

A Case Study of Primiparous Maternal and Infant Gorilla (*Gorilla gorilla gorilla*) Behavior

Jennie Y. Crosby

*Department of Biology
Northeastern Illinois University and
Lincoln Park Zoo
Chicago, Illinois*

Kristen E. Lukas

*Lincoln Park Zoo
Chicago, Illinois*

A primiparous mother and her infant were subjects of a longitudinal behavioral study at Lincoln Park Zoo in Chicago, Illinois. From November 1998 to November 1999, we collected a total of 100 hr of focal nonhuman animal instantaneous point sampling and all occurrence data on the mother and her infant. After 8 months, we introduced the 4-member focal group to an 8-member gorilla group, thus providing an opportunity to study the effect of the introduction on mother–infant behavior. Overall, time the pair spent physically apart was notably high with contact and proximate scores steadily decreasing over time. The infant was largely responsible for maintaining social proximity, rarely leaving the mother and frequently approaching her. In contrast, the mother left the infant frequently and approached the infant minimally. Maternal affiliative and nonaffiliative behaviors fluctuated throughout the study. Over time, both decreased. Despite a precarious maternal relationship, infant developmental trends were typical for captive gorillas. The results of this study suggest that allowing flexibility in judging maternal conduct can be of benefit to successful gorilla husbandry.

Among captive populations of western lowland gorillas (*Gorilla gorilla gorilla*), the mother–infant bond forms the basis of social breeding groups (Beck &

Power, 1988; Miller-Schroeder & Paterson, 1989). A close mother–infant relationship is beneficial not only to the development of the offspring but also to individual social groups and to the species as a whole. This relationship and the well being of mother and infant are believed to depend on several factors: (a) adequately complex social structure, with groups often composed of one or more dominant males, several females, and youngsters (Beck & Power, 1988; Meder 1990; Miller-Schroeder & Paterson, 1989; Nadler, 1974); (b) environmental complexity (Miller-Schroeder & Paterson, 1989); and (c) early social experience with conspecifics (Beck & Power, 1988).

During infancy, the relationships a gorilla forms with the mother and other group members are important components of appropriate social development (Enciso, Calcagno, & Gold, 1999; Hoff, Nadler, & Maple, 1981; Maple & Warren-Leubecker, 1983; McCann & Rothman, 1999; Miller-Schroeder & Paterson, 1989; Taylor, 1998). Thus, adequate social structure and mother–infant bonds enable properly functioning gorilla breeding groups. When examined in the context of captivity, the mother–infant bond is equally as important to the propagation of self-sustaining populations. Because of deficiencies in maternal behavior—often a result of insufficient captive environments—this maternal bond, in some cases, has proved a challenge to establish.

Human interventions associated with gorilla husbandry techniques sometimes are responsible for inadequately developed maternal behavior and subsequent problems with infant development (Miller-Schroeder & Paterson, 1989). Most wild-born, infant, captive founders were collected from the wild after mothers and entire troops were killed. These founders were traumatized as infants and thus did not benefit from prolonged exposure to appropriate social groups and mother–infant relationships. Infants who then were expected to develop into reproductive females in captivity faced a triad of difficulties: (a) captive environment that did not duplicate the social or environmental complexity found in nature; (b) lack of learned social and maternal skills; and (c) zoo managers who, as a rule, removed any infant born to be hand-reared, for fear of inadequate maternal care (Miller-Schroeder & Paterson, 1989).

Captive gorilla mothers often exhibit a variety of maternal behaviors—some considered appropriate, others inappropriate, and many confounding to caretakers. Typically, the bare minimum of appropriate maternal behavior has been judged to be (a) species-typical transport of the infant, (b) nursing within 72 hr of birth, and (c) close mother–infant proximity (Rosenthal, 1990). In contrast, leaving the infant alone for long periods of time, dragging the infant, rejecting nursing, and physically harming or allowing other group members to harm the infant represent a range of inappropriate behaviors—from neglect to abuse. In cases of extreme neglect or abuse, removal of infants from their mothers may be necessary to ensure an infant's survival. The decision to remove an infant from the mother is difficult and influenced by many factors that include the off-

spring's well-being, development, safety, and the mother's opportunity to gain maternal experience (Bloomsmith et al., 2003).

Because true norms for appropriate and inappropriate maternal behavior are lacking and—in a strict sense—may not exist, abuse and neglect can be, and often have been, prematurely assumed (Maple & Warren-Leubecker, 1983). The resulting high incidences of mother–infant separations further have exacerbated the dilemma of perceived maternal incompetence because the social and developmental benefits of mother rearing for both mother and infant are difficult to replicate with hand rearing (Beck & Power, 1988; Meder, 1989, 1990; Nadler, 1974; Ryan, Thompson, Roth, & Gold, 2002).

In an early review of 90 captive gorilla births, Nadler (1974) reported that more than 80% of live-born gorilla infants were separated from their mothers. Because each infant born was essential to perpetuating captive populations, fears of maternal abuse and neglect often compelled managers to pull infants from their mothers for hand rearing, particularly in primiparous females (Miller-Schroeder & Paterson, 1989; Nadler, 1974). High frequencies of hand rearing coincided with infant mortality rates reaching 66% between 1962 and 1979 (Kirchshofer, 1979).

In contrast, infant mortality in the wild during the 1960s and 1970s was reported to be only 27% in mountain gorillas (Fossey, 1979) and 23% in lowland gorillas (Schaller, 1963). These losses were attributed largely to human poaching and intergroup infanticide, although disease, stillbirths, and predation also contribute to infant mortality in the wild. The reported captive infant mortality rates, however, may have been due to gorilla infants not being reared by their mothers (Miller-Schroeder & Paterson, 1989) or may have been a result of whatever condition precipitated removal in the first place. When they do survive, hand-reared infants face challenges not encountered by mother-reared infants. Although many hand-reared infants develop into well-adapted and functioning adults, infants reared within a breeding group of conspecifics are from the outset exposed to, and developmentally benefit from, species-appropriate sexual behavior, maternal behavior, and association with adult peers (Meder, 1985, 1989, 1990).

The need for improved captive husbandry of gorillas became apparent in the early 1980s with reports of impending captive population crashes (Johnson, 1981; Kirchshofer, 1979). Captive gorilla populations had never thrived. By the late 1970s, many wild-born captive gorillas were entering states of reproductive senescence (Kirchshofer, 1979). Reproductive rates were low, and infant mortality rates were high. Thus, it was thought that a change in focus was needed in gorilla husbandry if the captive populations were to remain viable (Miller-Schroeder & Paterson, 1989). Reproductive and maternal behaviors were identified, and continue to be highlighted, as essential behaviors to understand thoroughly if captive populations are to grow and thrive (Beck, 1983; Beck & Power, 1988; Miller-Schroeder & Paterson, 1989).

During the last decade, research into the social lives of gorillas has led to improvements in captive gorilla husbandry. With the inception of the 1983 Gorilla Species Survival Plan®, the recommendation was made to encourage mother rearing of infant gorillas (Ryan et al., 2002). Ryan et al. reported that the rate of full and partial hand rearing varied considerably between 1970 and 1998 but decreased to less than 30% in 1998. Research continues to highlight the need for mothers and infants to stay together except in the most serious cases of maternal misconduct (Beck & Power, 1988; Hoff et al., 1981; Meder, 1990). Adequate social and environmental complexity has been identified as key to desirable maternal behaviors and infant development (Beck & Power, 1988; Miller-Schroeder & Paterson, 1989), but idiosyncrasies in maternal conduct remain understudied and a source of concern for caretakers.

What is clearer with each gorilla birth in captivity is that maternal deficiencies appear to be artifacts of captivity and to be related to individual differences in gorilla mothers. Husbandry decisions, therefore, must be based on more elastic criteria for maternal competence than have been used in the past (Beck & Power, 1988). Effective husbandry of gorilla requires carefully balancing species-typical norms of maternal behavior and individual differences in behavior.

LINCOLN PARK ZOO CASE STUDY

Zoo managers often question the parenting abilities of primiparous gorilla mothers (Beck, 1984; Nadler, 1974). In 1998, Lincoln Park Zoo in Chicago, Illinois, was faced with the challenge of a primiparous mother exhibiting questionable maternal skills. From the outset, the mother was seen regularly leaving the infant alone and allowing other group members to handle him roughly. When the infant was 12 days old, another adult female in the group injured the infant. Caretakers at Lincoln Park Zoo presumed maternal neglect enabled the injury because the infant was in the presence of the other adult female when the incident occurred (R. Elsner, personal communication, October 1998). Mother and infant were separated briefly to confirm the health status of the infant and to discuss how to deal with the apparently neglectful mother. One option considered was placing the mother and infant in a different, but less socially appropriate, group—one that lacked the vital presence of a silverback male. Should the mother continue to neglect the infant, the need to separate the two also was considered. Instead, caretakers decided to move the perpetrator of the injury to a different group, keep the mother–infant pair together in the original social group, and monitor the relationship closely. The mother continued to exhibit neglectful behaviors such as leaving the infant alone in a separate enclosure, allowing other members of the group to play roughly with him, and rejecting attempts at nursing and other forms of contact. To monitor the situation, the

mother–infant pair became the focus of a research project focusing on maternal behavior and infant development.

In October 1998, a longitudinal behavioral study was initiated with the goal of monitoring the mother–infant relationship over time, identifying milestones of infant development, and documenting the effects of social change on the pair when 4 adult females and 4 infants were introduced to the group when the study infant was 13 months old. The concern was whether casual observations of “infant neglect” by the mother would be backed up by quantitative data and, if so, would the infant suffer any behavioral repercussions.

This study assessed behavioral changes over time and the effects of an introduction on the mother–infant relationship, including (a) changes in mother–infant proximities over time; (b) maintenance of proximity between mother and infant; (c) maternal affiliative behavior (touching, nursing, carrying) and nonaffiliative behavior (dragging, ignoring, leaving alone); (d) infant social and solitary behaviors; and (e) mother–infant social play and social examination.

METHOD

Subjects

The focal group consisted of four Western lowland gorillas (*Gorilla gorilla gorilla*) residing at Lincoln Park Zoo: one captive-born, primiparous adult female and her 5-month-old male infant (see Figure 1); a silverback male; and one nulliparous adult female (see Table 1). The focal mother was mother-reared until she was 4 years of age. Eight months into the study, the group was introduced to an additional four infants and four adult females. Although data were collected on all members of the focal group and interactions between the focal infant and introduced members were noted, only data pertaining to the mother–infant relationship and infant solitary and social development are noted in this article.

The group was housed in a two-room, indoor enclosure. Room 1 was approximately 137 m² and approximately 6 m high. Room 2 measured 195 m² and approximately 9 m high. The gorillas also had access to a large, outside yard through an off-exhibit holding area that also contained space to occupy while their exhibits were being cleaned for 2 to 3 hr each morning. The enclosures were bedded heavily with straw, and food was routinely scattered and hidden in the straw to allow the gorillas to forage actively for food throughout the day (see Figure 2).

Data Collection

During the course of 12 months, approximately 50 hr of focal animal data were collected on each of the two focal subjects for a total of 100 hr. Data were col-



FIGURE 1 Data were collected on the mother–infant pair (8-year-old primiparous female and her 5-month-old male infant) over 1 year between 1998 and 1999. The pair is shown here in 2001 (Photo by S. Ross).

TABLE 1
LPZ Study Subjects and Social Group Members

<i>Subject</i>	<i>Birth History</i>	<i>Rearing History</i>	<i>Reproductive History</i>
Bahati*	9/20/90, captive (LPZ)	Mother reared	Primiparous female
Bengati*	6/1/98, captive (LPZ)	Mother reared	Infant male
Frank	Circa 1964, wild (Cameroon)	Mother/hand reared	Silverback, sire of 14 offspring
Tabibu	4/30/92, captive (LPZ)	Hand reared	Nulliparous female

Note. An asterisk (*) denotes mother–infant pair that was the focus of this study. LPZ = Lincoln Park Zoo.

lected at least four times per week across morning and afternoon sessions with a randomized focal animal order. Focal animal instantaneous point sampling (Altmann, 1974) with 15-min sampling periods at 1-min intervals was used. This method consisted of watching each focal animal individually for 15 min and using a stopwatch to record the exact behavior and physical state occurring at 1-min intervals. In addition to group proximities and location in the exhibit, the broad categories of social and solitary behaviors were noted at each interval.

Social proximity was categorized in the following ways: (a) contact (physically touching another animal), (b) proximate (within arm's reach of another animal),

(c) distant (out of reach of another animal but within the same enclosure), and (d) far (in a different enclosure). All-occurrence data were also collected on the following: (a) approaches; (b) leaves; (c) displacements (when one animal approached another animal, the other animal left and the first animal took the exact place of the approached animal); (d) avoidances (when one animal approached another animal and that animal moved away, maintaining a steady distance from the other); and (e) any interaction with the infant by group members (touch, drag, avoid, nurse, wean, carry). Baseline data were collected from November 1998 to June 1999, and postintroduction data were collected from June 1999 through October 1999. Data were recorded by hand on data sheets, then transferred to Microsoft Excel (Microsoft Office 2000) spreadsheets and summarized using Systat® (Wilkinson, 2002) and Microsoft Excel®.

Data Analysis

Mean monthly percentages of time engaged in each behavior for each subject were calculated for the instantaneous point-sampling data, and all-occurrence data were summarized as monthly rates (mean number per 15-min sample periods). Systat was used to perform all analyses. Linear regression analysis was applied to assess all behavioral changes over the 12 months of study. An analysis of variance (ANOVA) for repeated measures determined changes in behavior that may have been influenced

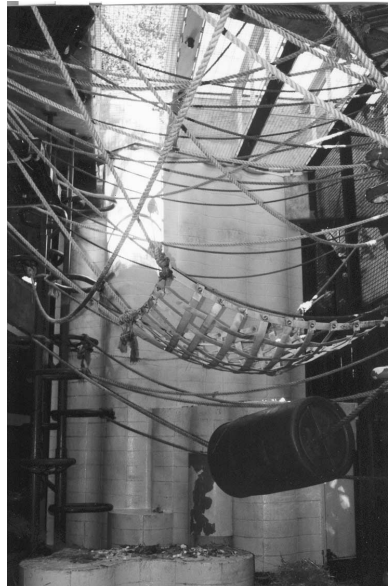


FIGURE 2 One room of the gorilla exhibit at Lincoln Park Zoo (Photo by K. Lukas).

by the introduction over the 3-months pre-, during, and postintroduction (Months 12, 13, and 14). Because the months included in the repeated measures ANOVA had disparate numbers of samples (Month 12 had 9, Month 13 had 17, and Month 14 had 16), 9 samples were chosen randomly from Months 13 and 14 to compare with Month 12 in the analysis. *T* tests were used for analysis of overall maternal affiliative and maternal nonaffiliative behaviors and differences in mother–infant maintenance of proximity (paired samples *t* test) as well as mother–infant approaching and leaving behavior (two-sample *t* test).

For all statistical tests, alpha was set at .05. Data that did not produce statistically significant *p* values, but that did offer graphic evidence of trends, are referred to as notable. Data are graphically reported as mean values by infant age in months.

RESULTS

Mother–Infant Social Proximity Over Time

During the course of the 12 months of study, mother and infant spent, on average, more time distant from one another than in any other spacing category (see Table 2). The distant category became the predominant spacing category between mother and infant beginning at infant age 11 months and rose steadily throughout the following months (see Figure 3). At 5 months of age, the infant was spending only 35% of time distant from the mother; by 14 months, the infant was distant 70% of the time. Time mother and infant spent in far and proximate spacing categories fluctuated throughout the 12 months but remained lower than distant throughout the study.

Mother–Infant Approaches and Leaves Over Time

Over time, there was a significant increase in both infant approach mother and infant leave mother (see Table 2). The infant also approached the mother significantly more often than the mother approached the infant, $t(22) = 4.565, p < .001$. The infant left the mother significantly less often than the mother left the infant, $t(22) = 4.839, p < .001$, and the infant approached the mother significantly more often than the infant left the mother, $t(11) = 8.579, p < .001$. The mother, however, approached the infant significantly less often than she left him, $t(11) = 3.489, p = .005$.

Infant Solitary and Social Behaviors Over Time

Over time, there was a significant increase in infant solitary play (see Table 2 and Figure 4) and feed foraging (see Table 2). The percentage of time the infant exhibited locomotion and inactivity significantly decreased over time, but there

TABLE 2
Results of Linear Regression Analyses on Behavior Changes Over Time

<i>Behavior</i>	<i>M</i>	<i>+/- SE</i>	<i>R</i> ²	<i>Coefficient</i>	<i>F</i>	<i>p</i>
Mother–infant proximity (mean percentage of time)						
Contact	16.00	2.15	.090	-.230	18.646	< .001
Proximate	12.14	1.16	.001	.017	0.222	<i>ns</i>
Distant	53.36	3.15	.071	.294	6.418	< .001
Far-distant	14.51	2.55	.005	.060	1.024	<i>ns</i>
Nonvisible	3.01	1.09	.006	.039	1.109	<i>ns</i>
Mother–infant approaches and leaves (mean no. per hour)						
Infant approach mother	8.48	2.17	.074	.178	15.052	< .001
Infant leave mother	2.20	0.81	.083	.073	16.971	< .001
Mother approach infant	3.62	1.14	.007	.002	1.309	<i>ns</i>
Mother leave infant	6.29	1.71	.007	.042	1.368	<i>ns</i>
Mother–infant social behavior (mean percentage of time)						
Social play	0.401	0.13	.048	.004	0.437	<i>ns</i>
Social examination	0.453	0.13	-.154	.012	4.577	.034
Maternal affiliative and nonaffiliative behavior (mean no. per hour)						
Maternal affiliative	2.72	0.99	.041	-.058	8.057	.005
Maternal nonaffiliative	1.97	0.84	.003	-.014	0.589	<i>ns</i>
Infant behavior (mean percentage of time)						
Locomote	15.29	3.68	.037	-.123	7.265	.008
Feed/forage	19.50	5.01	.068	.238	13.837	< .001
Self-directed behavior	0.31	0.10	.000	.000	0.002	<i>ns</i>
Object examination	8.57	2.61	.001	-.015	0.186	<i>ns</i>
Solitary play	3.63	1.43	.117	.101	24.149	< .001
Inactive	28.46	7.36	.077	-.362	15.732	< .001
Social play with natal group	3.32	1.73	.077	.040	1.262	<i>ns</i>
Social behavior	12.06	3.80	.153	.312	34.030	< .001

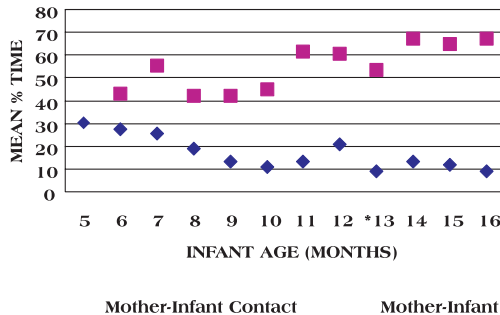


FIGURE 3 Mother–infant proximity: Mean percentage of time spent in contact and distant proximity categories as a function of infant age. Contact between mother and infant significantly increased over time, and distance between mother and infant significantly decreased over time (see Table 2). The asterisk denotes month of introduction.

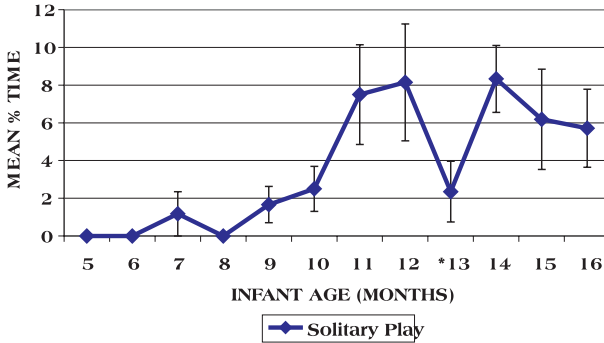


FIGURE 4 Infant solitary play over time. Points represent the mean monthly percentage of time the infant spent playing by himself without interacting with inanimate objects. Over time, solitary play significantly increased (see Table 2). A notable drop in solitary play in Month 13 and then rise back to preintroduction levels in Month 14 was also observed. The asterisk denotes month of introduction.

were no significant changes in self-directed behavior or object examination over time (see Table 2). The infant's total social behavior increased significantly over time (see Table 2 and Figure 5).

Mother–Infant Social Behavior Over Time

Of all potential social behaviors between mother and infant, the two observed most frequently were social play and social examination. Over time, a significant decrease in social examination between mother and infant occurred, particularly after the infant reached 9 months of age (see Table 2 and Figure 6).

Maternal Affiliative and Maternal Nonaffiliative Behavior Over Time

No significant difference in the rate the mother exhibited maternal affiliative (nurse, touch, carry) and maternal nonaffiliative (drag, leave alone, ignore) behaviors were found. There was, however, a significant decrease in maternal affiliative behavior during the 12 months of the study (see Table 2). Maternal nonaffiliative behavior did not significantly decrease over time but did trend upward for Months 5 through 7 and then sharply downward during Months 7 through 16 (see Figure 7). Both behaviors fluctuated throughout the study.

Behavioral Change as a Result of Introduction

A multivariate analysis of variance (MANOVA) for repeated measures revealed a significant change in overall proximity between Months 12, 13, and 14, $F(11, 88) = 12.330, p < .001$. However, a subsequent repeated measures analysis of variance found no significant changes in time spent in contact, proximate, distant, or far categories across the 3 months encompassing the pre-, during, and postintroduction time period (Months 12, 13, and 14, respectively). There was, however, a notable drop in mother–infant contact in Month 13 (see Figure 3). No significant differences in rates of maintaining proximity (approaches and leaves) were found between mother and infant in the months prior to, during, or

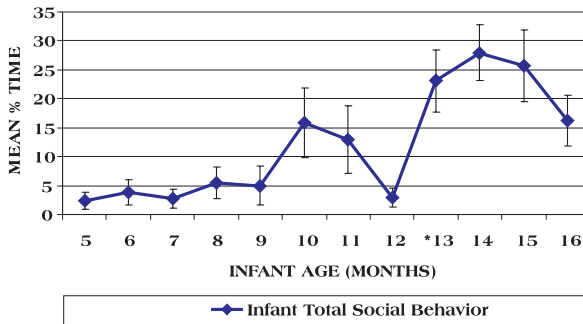


FIGURE 5 Mean monthly percentage of time the infant spent engaging in all social behaviors. Over time there was a significant increase in total social behaviors. Comparison of Months 12, 13 and 14 (months pre-, during, and postintroduction), revealed an overall significant change in social behavior. Social behavior was significantly greater in Months 13 and 14 than in Month 12. The asterisk denotes month of introduction.

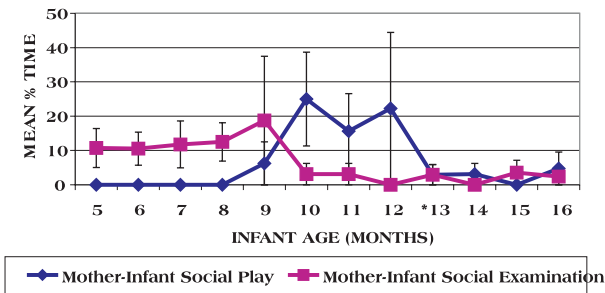


FIGURE 6 Mean monthly percentage of time mother and infant engaged in social play and social examination. Over time, a significant decrease in social examination occurred (see Table 2). The asterisk denotes month of introduction.

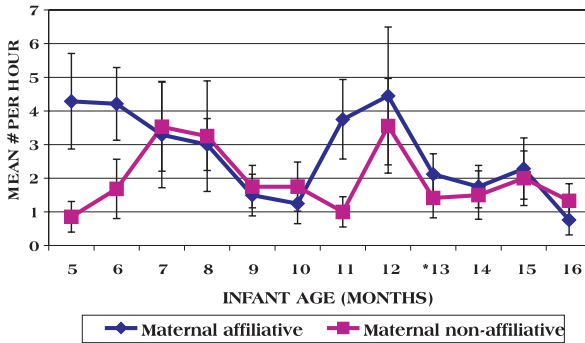


FIGURE 7 Maternal affiliative (touch, nurse, carry) and nonaffiliative (drag, leave alone, ignore) behaviors over time. Points represent the mean monthly occurrences per hour as a function of infant age. Over time, a significant decrease in maternal affiliative behavior occurred (see Table 2). The asterisk denotes month of introduction.

following the introduction. However, there was a notable drop in mother leaving infant in Month 13 and a notable increase in infant approaching mother in Month 13.

No statistically significant changes in infant solitary behavior were found between the months prior to, during, and immediately following the introduction. However, a notable decrease in solitary play did occur during the month of introduction (from 8% to 2.5% of time) followed by an immediate return to the baseline level (8%) in the subsequent month (see Figure 4).

Comparison of Months 12, 13, and 14 (pre-, during, and postintroduction) showed an overall significant change in infant social behavior, $F(2, 16) = 5.143$, $p = .019$ (see Figure 5). Compared with preintroduction Month 12, social behavior was significantly greater in Months 13, $F(1, 8) = 7.043$, $p = .029$, and 14, $F(1, 8) = 18.626$, $p = .003$, than in 12. Overall, social behavior between the mother and infant decreased during the month of the introduction and stayed low throughout the remainder of the study (see Figures 6 and 7).

DISCUSSION

Although they observed precarious maternal behavior, Lincoln Park Zoo management staff chose to keep a mother and her first infant together in a social group rather than remove the infant for hand rearing. One year's worth of data and anecdotal observations suggest that keeping the mother and infant together did not affect the infant detrimentally and may have afforded both mother and infant developmental and social benefits. A lack of abundant information on go-

rilla infant development and maternal behavior makes direct comparisons with other studies difficult, but the results of this study add to a growing body of knowledge about the importance of allowing for flexibility in judging maternal competence. Longitudinal observations on social proximity, infant social and solitary behaviors, and maternal interactions with the infant indicate that the infant exhibited appropriate developmental trends and that the mother was adequately responsive.

Gorilla infant development is characterized by a gradual decrease in the intensity of the overall mother–infant relationship (Hoff et al., 1981; Hoff, Nadler, & Maple, 1983; Shepherd, 1993; Taylor, 1998). A decrease in mother–infant contact is one of the most prevalent indexes of infant development (Fossey, 1979; Hoff et al., 1981, 1983; Shaller, 1963; Taylor, 1998). The mother–infant pair in this study exhibited a decrease in physical closeness over time that agrees with other reports of infant development (Hoff et al., 1981; Maestripieri, Ross, & Megna, 2002; Shepherd, 1993; Taylor, 1998). As in Hoff et al. (1981), mother and infant spent the most overall time distant from one another, 1 to 5 m apart in Hoff et al. (1981) and 1 to 10 m apart in this study; over time, distant increased while mother–infant physical contact decreased. Distant became the predominant spacing category by the time the infant was 6 months of age and then rose steadily and significantly. Proximate and far distance categories did not change significantly over time.

This differs from the Hoff et al. (1981) study in which, between the ages of 14 and 16 months, infants were far distant from their mothers nearly as often as they were distant and in which proximate scores were on a steady decline by 12 months of age. The mother and infant in this study often were seen out of contact and far distant from one another. This contrasts with other studies of gorillas both wild and captive in which infants were not seen more than 5 m away from mothers until the age of 8 to 18 months (Fossey, 1979; Hoff et al., 1981; Shaller, 1963). The infant in this study exhibited an earlier outset of independence that may have been attributable partly to the distance the mother maintained from the infant at an early age.

The introduction of eight new social group members did not elicit, as expected, a sudden increase in contact and proximity between mother and infant. Rather, the far distant category decreased slightly and distant increased, thus only somewhat lessening the spatial gap between mother and infant. Hoff, Hoff, Horton, and Maple (1996) reported similar findings following an introduction. The introduction had very little effect on mother–infant proximity, other than producing a notable drop in contact. Yet, the infant suffered no adverse consequences during this study period such as physical harm or evidence of antisocial or other unusual behaviors.

Gorilla infants in the wild and captivity have been observed to be largely responsible for maintaining proximity with their mothers (Fossey, 1979; Hoff et al., 1981). Hoff et al. reported that instances of mothers leaving and approaching infants were generally less frequent than infants leaving and approaching mothers.

Both leaving and approaching behaviors have been reported as being closely linked in frequency (Hoff et al., 1981).

In this study, however, the disparity between frequency in leaving and approaching behaviors was large for both the mother and infant. The infant spent significantly more time approaching the mother than leaving the mother. The mother, conversely, left the infant significantly more often than she approached him. Over time, the infant approached and left the mother with increasing frequency, indicating heightened infant activity and independence from his mother. The observed patterns of maintaining proximity indicate that the infant was attempting to maintain proximity with his mother, but mainly in the form of approaching her. The mother, on the other hand, controlled proximity with her infant mainly by leaving him. Maestripieri et al. (2002) reported that a mother's age might influence time spent in proximity with an infant because older mothers spend more time in proximity with infants than do younger mothers. That this young mother left the infant so frequently may have contributed to an early onset of infant independence.

Increasing solitary behaviors such as object examination often accompany infant independence from maternal influence (Hoff et al., 1981) and solitary play (Hoff et al., 1981; Taylor, 1998). The focal infant in this study was no exception to this pattern, as he exhibited a significant increase in solitary play and a rising trend in object examination with increasing age. The onset of his independence, however, was earlier than reported in Fossey (1979) and Hoff et al., in which infants began to explore environments away from their mothers around 1 year of age. The infant in this study exhibited elevated levels of object examination and solitary play beginning around 7 months of age. Concurrently, overall inactivity levels significantly decreased over time. Self-directed behaviors were infrequent and showed no significant change over time. In contrast, high frequencies of self-directed behavior in socially deprived (Fossey, 1979) and hand-reared (Gold, 1992) gorilla infants have been reported, indicating that the infant in this study was engaging in developmentally appropriate behaviors.

Object examination became the infant's most frequent solitary behavior over time, followed by solitary play. Both of these behaviors decreased substantially with the introduction of the new group, as the infant shifted his focus from his environment to his new cage-mates. Yet by the end of the study, both solitary play and object examination were once again trending back toward preintroduction levels, indicating that the introduction did not disrupt the positive developmental trajectory the infant had been on prior to the introduction.

Another indication that the infant was developing along species-typical lines was his ability for appropriate social interaction and the lack of aggression observed. Overall, the total affiliative social behavior of the infant significantly increased over time, and he was observed engaging in only affiliative social behaviors. In contrast to the infant in this study, human-reared gorilla infants have

been reported to exhibit frequent, unprovoked aggressive display behaviors (Gold, 1992) as have infants deprived of maternal care (Meder, 1989).

Social interaction between the infant and the introduced group quickly surpassed baseline levels. Social play with the new group members dominated the social behaviors of the infant. Meder (1990) reported social play among newly introduced infant gorillas as being indicative of a successful integration of members into a new social environment. By 13 months of age, the infant was sufficiently independent to assimilate into a social setting that was much more complex than he previously had experienced. Moreover, the infant was able to do this with minimal maternal protection as reflected by indexes of maternal behavior that did not indicate a sudden increase in mother–infant affiliative interactions. Although likely a major event in the life of the infant, the introduction to eight new gorillas did not prove to be too disruptive to the infant. Rather, by the completion of the study, spikes seen in sociability following the introduction were gradually decreased to preintroduction levels.

The two predominant interactions between mother and infant were social examination and social play. Although both behaviors fluctuated, a significant, overall decrease in social examination occurred during the 12 months of the study. Social examination began to drop precipitously at 9 months of age. This agrees with Hoff et al. (1981), in which mother–infant social examination began to decrease rapidly around 8 months of age and remained at negligible levels from that point forward.

A decided shift in interactions occurred between the 5th and 12th month, in which the focus changed from social examination to social play. The passive, mutual examination of one another was replaced by a more playful relationship as the infant matured and became more active and more of a social play partner to his young mother. This contrasts to other captive studies (Hoff et al., 1981; Maple & Zucker, 1978) in which social play between mother and infant was infrequently observed. Social examination and social play between the dyad plummeted when the new group was introduced, as mother and infant focused their attention away from one another and toward new social partners.

As zoo husbandry techniques advance, the need for greater understanding of social relationships among captive animals increases. Captive situations rarely duplicate the environmental and social complexity found in nature. As a result, captive animals continue to “evolve” into animals behaviorally distinct from their wild counterparts. Gorilla maternal behavior is one example of a behavior that may be affected adversely by the captive environment. Because norms do not always exist against which to measure appropriate and inappropriate maternal behaviors, mothers and infants needlessly may have been separated in the past. Studies such as the one conducted by Bloomsmith et al. (2003) that empirically identify behaviors of successful primiparous chimpanzee mothers are important for determining factors that indicate maternal competence. Managers of captive gorillas must de-

pend on species-typical indexes of successful maternal behavior, particularly for primiparous females, but also acknowledge and allow for idiosyncratic differences in individuals that might suggest taking a risk toward permitting a questionable mother to raise her own offspring. With careful monitoring and support, the result may be one more mother-reared, socially competent individual in the captive gorilla population.

CONCLUSIONS

In the early days of gorilla husbandry, the majority of infants were taken from their mothers for hand rearing (Kirchshofer, 1979; Nadler, 1974). Present-day evidence of maternal naiveté, neglect, and abuse may, therefore, be a direct result of well-intended but misguided human interventions. The result appears to be a variety of maternal behaviors, some considered appropriate and others inappropriate. Effective husbandry of *G. g. gorilla* must therefore recognize, and allow for, the fact that gorillas have individualistic mothering styles. Some likely are artifacts of captivity and others merely due to personality differences in mothers. For primiparous mothers, both human- and mother-reared, the first maternal experience may be key to rearing subsequent offspring successfully. The mother in this study offers a good example of a female who exhibited a somewhat negligent, but adequate, mothering style. What appeared to be maternal neglect (leaving the infant alone in a room for long periods of time) may simply reflect one extreme of the spectrum of adequate maternal care.

Despite anecdotal suspicions of severe maternal neglect in the focal primiparous mother at Lincoln Park Zoo, the data suggested that the mother was able to provide adequate maternal care and successfully rear her first infant through his first year. Although the mother did not demonstrate typical protectiveness for her infant compared to the Fossey (1979) and Hoff et al. (1981, 1983) studies, no further injuries occurred, and the infant developed along somewhat species typical lines. The data did not indicate total maternal incompetence or infant developmental problems but rather a mothering style that, nonetheless, produced a well-functioning, socially adapted infant. This case study supports growing evidence that each mother–infant relationship is unique and that the benefits of keeping borderline mothers and infants together may, in some instances, outweigh the risks of hand rearing.

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REFERENCES

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behavior*, *49*, 227–267.
- Beck, B. B. (1983). Managerial strategies in the captive propagation of endangered species. *Zoo Biology*, *2*, 253–257.
- Beck, B. B. (1984). The birth of a lowland gorilla in captivity. *Primates*, *25*, 378–383.
- Beck, B., & Power, M. (1988). Correlates of sexual and maternal competence in captive gorillas. *Zoo Biology*, *7*, 339–350.
- Bloomsmith, M. A., Kuhar, C., Baker, K., Lambeth, S., Brent, L., Ross, S. R., et al. (2003). Primiparous chimpanzee mothers: Behavior and success in a short-term assessment of infant rearing. *Applied Animal Behaviour Science*, *84*, 235–250.
- Enciso, A. E., Calcagno, J. M., & Gold, K. C. (1999). Social interactions between captive adult male and infant lowland gorillas: Implications regarding kin selection and zoo management. *Zoo Biology*, *18*, 53–62.
- Fossey, D. (1979). Development of the mountain gorilla (*Gorilla gorilla berengei*): The first thirty-six months. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 139–184). Menlo Park, CA: Benjamin Cummings.
- Gold, K. (1992). Nonsocial behavior of captive infant gorillas. *American Journal of Primatology*, *26*, 65–72.
- Hoff, M., Hoff, K., Horton, C., & Maple, T. (1996). Behavioral effects of changing group membership among captive lowland gorillas. *Zoo Biology*, *15*, 338–393.
- Hoff, M. P., Nadler, R. D., & Maple, T. L. (1981). Development of infant independence in a captive group of lowland gorillas. *Developmental Psychobiology*, *14*, 251–265.
- Hoff, M. P., Nadler, R. D., & Maple, T. L. (1983). Maternal transport and infant motor development in a captive group of lowland gorillas. *Primates*, *24*, 77–85.
- Johnson, D. (1981). Atlanta ape fertility conference. In *American Association of Zoological Parks and Aquariums Annual Conference Proceedings* (pp. 261–263). Wheeling, WV: American Association of Zoological Parks and Aquariums.
- Kirchshofer, R. (1979). *International studbook for the gorilla (Gorilla gorilla)*. Frankfurt, Germany: Frankfurt Zoological Garden.
- Maestripieri, D., Ross, S. K., & Megna, N. L. (2002). Mother–infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): Spatial relationships, communication, and opportunities for social learning. *Journal of Comparative Psychology*, *116*, 219–227.

- Maple, T. L., & Warren-Leubecker, A. (1983). Variability in the parental conduct of captive great apes and some generalizations to humankind. In M. Reite & N. G. Caine (Eds.), *Child abuse: The nonhuman primate data* (pp. 119–137). New York: Liss.
- Maple, T. L., & Zucker, E. L. (1978). Ethological studies of play behavior in captive great apes. In E. O. Smith (Ed.), *Social play in primates* (pp. 113–142). New York: Academic.
- McCann, C. M., & Rothman, J. (1999). Changes in nearest-neighbor associations in a captive group of western lowland gorillas after the introduction of five hand-reared infants. *Zoo Biology, 18*, 261–278.
- Meder, A. (1985). Integration of hand-reared gorilla infants in a group. *Zoo Biology, 4*, 1–12.
- Meder, A. (1989). Effects of hand rearing on the behavioral development of infant and juvenile gorillas (*Gorilla g. gorilla*). *Developmental Psychobiology, 22*, 357–376.
- Meder, A. (1990). Integration of hand-reared gorillas into breeding groups. *Zoo Biology, 9*, 157–164.
- Miller-Schroeder, P., & Paterson, J. D. (1989). Environmental influences on reproduction and maternal behavior in captive gorillas: Results of a survey. In E. F. Segal (Ed.), *Housing, care and psychological well-being of captive and laboratory primates* (pp. 389–415). Park Ridge, NJ: Noyes.
- Nadler, R. D. (1974). Determinants of variability in maternal behavior of captive female gorillas. In S. Kondo, M. Kawai, A. Ehara, & S. Kawamura (Eds.), *Proceedings of the Symposium of the 5th Congress of the International Primatological Society* (pp. 207–216). Tokyo: Japan Science Press.
- Rosenthal, M. A. (1990). To be a gorilla: The management of lowland gorillas in captivity. In *American Association of Zoological Parks and Aquariums Annual Conference Proceedings* (p. 580). Wheeling, WV: American Association of Zoological Parks and Aquariums.
- Ryan, S., Thompson, S. D., Roth, A. M., & Gold, K. C. (2002). Effects of hand-rearing on the reproductive success of Western lowland gorillas in North America. *Zoo Biology, 21*, 389–401.
- Schaller, G. B. (1963). *The mountain gorilla*. Chicago: University of Chicago Press.
- Shepherd, T. (1993). *Infant independency as a function of contact behavior in a group of captive Western lowland gorillas* (*Gorilla gorilla gorilla*). Unpublished master's thesis, George Fox College, Newberg, OR.
- Taylor, W. (1998). Social development of an infant lowland gorilla raised without age mates. *Animal Keeper's Forum, 25*, 70–77.
- Wilkinson, L. (2002). Systat (version 10.2) [Computer software]. Richmond, CA: Systat Software.