do not actively encourage or discourage infants' behavior in the contexts of feeding, object manipulation, or social communication. In contrast, both younger and older infants are relatively active in requesting the mother's participation in their activities or in observing and repeating their mother's behavior.

Discussion

The amount of time spent in contact by lowland gorilla mothers and infants appears to be the product of both social and nonsocial factors. Clearly, infant age is an important determinant of time spent in contact; as the youngest infant, Lulu, in this study spent a much higher amount of time in contact with her mother than the older infants that ranged in age from 2 to 4 years. On average, 2- and 4-year-old infants spent less than 10% of the observation time in contact with their mothers, despite the fact that most of the 2-year-olds were still nutritionally dependent on their mothers. Among the 2- and 4-year-olds, there were few or no age-related fluctuations in time in contact across the 12 months of the study period, suggesting that within this age range, time in contact is unlikely to show significant developmental changes. This is consistent with data from Old World monkeys in which the most significant changes in time in contact occur in the 1st year of life (e.g., Hinde & Spencer-Booth, 1967). The only consistent temporal changes in time in contact were observed among the mother-infant dyads housed at ZA in relation to seasonal fluctuations in ambient temperature. Because these gorillas were housed outdoors, time spent in contact showed a clear inverse relation with temperature, being low in the warm summer months and high in the cold winter months. Furthermore, time in contact was significantly higher among the gorillas housed outdoors at ZA than among those housed indoors at LPZ, where the temperature was held constant throughout the year. Thus, although we cannot rule out that other variables could have contributed to differences between the two locations (e.g., the size and structure of the

enclosures, the type of substrate, the possible differences in activity patterns and provisioning, and the fact that one of the ZA groups lost its silverback male), the data strongly suggest that temperature may have affected mother–infant contact. Studies of macaques have failed to report a clear effect of ambient temperature on mother–infant contact time (e.g., Schino & Troisi, 1998), suggesting that the thermoregulatory function of body contact may be more significant among gorillas than among macaques.

With the exception of the youngest infant, Lulu, who spent a great deal of time in contact with her mother but little time in proximity, there was a negative correlation between infant age and time in proximity such that the 2-year-olds generally spent more time in proximity to their mothers than the 4-year-olds. This finding suggests that for infants in this age range, time spent in proximity is a more meaningful indicator of the mother–infant relationship than time spent in contact. In other words, even though infants in the 2–4 years age range spend most of their time out of contact with their mothers and playing with their peers, for the younger infants, the mother is still an important source of protection and support. Individual differences in time spent in proximity probably resulted from differences in both infant and maternal behavior. Although we did not assess the relative roles of mother and infant in maintaining proximity, time in proximity was significantly correlated with the mother's age, irrespective of parity, so that older mothers spent more time in proximity to their infants than younger mothers. The mother's age is also an important source of individual differences in parenting styles of Old World monkeys (e.g., Schino, D'Amato, & Troisi, 1995). However, whereas among Old World monkeys, older mothers tend to spend less time in contact and proximity with their infants, among the lowland gorillas of this study, the mother's age had an opposite effect on proximity.

The mother's dominance rank did not significantly affect any mother–infant interactions, whereas infant sex accounted for only some variability in the frequency of maternal restraining, with male infants being restrained more by their mothers than female infants. This is another potential difference between lowland gorillas and Old World monkeys, as some studies of Old World monkeys have reported that female infants are restrained by their mothers more than male infants (e.g., Itoigawa, 1973; Mitchell, 1968). Differences in maternal protectiveness with sons and daughters in gorillas and macaques could be potentially accounted for by differences in social systems and sex-typical life histories. Whereas macaque female infants may represent future competitors for adult females and their offspring within their group and therefore be targeted by the adult females (Silk, 1980), both male and female gorilla infants may be at risk of infanticide (Watts, 1989). Higher maternal protectiveness of male infants or juveniles may be associated with infant's higher tendency to play away from their mothers and interact with older gorillas (Fossey, 1979).

Although gorilla mothers may be an important source of protection and support for their offspring up to 4 years of age and beyond, mothers do not appear to take an active role in creating opportunities for their infants' social learning, at least under the particular circumstances of this study. Clear cases of maternal encouragement or discouragement of infant behavior were rarely observed. Most of these cases involved the dyad with the youngest infant and occurred in the context of locomotion, that is, walking or climbing (see also Hess, 1973; Whiten, 1999). Although

mother–infant food sharing was relatively common among all dyads, it was almost invariably initiated by the infants, and the mother's role was one of passive tolerance (see also Watts, 1985). Object manipulation was generally rare among adults or infants. Gorillas have been reported to engage in tool use less frequently than chimpanzees and orangutans both in captivity and in the wild (van Schaik, Deaner, & Merrill, 1999; but see Boysen, Kuhlmeier, Halliday, & Halliday, 1999), and to date, there have been no reports of tool use by wild gorillas in the context of food processing. In this study, mothers were never observed to encourage their infants to interact with objects present in their enclosure, and only in a few occasions were mothers observed to take nonedible objects out of their infants' hands. Mothers were never observed to encourage or discourage the use of facial expressions or other signals and were never observed to encourage social interactions between their infants and other gorillas. On a few occasions, however, mothers retrieved their infants from potentially dangerous situations such as a bout of rough play or close proximity to dominant gorillas, particularly the male silverback. Thus, the general picture emerging from these findings is that gorilla mothers with offspring in the 2–4 years age range are generally uninvolved in their infant's social and nonsocial activities unless their infants are at risk from other gorillas and maternal intervention is required. Refraining from intervening in the infant's activities (e.g., social play) may, in itself, foster individual learning and therefore be considered a form of scaffolding (West & Rheingold, 1978). However, at this stage of investigation of this process in primates, it may be more profitable to define scaffolding in positive rather than in negative terms (i.e., doing something vs. not doing something).

In contrast to the mothers' relative lack of involvement, infants often showed a keen interest in their mothers' activities. For example, infants intensely observed their mothers during feeding activities, inspected the food being eaten (including, on some occasions, food that had been regurgitated and was about to be reingested), and requested some of this food with begging gestures. On a few occasions, infants also repeated the actions that their mothers had just performed in the context of feeding or object manipulation. Finally, infants encouraged their mothers to follow, to move to a different location within their enclosure, or to play with them with a combination of eye gaze, hand gestures, and body postures. Infant requests for food were more common among younger infants, whereas requests to follow were more common among older infants. This suggests that older infants may view their mothers as important participants in their daily activities beyond their mothers' role as providers of food or support. Requests of food among older infants may become less frequent because of their mother's increasing intolerance of food sharing.

The use of eye gaze and gestures to request food or maternal participation in infant activities has been previously reported for all four species of great apes (Bard, 1992; Hiraiwa-Hasegawa, 1990; King, *in press*; Plooi, 1979), but it is rarely, if ever, observed among primates other than the great apes. In some cases, this type of infant behavior has been interpreted as an example of intentional communication, that is, the use of other apes as social agents (Bard, 1992; Gomez, 1990; Tomasello et al., 1997). Although it is difficult to make any inferences about the infant's cognitive processes from observations of their communicative behavior, it is reasonable to conclude that infants take an active

role in creating situations in which transfer of information can potentially occur. In contrast, with the possible exception of early interactions in the context of infant locomotion, mothers do not attempt to facilitate learning either by direct instruction (teaching) or by indirect instruction, that is, creating learning opportunities for their infants (scaffolding).

Great ape infants are dependent on their mothers for a much longer period of time than infants in other primate species. Moreover, great ape infants actively initiate interactions with their mothers such as food sharing and play that are very rare or nonexistent in other primate species. Finally, great ape infants, particularly chimpanzees, use facial expressions and hand gestures (e.g., food begging, play initiation, and pointing; Leavens & Hopkins, 1999; Maestriperieri & Call, 1996; Plooij, 1979) that are not observed in other species. Altogether, these characteristics suggest that great ape infants may be predisposed to create opportunities for their own social learning in the context of interaction with their mothers and other conspecifics.

It is likely that in the course of human evolution, qualitative changes in parent-offspring interactions occurred as a result of changes in both parenting behavior and offspring social and cognitive abilities. Although it is possible that active parental instruction did not emerge or did not become prominent in human evolution until after the pongid-hominid split, evolutionary changes in the infants' potential for social learning may have begun much earlier in human evolution, and some of the precursors to these changes could be observable in the extant species of great apes. Although controlled laboratory experiments are important to assess the cognitive abilities of the great apes and the specific mechanisms underlying social learning, naturalistic observations of mothers and infants across different stages of development can provide important information on the situations in which social learning is most likely to occur and the selective pressures that resulted in evolutionary changes in social and cognitive development among hominid primates.

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Appendix

Behavioral Definitions

Maternal Scaffolding of Infant Behavior

1. *Locomotion*: Encouragement included any attempts by the mother to stimulate the infant’s locomotor activity (crawling, walking, climbing, or following). Maternal behaviors included body postures, eye gaze, facial expressions, vocalizations, touch, or direct physical support. Discouragement included any attempts by the mother to discourage the infant from activities such as climbing a fence, tree, or large boulder. Maternal discouragement of infant attempts to break contact (e.g., by holding the infant’s body or limbs) was recorded in the category *mother restrains* (see *Procedure*). Thus, discouragement of infant locomotion was differentiated from restraining, because in the former case, the infant was already out of contact, whereas in the latter, the infant was in contact with its mother.

2. *Food sharing and processing*: Encouragement included any attempts by the mother to direct the infant’s attention to food with eye gaze, facial expressions, vocalizations, or tactile interactions and by offering food to the infant with one hand or mouth; helping the infant process food in various ways, for example, including offering food partly processed; demonstrating the actions involving food processing or shaping the infant’s hands in the correct position. Discouragement of food sharing included the mother’s aggression or avoidance in response to the infant’s attempts to obtain food from her. If the mother allowed the infant to obtain food from her hand or mouth, this interaction was recorded as passive food sharing.

3. *Object manipulation*: Encouragement included any attempts by the mother to encourage infant interactions with nonfood objects present in the cage or outdoor enclosure including sticks, rocks, or toys. Object manipulation also included handling materials that can be used for nest building such as twigs, hay, or grass. Encouragement could be indirect (e.g.,

attention getting, orientation) or direct (active maternal involvement in the activity). Discouragement included any attempts by the mother to discourage infant interactions with objects present in the cage or outdoor enclosure including sticks, rocks, or toys. Discouragement took the form of taking the object out of the infant’s hands or mouth and dropping it or throwing it away.

4. *Communication and social interaction*: Encouragement included any attempts by the mother to facilitate the performance of signals such as facial expressions, hand gestures, body postures, or vocalizations in the infant. It included, for example, displaying a signal to the infant, waiting for the infant to repeat it, then displaying the signal again to reinforce the infant’s performance. It also included reinforcement or punishment of the infant for displaying a signal (e.g., a food-begging gesture) in the correct or incorrect form or in an appropriate or inappropriate context. Encouragement of social interaction included any attempts by the mother to encourage interactions between the infant and the other gorillas, for example, by placing the infant in close proximity to another infant and encouraging play. Discouragement included events in which the mother interrupted a play bout between the infant and another gorilla and/or pulled the infant away from a dangerous gorilla.

Infant-Initiated Interactions

1. *Locomotion*: Any attempt by the infant to encourage the mother to follow and move to another location by pulling her hand or arm, touching her body then walking and checking whether the mother followed, or alternating gaze from the mother to another location while walking.

2. *Food sharing*: Any attempt by the infant to obtain food from its mother either directly (e.g., by taking food from her hand or mouth) or

indirectly (e.g., by using facial expressions, begging gestures, or touching). Direct attempts included taking the food from the mother's hand or mouth. Indirect attempts involved using facial expressions (pout face), vocalizations (coos and whimpers), or gestures (holding its hand under the mother's chin in a begging gesture) or by briefly touching the mother's mouth with the hand holding the food (see also Bard, 1992, and Tomasello et al., 1997, for definitions).

3. *Repeating*: Any instances in which the infant observed and repeated some aspects of the mother's behavior within 10 s after the occurrence of

the mother's behavior (e.g., picking up an object that the mother had just picked up and dropped, eating grass after observing the mother do the same, or displaying a facial expression or gesture following a similar signal by the mother).

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The Publications and Communications (P&C) Board has opened nominations for the editorships of *Contemporary Psychology: APA Review of Books*, *Developmental Psychology*, and *Psychological Review* for the years 2005–2010. Robert J. Sternberg, PhD, James L. Dannemiller, PhD, and Walter Mischel, PhD, respectively, are the incumbent editors.

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