1986

Influences of Captivity on Gorilla and Orang-Utan Behavior

Coquette Elliott
Loyola University Chicago

INFLUENCES OF CAPTIVITY ON GORILLA AND ORANG-UTAN BEHAVIOR

by

Coquette Elliott

A Thesis Submitted to the Faculty of the Graduate School

Of Loyola University of Chicago in Partial Fulfillment

of the Requirements for the Degree of

Master of Science

September

1986

ACKNOWLEDGEMENTS

I wish to express my deepest gratitude to my co-advisors, John Janssen and Melvin Neville, who took such a personal and enthusiastic interest in my project. I also thank committee members Sheryl Coombs, Jan Savitz, and Nancy Garwood for their invaluable advice and support.

The directors and personnel at Brookfield Zoo, Lincoln Park Zoo, and Milwaukee County Zoo deserve many thanks for granting me the permission to conduct my research and for all of their cooperation and assistance in gathering pertinent information. Of course, the most special thanks to my parents, William and Lorraine Elliott, who have always encouraged me to pursue my dreams.

VITA

The author, Coquette Elliott, is the daughter of Lorraine E. Elliott (Jacobs) and William W. Elliott. She was born June 28, 1959 in Chicago, Illinois.

Her elementary education was obtained in the public schools of Lincolnwood and Niles and was completed in 1976.

In September of 1976, Ms. Elliott attended Oakton Community College for one year and then transferred to Lake Forest College where she received the degree of Bachelor of Liberal Arts, majoring in Biology, in May, 1980.

In 1982, Ms. Elliott decided to continue her education at Loyola University. She was granted an assistantship in 1983, which enabled her to complete the Master of Science in biology in 1986.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

INTRODUCTION

Past studies have indicated that behaviors involved in social interactions may change in great apes according to the environment. For example, in captivity orang-utans (Pongo pygmaeus) spend more time and energy in sexual activities compared to those in the wild (MacKinnon, 1974) and adult male lowland gorillas (Gorilla gorilla gorilla) engage in more contact with offspring compared to wild mountain gorillas (Gorilla gorilla beringei) (Tilford and Nadler, 1978). This suggests that there is a certain amount of plasticity in great ape behavior that is dependent upon a number of environmental factors such as food availability and the absence of potential predators.

One way to assess environmental affects on social interactions has been to compare behaviors between wild and captive animals (Erwin and Deni, 1979). While there are a number of studies on social interactions among wild mountain gorillas (Fossey, 1971; Schaller, 1963), fewer studies exist on other great apes, such as orang-utans and lowland gorillas, the most common species in captive environments. In addition, studies of captive animals, namely those conducted in zoos, have focused on isolated behaviors, making it difficult to evaluate complex behavioral repertoires involved in social interactions.

The focus of this study, then, was to compare the social interactions of captive lowland gorilla and captive orang-utan groups

and to determine how captivity alters behaviors normally observed in wild animals.

Zoo exhibits with different species specific social groupings of orang-utans and gorillas were chosen as captive environments for study. Observations on several types of behaviors were made to assess social interactions.

I observed behaviors both typical and atypical to those exhibited by wild animals. Typical behaviors included adult female/adult female gorilla tolerance toward one another, closer bonding between related adult female gorillas, adult female gorilla interest in infants, juvenile interest in infants, and juvenile and infant interest in social play with similar aged peers. Behaviors such as adult male orang-utan/adult female social play and adult female/unrelated infant care may or may not be typical behaviors in the wild. Atypical behaviors observed include paternal care, social play bewteen adult gorillas, and adult female orang-utan/adult female tolerance and food sharing.

These results show that both captive and wild orang-utans and gorillas have certain behaviors in common, but that other behaviors are quite different in the captive environment. Behaviors atypical of the wild may be due to increased social contact provided by the captive environment and an increase in "leisure time" made available by a constant and plentiful food supply and the absence of predators.

CHAPTER II

METHODS

Comparisons of gorilla and orang-utan social behavior were conducted at Brookfield Zoo, Brookfield, Illinois; Lincoln Park Zoo, Chicago, Illinois; and Milwaukee County Zoo, Milwaukee, Wisconsin. From approximately 1 September 1983 until 31 May 1984 most of the 29 animals included in the study were observed 10 times each for a total of approximately 5 hours of observation per animal. The scheduling of observation periods was randomized, and animals were observed in groups of 2 to 8 individuals using the Focal-Animal Sampling method (Altmann, 1974). During each day of observation the location and behavior of a given (focal) individual was recorded every 30 seconds for a total of 30 minutes. Observations were then focused on a second individual for the next 30 minutes and so on until observations were finished for that particular group. The order of animals to be observed within a group was determined randomly. On some occasions not all of the animals on exhibit were observed on a particular day due to unavoidable circumstances, i.e., zoo closing, visitor disruption.

Behaviors observed and subsequently included in the data analysis as social interactions were grouped into 3 categories of: (1) physical contact (i.e., touching, holding, grooming, does not include aggressive, submissive or sexual contacts), (2) close proximity (any non-aggressive or non-submissive behavior that occurred within 3 feet of another

individual) and (3) social play (i.e., wrestling, chasing, pushing, see Maple and Zucker, 1978; Maple, 1980; and Zucker, et al., 1986).

Any behavior which qualified for both the contact and close proximity categories was placed in the contact category. In addition, although it rarely occurred, social play and close proximity was placed in the social play category. While other behaviors, such as aggression, submission, and nonsocial behaviors (i.e., self play) were seen, these behaviors were so infrequent that they were excluded from the data analysis.

I studied 14 lowland gorillas and 15 orang-utans housed in varying social groups or alone at zoos (information on the subjects are in Tables 1 and 2). During the study, social groupings of gorillas at Lincoln Park Zoo, Milwaukee County Zoo, and orang-utans at Brookfield Zoo were changed several times (between 5 and 7) by zoo personnel, but only twice for orang-utans at Lincoln Park Zoo. Animals born or introduced after the onset of this study were not focal subjects, although interactions between them and the other subjects were recorded. Group compositions are in Tables 3 and 4.

Analysis

The frequency of behaviors resulting in actual contact between individuals, close proximity between individuals, and social play between individuals was used to assess the degree of interaction between

individuals of different sexes and age. Gorillas were placed in 5 general age groups (infant, juvenile, subadult and adult females, black-backed males, and adult silver-backed males) according to Schaller (1963). Orang-utans were placed in 6 general age groups (infant, juvenile, adolescent, subadult males, adult females, and adult males) according to MacKinnon (1974).

CHAPTER III

RESULTS AND DISCUSSION

Interactions between individuals of different sexes and ages are presented below with a brief discussion of how these interactions for captive animals are related to findings in wild animals (see Table 5).

A) Adult male orang-utan/infant interactions

In general, adult male orang-utans spent a considerable amount of time in contact (up to 40 percent of total number of observations) or in close proximity with their infant offspring (Table 6). Aggressive behavior between adult male orang-utans and infants was never observed.

Objects, attracting attention, such as crates and tires, sometimes accounted for the close proximity between adult male Dick and his infant son, Thomas-O, although contact was also made when no objects were involved.

The adult male Sam's total contact occurred with Pongo, his infant son. Prior to the removal of Pongo's mother, Hahna (removed from the exhibit in June 1984, following 5 groups observations), Pongo was usually in contact with or near his mother. Following her removal, Pongo and Sam were in almost constant contact. Since Sam was out of sight 30 percent of the total observation time, and Pongo was out of sight 25 percent of the total observation time, the contact between them was probably higher than reported. Sam never attempted to discourage

the contact with his son. On occasion when Sam was in close proximity to Pongo, he would reach for him and then cradle him.

No interactions were observed between the adult male Stanton and his newly born offspring, but observations were limited to a single half hour session.

Since orang-utans in the wild are usually solitary, except for females with their young, it is interesting that Pongo sought the vicinity of his father rather than that of the unrelated adult female, Katy. Katy was raising two unrelated offspring (Pepper and Herbie), but it is not unusual for adult females in captivity to mother as many as three unrelated orphaned offspring at a time (Maple, 1980). It is possible that Pongo avoided Katy because she had been aggressive toward his mother (Hahna).

Intense social interactions between a captive adult male orang-utan and his male offspring were also observed by Zucker, et al. (1978) at the Grant Park Zoo (Atlanta, Georgia). Adult male/offspring interactions were primarily classified as playful with the most frequent behavior being non-aggressive biting.

These findings suggest that male orang-utans are capable of more social interactions that has been observed in the wild. This is very intriguing especially considering fossil evidence that more primitive orang-utans were more social and may have had societies of a single protective male and several females with young (Maple, 1980) as is similar to that in gorillas (Eisenberg, et.al., 1979). Fossil evidence showing that males had larger body and canine tooth size clearly

indicates sexual dimorphism, suggesting that primitive orang-utans lived in groups (Hooijer, 1949).

B) Adult male gorilla/infant interactions

Gorilla fathers rarely or never made contact with their offspring, however they were sometimes in close proximity (table 6). The highest percentage of adult male Frank's total close proximity was near his newly born son, Brook.

The adult male, Samson, occasionally played with both Becky (infant male offspring) and Aqualina (infant female offspring) (Table 6). In the wild, adult male gorillas do not interact with offspring to any appreciable extent (Schaller, 1963). However, infants sometimes leave their mother to sit by or play on the dominant male (Schaller, 1963) and captive studies suggest that adult male gorillas possess the potential for intense social interactions with their offspring (Hoff, et al., 1977).

Of Samson's total social play, 92 percent included either Babs, an adult female, or Becky (Babs and Samson's son). Tilford and Nadler (1978) suggested that an affiliative bond between a male and female may increase the male's attraction toward her infant. In contrast, Samson did not spend as much time with his daughter, Aqualina, or with his daughter's mother, Alpha. Since Babs was never observed to interfere with Samons's opportunities to interact with Alpha (Babs' mother), it is likely that Samson preferred contact and close proximity with his male offspring as opposed to his daughter (see Tilford and Nadler, 1978), and

therefore was more attracted to Babs, his son's mother, than to Alpha, his daughter's mother.

C) Adult male/juvenile interactions

Adult males did not interact with juveniles to any appreciable extent (Table 7). The adult male orang-utan, Stanton, played exclusively with his son Ray only once. However, Stanton played with both Ray and Donna (Stanton's young adult female daughter) together on 21 occasions. It appeared that Ray joined Stanton and Donna after the onset of their play bouts.

The adult male gorilla, Frank, was occasionally seen to be in close proximity to Kivu (unrelated juvenile female). However, he was rarely observed to be near Kowali (his juvenile daughter) or Gino (unrelated juvenile male).

In the wild, adult male orang-utans occasionally interact with juveniles while consorting with their respective mother. Juveniles sometimes ignore or are ingored by the adult male. However, on several occasions juveniles have been observed to attack adult males who are attempting to mate with their mother. The adult male is very tolerant of these actions (MacKinnon, 1974).

Adult male gorillas in the wild, like orang-utans, rarely respond to the presence of juveniles (Schaller, 1963). Juveniles sometimes seek the vicinity of the silverbacked male (Schaller, 1963). However, when both males and females approach adolescence, they normally leave their natal group and therefore possible interaction with the adult male in

their natal group no longer occurs. While adolescent males travel alone and try to establish a harem (often by resorting to infanticide - see Fossey, 1979), adolescent females transfer directly to a new group (Harcourt, et al., 1976). Thus, in the wild it is more likely that adult males will encounter unrelated adolescent females than related adolescent females. In this respect, it is interesting that the adult male Frank was observed to be near the unrelated Kivu (approaching adolescence) more that he was near his own juvenile daughter, Kowali (approaching adolescence).

D) Adult male orang-utan/adult female interactions

Although some adult females were occasionally observed in close proximity to unrelated adult males, they seldom had any interactions involving bodily contact or social play with unrelated adult males (Table 8). For example, Stanton was never observed to engage in contact of social play with the unrelated adult female Erica. She was pregnant via Stanton at the onset of this study, so her pregnancy may have depressed proximity initiation toward Stanton (see Maple, et al., 1979). In addition, Stanton's participation in contact and social play did not include the unrelated adult female Tanga, who was still mothering Ray (Tanga and Stanton's son). I never observed any female to interfere with other females' desire to interact with the adult male.

However, interactions between a related adult male and female were observed. The adult male, Stanton, had a considerable amount of contact, close proximity, and social play with his daughter Donna (young

adult female). Of Donna's 43 counts of social play with Stanton, 22 counts were exclusively with Stanton, and 21 counts included juvenile Ray. There are 2 possible explanations for Stanton's association with Donna: 1) precopulatory behavior and 2) paternal interest.

Play behavior between cooperative consort pairs in the wild sometimes occurs prior to copulation (MacKinnon, 1974). Close proximity initiated by a female orang-utan in captivity may be used to show that she is in estrus (Beach, 1976; Maple, et al., 1979). Typical male behaviors that occur prior to copulation include a precopulatory chase after the female followed by grabbing and eventual restraint of the female. Following a precopulatory chase, females have been known to assume a copulatory position (Fox, 1929; MacKinnon, 1974; Zucker, et al., 1976). These behaviors, whether cooperative or forced by the male, then lead to copulation (MacKinnon, 1974; Mitani, 1985). Social play observed between Stanton and Donna consisted of behaviors similar to some of these precopulatory behaviors. However, this play behavior between Stanton and Donna never led to copulation. Since Stanton obviously copulated with unrelated adult females Erica and Tanga, but not with his daughter Donna, it is conceivable that a father-daughter incest taboo exists. However, fraternal twins that were raised together at the Seattle Zoo successfully mated (Maple, 1980), suggesting that incest behavior among orang-utans cannot be ruled out.

A second possibility is that Stanton's interactions with Donna were purely due to a paternal rather than sexual attraction. However, since female offspring are frequently separated from their fathers in

captive environments, it is difficult to evaluate this hypothesis.

E) Adult male gorilla/adult female interactions

Most adult male gorillas, like most adult male orang-utans, had little or no interactions involving bodily contact with adult females (Table 8). However, some adult females were occasionally observed to be in close proximity to the adult male. In one case, the adult male Frank, was observed to be in close proximity to the adult female, Kumba, only after the birth of their son, Brook.

In the wild, feeding competition among individuals within the group may have an affect on the spacing behavior between members (Watts, 1985). Although females watch the actions of the dominant male, interactions involving bodily contact are rare (Schaller, 1963). Females with dependent offspring spend more time near the dominant silverbacked male that those without dependent offspring (Harcourt, 1979). This phenomenon may account for Frank's frequent proximity to his newly born son, Brook. However, since Brook was often near Frank without a female, it may be the adult male or the infant and not the female that is initiating proximity.

Unlike what has been observed in the wild (Schaller, 1963), social play between adult females and males was observed in two of the captive populations. The adult female/adult male social play observed at Brookfield Zoo was only between Samson and Babs. Of Samson's total social play, 42 percent occurred with Babs, and 83 percent of Babs' social play occurred with Samson. As mentioned previously, this social interaction

may be related to the fact that Babs is the mother of Samson's son with whom he also engaged in a considerable amount of close proximity and social play (Table 6).

It is unclear what factors are involved in social play, but it is interesting to note that social play occurred primarily in the Brookfield Zoo population and never at the Milwaukee Zoo. It is possible that the absolute absence of social play at Milwaukee was due to the small cage size or the small size of the social unit. While social play was never observed at Milwaukee Zoo, copulation was.

F) Adult female/infant interactions

The majority of adult female/infant interactions for both gorillas and orang-utans occurred between mother and natural or adopted infant (Table 9). In comparison to the other adult female gorilla mothers observed, the maternal care exhibited by one particular adult female, Kumba (Brook's mother), did not appear to be as intense. I estimate that the frequency of contact between Kumba and Brook would probably have been even lower than reported if Brook had been observed more often. On several occasions I observed Kumba leave Brook alone on an elevated ledge. In a few instances, Brook fell to the ground. The lack of suitable maternal care exhibited by Kumba may have been because she was nursery reared. Nadler (1974; 1980) found that gorillas reared by their mothers in complex social groups are more likely to develop suitable maternal care.

On occasion, other female group members would "babysit" for Kumba

(Tables 9 and 13). The nulliparous adult female Terra, contacted Brook (Kumba's infant) on 55 occasions (100 percent of Terra's total contact), and the nulliparous adult female Debbie, was in contact with Brook on 31 occasions (94 percent of Debbie's total contact). This is consistent with Harcourt's (1979) and Stewart's (1977) findings that a newborn attracted other group members. In Harcourt's study the greatest interest in the newborn was exhibited by nulliparous females. Aside from Kumba, the remaining females in the Lincoln Park group were nulliparous, therefore a direct comparison between nulliparous and pipivarous gorillas cannot be made. The adult female gorilla mothers at Brookfield Zoo occasionally contacted the other females' infant.

Harcourt also reported that attraction toward a newborn from other group members tended to increase the avoidence behavior of the mother toward the other group members. Surprisingly, Kumba did not react in this fashion. When another female group member made contact with Brook I never observed Kumba to display aggression or try to retrieve her infant.

With the exception of the young adult female Donna, the adult female orang-utans that I observed had young offspring or young adopted offspring. Therefore, comparisons between nulliparous gorilla female/infant interactions and nulliparous orang-utan female/infant interactions cannot be made.

Aside from contact interactions, adult female orang-utans never engaged in social play with their infant. Although the juvenile male Ray played simultaneously with Erica and her infant on eight occasions,

Erica was actively playing with Ray, and not her infant. Active adult female/infant social play (neither individual was a passive recipient of play) was observed only between the gorillas at Brookfield Zoo. In the wild, active social play between adult female gorillas and infants is rare (Schaller, 1963). Schaller noted only one instance in which a female reciprocated active social play with an infant. Orang-utan mothers in the wild occasionally play with their young (Rijksen, 1978).

G) Adult female/juvenile interactions

Unlike adult female gorillas, adult female orang-utans were often in contact or close proximity to their juvenile offspring or adopted offspring (Table 10). However, a direct comparison between the two species cannot be made because of the age differences of the animals involved and also because the juvenile gorillas were not on exhibit with their mother or foster mother on several occasions.

With the exception of Gino (juvenile male gorilla) and Ray (juvenile male orang-utan), juvenile gorillas and orang-utans rarely or never had social play with an adult female. Ray's highest percentage of social play occurred with Donna (his young adult sister).

In the wild, the social break between a gorilla female and her juvenile occurs largely because juveniles actively seek contact with other group members as they grow (Schaller, 1963). Since orang-utans do not live in social units, juvenile orang-utans are not given as many opportunities as juvenile gorillas to interact with conspecifics other than their mother. Within their own subgroup, the juvenile orang-utan

can only play alone, with its mother, or perhaps a younger sibling (MacKinnon, 1974; Rijksen, 1978). When given the opportunity, the juvenile crosses over to a nearby subgroup to play with a similar aged peer (MacKinnon, 1974). In a captive setting it seems that both juvenile gorillas and juvenile orang-utans prefer to indulge in social play with similar age mates. (Tables 12 and 13).

H) Adult female orang-utan/adult female interactions

Aside from the antagonistic behavior exhibited between Katy and Hahna (two adult females that had to be separated, due to aggressive behavior, by zoo keepers at Brookfield Zoo), adult female orang-utans were quite tolerant of each other. Tanga, the oldest, largest, and most dominant of the females (determined by displacement of subordinate animals by dominant animals for preferred location and food) at Lincoln Park Zoo, often made contact or was in close proximity to Donna (her young adult daughter) and Erica (unrelated adult female) (Table 11). Erica often "begged" for food from Tanga, and she complied by allowing Erica to eat directly from her mouth.

There have been many reports on active food sharing by mothers with young, and between adult heterosexual pairs in captivity (Maple, 1980). Food sharing among unrelated adult females, however, is quite unusual.

In the wild, juveniles play with members of other subgroups, but respective females stay apart or do not meet (MacKinnon, 1974). When adult females do meet they are most likely to be related and thus more

tolerant of one another (Maple, 1980; Galdikas, 1984). Aggressive displays and fighting among adult females (probably unrelated) has been observed in the wild (MacKinnon, 1974; Galdikas, 1984), and in captivity (Maple, 1980).

I) Adult female gorilla/adult female interactions

With the exception of Alpha and Babs (Brookfield Zoo), adult female gorillas never made contact and were seldom in close proximity (Table 11). Although Kumba and Debbie (Lincoln Park Zoo) often changed location to avoid close proximity to Terra, the largest and most dominant female (determined by displacement of subordinate animals by dominant animals for preferred locations and food), Terra also seemed to prefer keeping her distance from them. Terra was pregnant during this study which could account for her asocial behavior. She spent a considerable amount of time in the sleeping quarters where she could not be observed. Pregnancy often alters the typical behavior patterns of gorillas whereby females become less active and more reclusive (Rumbaugh, 1965).

A very close relationship appeared to exist between Alpha and her older daughter, Babs. They were almost always seen on the same side of the exhibit within view of each other. Alpha and Babs engaged in social play and were often in close proximity. The frequency of close proximity behaviors between Alpha and Babs is even greater than indicated in Table 11. This is because the behavior "contact with one individual while near another" is only analyzed under the contact category. When

this behavior is included in the close proximity category, Alpha was seen to be in contact with her infant while being near Babs on 73 occasions. Babs was seen to be in contact with her infant while being near Alpha on 27 occasions.

In the Virunga Volcanoe region, Harcourt (1979) observed that related female gorillas spend more time together than unrelated or unfamiliar females, although in general adult females spend more time near the adult male that they do with each other and that it is the male's presence which accounts for proximity between females. Schaller (1963) observed that female gorillas, within the same harem, usually rest near each other, and are closely and continuously associated.

J) Adolescent orang-utan/adolescent interactions

In my study the adolescent orang-utans (Robin and Ronald) were not often in contact or close proximity, although there was a high percentage of social play between them. Of 399 observations of Robin and Ronald, 9 were of contact, 7 of close proximity, 125 of social play, and 3 of mutual homosexual behavior that occurred immediately after a play bout.

The adolescent orang-utan in the wild, although it may still travel with its mother, seeks contact with similar aged peers, plays with them, and may move about with them in adolescent groups (Rijksen, 1978). Field reports do not mention any incidences of homosexual behavior, however homosexuality between adult males has been observed in captivity (Maple, 1977). As mentioned previously, a play bout may be a

prerequisite for successful heterosexual copulation in orang-utans. It is possible that one of the functions of peer play is to facilitate the learning of successful reproductive behaviors. Laboratory reared infant and juvenile rhesus monkeys have been observed to exhibit rudimentary adult heterosexual behaviors during play bouts (Harlow, 1962).

K) Juvenile gorilla/juvenile interactions

Juveniles were occasionally observed to be in contact or in close proximity with each other (Table 12). The majority of gorilla juvenile social play occurred with similar age mates. At the Lincoln Park Zoo the juvenile females, Kivu and Kowali, both preferred the juvenile male, Gino, as a play partner. This is consistent with Freeman and Alcock's (1973) findings that the majority of social play of young captive gorillas was heterosexual in nature.

L) Juvenile gorilla/infant interactions

Although the juvenile gorillas at Lincoln Park Zoo were seldom on exhibit with the infant (Brook, male), when given the opportunity most made contact or engaged in social play with him (Table 13). Of the juvenile female Kowali's total contact, 93 percent occurred with her infant brother Brook. The juvenile male, Gino, also took an interest in Brook (unrelated to Gino) and was observed to play with him on several occasions. Brook was never observed to play with any other group member.

Juvenile interest in infants is consistent with Harcourt's (1979)

observations in the wild. He found that immature group members were greatly attracted to a newborn infant.

M) Juvenile orang-utan/infant interactions

It appears that juvenile orang-utans, like juvenile gorillas, may also be attracted to newborns. As mentioned previously, the juvenile male Ray, at Lincoln Park Zoo, was observed to play with the adult female, Erica, and her infant on 8 occasions. Prior to the birth of Erica's child, Ray and Erica had little contact.

Juvenile orang-utan/infant social play was also observed at Brookfield Zoo. The infant male, Pongo, did not engage in social play prior to the introduction of an infant and a juvenile (Pepper and Herbie). The lack of a similar aged peer (infant or juvenile) within Thomas-O's (Tables 6 and 9) environment could have accounted for his low percentage of social play.

Since social play occurs within the orang-utans natural habitat it may serve a function in social development of an individual much as Harlow (1971) found that peer experience is an important element toward normal social development in rhesus monkeys.

N) Infant/infant interactions

The infant gorillas observed were seldom in contact with each other, although they were occasionally in close proximity (Table 14). The infant orang-utans were never observed to be in contact (Table 14). Both orang-utan and gorilla infants occasionally left their mother to

engage in social play with another group member, however, with the exception of the infant male Thomas-O and adult male Dick's, one incident of social play, orang-utan infants only played with similar aged peers (see Zucker, et al., 1986).

O) Orang-utan/macaque interactions

The crabeating macaques (Macaca fascicularis), which reside in Brookfield Zoo's "Asia Tropic World," found their way into the orang-utan portion of the Asian exhibit. Surprisingly, 6 percent of juvenile Pepper's total contact, and 15 percent of her close proximity was with a crabeating macaque. Pepper's non-aggressive behavior toward the other species exceeded the 0.2 percent (of Pepper's total observation time I observed only 1 count of aggression) of aggressive acts (apparently very subtle) towards the macaques. It is interesting, considering the size disparity of the animals, that a macaque was twice aggressive toward Pepper (0.3 percent of total observations on Pepper).

The adult male, Sam, was also tolerant of the crabeating macaques. On 2 occasions a crabeating macaque was in close proximity to Sam and he simply looked at the macaque and made no attempt to displace it.

Field studies indicate that orang-utans usually show no reaction to macaque monkeys (MacKinnon, 1974). Rijksen (1978) observed that in general, orang-utan and long tailed macaque interactions were peaceful and on several occasions he observed mutual grooming between 2 young rehabilitant orang-utans (human dependent orang-utans that were placed into a program designed to relocate them into the wild) and a long

tailed macaque. Maple (1980) feels that wild orang-utans are probably too busy supporting their own food habits and it is not energetically worthwhile to interact with other species. However, those with time to spare, i.e., rehabilitants (where food is available at the rehabilitation station), take greater interest in their surroundings.

Peaceful interactions between an orang-utan and another species has also occurred in captivity. At the Baltimore Zoo, an adult male orang-utan lived compatibly with chimpanzees and occasionally played with them (Maple, 1980).

CHAPTER IV

GENERAL DISCUSSION

In my study some of the gorillas and orang-utans exhibited behaviors that would be considered atypical in the wild. These include paternal care and social play with offspring, adult male/adult female gorilla social play, adult female/infant gorilla social play, adult female/adult female gorilla social play, and food sharing among unrelated adult female orang-utans. Since these behaviors are apparently not exclusive to captive born animals, it seems that feral born animals are capable of acquiring these behaviors in captivity.

Many primates show different behaviors under different environmental conditions, some of which may have been shaped by natural selection and others which clearly do not involve an evolutionary time scale. For example, environmental conditions similar to those encountered by captive primates have been known to affect behavioral changes in open country baboons (Papio anubis) (Harding, 1977). These baboons lived on a cattle ranch which provided constant water supply and predator protection. Consequently they did no show the tight troop structure that was described in earlier baboon studies (DeVore and Washburn, 1963) presumably because rigid social organization was no longer needed as an anti-predator strategy used when traveling over long distances for water.

Social organization and the degree of social interaction may also be related to ecological factors, especially those determining food supply, food preference, and the extent of potential predators. Differences in troop size between black and white colobus monkeys (Colobus guereza) and red colobus monkeys (Colobus badius) for example, may be related to food supply. Black and white colobus monkeys inhabiting the Kibale Forest in Uganda feed exclusively on a limited number of tree species (Clutton-Brock, 1974). They consume both mature leaves and flower and shoot stages so that a small area of forest is sufficient to support their small troop size of 5 to 10 animals. The food resources are dependable and predictable and therefore worth defending. With the exception of maturing males that leave or are forced from the group or a harem male that may be replaced by a young adult, black and white colobus group membership is stable. Members are closely spaced and cooperate in group defense of their territory against other troops competing for food. Females often handle infants other than their own which probably helps integrate the infant into the type of cohesive social grouping that these animals display (Struhsaker and Oates, 1975).

In contrast to the black and white colobus, the red colobus monkeys inhabiting the Kibale Forest in Uganda and at the Gombe National Park in Tanzania, travel over longer distances to maintain a constant supply of trees in the flowering or fruit stages (Clutton-Brock, 1974). Because their food grows in sizable clumps in different parts of their range at different times, each area provides an adequate amount of food for a large multi-male/multi-female troop of 40 or more individuals.

However, the range that they must travel for food is too large to be efficiently defended. A large group size may be advantageous to red colobus monkeys because it better enables them to find food and to detect and defend themselves against predators. In fact, red colobus monkeys are know to cooperatively defend themselves against chimpanzees, a common predator (Clutton-Brock, 1974). Unlike the black and white colobus, which maintain a very stable group, red colobus females leave the group at maturity and males either leave or attain membership (Kavanagh, 1983).

A similar phenomenon involving food availability may account for behavioral differences noted between wild and captive orang-utans. Unlike the more social gorilla, orang-utans are more or less solitary animals with the exception of a mother and young. This is probably because their diets are composed mainly of fruits. Since the orang-utan is a frugivore that requires a substantial amount of food, a given area can only accommodate a few individuals. These conditions change in captivity however, where food supplies are plentiful and predictable. As was shown in my study, orang-utans void of natural environmental pressures can and do behave socially.

Similarly, pair bonding or the amount of time which mates spend together may be a function of food availability and predation. MacKinnon (1974) observed that adult female/adult male pairing in Borneo, where food supplies were plentiful, was maintained for only short periods of time. In contrast, pairing was maintained for longer periods of time in Sumatra, where food was less abundant yet predation was high. MacKinnon

(1974) observed a high frequency of Sumatran females with young being accompanied by an adult male whose function may have been to protect limited food supplies and defend against predators.

In captivity, where natural environmental pressures are alleviated, animals seem to show behaviors different from those observed in the wild. Some of the behaviors exhibited by captive orang-utans and gorillas in this study were surprisingly similar. Both gorilla and orang-utan fathers took an interest in their offspring. This could be because paternal certainty is high or undeniable, or simply that the adult male has more time to spare in a captive environment. Some of the adult males observed had a considerable amount of contact, close proximity, or social play with their respective infant which indicates that they do have the potential to care for their young.

Another behavior normally not observed in the wild is social play between adult male and female gorillas. In orang-utans, play may typically occur prior to copulation (MacKinnon, 1974). In my study some adult males of both species showed an active interest in social play with conspecific adult females. There could be a variety of reasons for this behavior such as strengthening and maintaining familiarity (see Poirier, et al., 1978), or simply to "fill spare time." However, in the case of adult female orang-utans, the willingness of the female to participate in social play with an adult male may serve as a social signal to indicate that she is in estrus. Perineal swelling is extremely small in female gorillas and is also small or absent in female orang-utans and therefore unlikely to serve as a major stimulus. Unlike

the female gorilla, which is known to show postures indicating sexual receptivity (Maple, 1980), it is not certain whether this is true for female orang-utans (Beach, 1976; Maple, 1980).

Although male orang-utans are basically solitary individuals, when consorting they do so with only one adult female at a time and therefore it would be to the male's benefit, reproductively, to be able to determine if the female is in estrus. If the female does not respond appropriately to his actions, he can then move on and ultimately make contact with a female that is ovulating.

In the wild, orang-utan juveniles without a sibling rarely have the opportunity to play with a similar aged peer. In captivity it seems that both gorilla and orang-utan infants and juveniles prefer to endulge in play with a similar aged mate. Both of the juvenile female gorillas observed preferred the smaller and younger juvenile male as a play partner. The play bouts observed between the adolescent orang-utans led to mutual homosexual behavior, suggesting that peer play may aid in the learning of appropriate adult sexual behavior (see Harlow, 1962; Nadler, 1986; Zucker, et al., 1986).

During my observations, adult female gorilla interactions were peaceful. Although the Lincoln Park group had an apparent dominance hierarchy, overt physical aggression was never observed. The two related adult female gorillas at Brookfield Zoo seemed to have a close relationship and they sometimes engaged in social play. The adult male may be partly responsible in keeping aggressive levels between adult females to a minimum. Although I never observed an adult male to

interfere with adult female interactions, it has been shown that removal of the dominant male in a captive group causes an immediate increase in aggressive behaviors between adult females (Hoff, et al., 1982). It is also possible that aggressive levels are low because zoo personnel can manipulate group compositions.

Adult female/adult female orang-utan interactions were far more peaceful than some observed in the wild, although, obviously aggressive encounters occur in captivity since females have been separated because of it. The female orang-utans at Lincoln Park Zoo had an apparent dominance hierarchy but were quite tolerant of each other. It would be interesting to determine if the adult male orang-utan, like the adult male gorilla, may also play a role in the level of aggressive interactions between adult females in captivity,

My findings suggest that gorillas and orang-utans show behaviors atypical of those observed in the wild in addition to those behaviors that naturally occur in the wild. Some of the typical behaviors observed in the wild and in this study include adult female gorilla interest in infants other than their own, closer bonding between related adult female gorillas, juvenile and infant orang-utan and gorilla interest in similar aged play partners, and possibly adult male orang-utan/adult female social play.

The purpose of this study was to show how captivity may affect social interactions in gorilla and orang-utan groups and to demonstrate how different types of social groupings can affect an individual's behavior. Although I have shown that there are several unusual

behaviors that occur in captive animals, it is presently unclear whether these behaviors arise de nova or are merely expressed at a much lower frequency in the wild. In addition, it is not clear to what extent individual differences play in the behaviors observed. Finally, it is not clear which features of the captive environment are most important in affecting behavior.

Table 1. Gorilla subject information. B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo, ?=unknown information, *=not a focal individual. For animals caught wild, the approximate age when the animal was caught is indicated.

Name	Sex	Age Group (actual age)	Zoo	Parentage (mother x father)
Samson	male	adult (23 yrs.)	B	wild, 2 yrs.
Alpha	female	adult (23 yrs.)	B	wild, 2 yrs.
Babs	female	adult (9 yrs.)	B	Alpah x ?
Becky	male	infant (2 yrs.)	B	Babs x Samson
Aqualina	female	infant (2 yrs.)	B	Alpha x Samson
Frank	male	adult (19 yrs.)	L	wild, 1 yr.
Terra	female	adult (25 yrs.)	L	wild, youth
Debbie	female	adult (18 yrs.)	L	wild, 1 yr.
Kumba	female	adult (13 yrs.)	L	raised by mother Mumbi for 28 days, then nursery reared fathered by Kisoro
Kowali	female	juvenile (5 yrs.)	L	Kumba x Frank
Kivu	female	juvenile (5 yrs.)	L	Banga x Otto
Gino	male	juvenile (3 yrs.)	L	hand raised for 2 yrs.
Brook*	male	born Sep. 1983	L	Kumba x Frank
Kounda*	male	sub-adult (10 yrs.)	L	?
Tanga	male	adult (23 yrs.)	M	wild, youth
Diane	female	adult (18 yrs.)	M	wild, youth

Table 2. Orang-utan subject information. B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo, ?=unknown information, *=not a focal individual. For animals caught wild, the approximate age when the animal was caught is indicated.

Name	Sex	Age Group (actual age)	Zoo	Parentage (mother x father)
Sam	male	adult (23 yrs.)	B	wild, 2 yrs. (Sumatran)
Katy	female	adult (23 yrs.)	B	wild, 2 yrs. (Sumatran)
Hahna	female	adult (10 yrs.)	B	Ginger x Yogi, Como Zoo nursery reared (Sumatran x Bornean)
Ronald	male	adolescent (9 yrs.)	B	Katy x Sam
Robin	male	adolescent (7 yrs.)	B	Ginger x Yogi, Como Zoo
Pepper	female	juvenile (3 yrs.)	B	Ginger x Yogi, Como Zoo
Pongo	male	infant (1 yr.)	B	Hahna x Sam
Herbie*	male	infant (1 yr.)	B	?
Stanton	male	adult (23 yrs.)	L	wild, youth (Bornean)
Tanga	female	adult (33 yrs.)	L	wild, 1 1/2 yrs.
Erica	female	adult (9 yrs.)	L	Billy x Jean nursery reared
Donna	female	adult (8 yrs.)	L	Tanga x Stanton
Ray	male	juvenile (3 yrs.)	L	Tanga x Stanton
?*	?	born Feb. 1984	L	Erica x Stanton
Dick	male	adult (15 yrs.)	M	Tia x Chang
Saba	female	adult (12 yrs.)	M	? x Billy (Sumatran x Bornean)
Thomas-O	male	infant (1 yr.)	M	Saba x Dick

Table 3. Composition of the gorilla groups. The number of observations refers to the number of times that a particular group composition was on display. B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo.

Group No.	Animal	Zoo	No. Obs
1	Samson (adult male)	B	10
	Alpha (adult female)		
	Babs (adult female)		
	Becky (infant male)		
	Aqualina (infant female)		
2	Frank (adult male)	L	2
	Terra (adult female)		
	Kumba (adult female)		
	Debbie (adult female)		
	Kowali (juvenile female)		
	Kivu (juvenile female)		
	Gino (juvenile male)		
3	Frank (adult male)	L	3
	Terra (adult female)		
	Kumba (adult female)		
	Debbie (adult female)		
	Kowali (juvenile female)		
	Kivu (juvenile female)		
	Gino (juvenile male)		
	Brook (infant male)		
4	Frank (adult male)	L	4
	Terra (adult female)		
	Kumba (adult female)		
	Debbie (adult female)		
	Brook (infant male)		
5	Kowali (juvenile female)	L	4
	Kivu (juvenile female)		
	Gino (juvenile male)		
6	Frank (adult male)	L	1
	Terra (adult female)		
	Kumba (adult female)		
	Debbie (adult female)		
	Gino (juvenile male)		
	Brook (infant male)		
7	Kowali (juvenile female)	L	1
	Kivu (juvenile female)		
	Koundu (sub-adult male)		
8	Tanga (adult male)	M	5
	Diane (adult female)		
9	Tanga (adult male)	M	5
10	Diane (adult female)	M	5

Table 4. Composition of the orang-utan groups. The number of observations refers to the number of times that a particular group composition was on display. B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo, ?=unknown information.

Group No.	Animal	Zoo	No. Obs
1	Sam (adult male)	B	4
	Hahna (adult female)		
	Pongo (infant male)		
2	Katy (adult female)	B	3
	Ronald (adolescent male)		
	Robin (adolescent male)		
	Pepper (juvenile female)		
3	Ronald (adolescent male)	B	1
	Robin (adolescent male)		
4	Sam (adult male)	B	3
	Katy (adult female)		
5	Hahna (adult female)	B	1
	Pongo (infant male)		
	Pepper (juvenile female)		
6	Sam (adult male)	B	8
	Katy (adult female)		
	Pepper (juvenile female)		
	Pongo (infant male)		
	Herbie (infant male)		
7	Hahna (adult female)	B	1
	Ronald (adolescent male)		
	Robin (adolescent male)		
8	Stanton (adult male)	L	7
	Tanga (adult female)		
	Erica (adult female)		
	Donna (adult female)		
	Ray (juvenile male)		
9	Stanton (adult male)	L	2
	Erica (adult female)		
	Donna (adult female)		
10	Stanton (adult male)	L	1
	Tanga (adult female)		
	Erica (adult female)		
	Donna (adult female)		
	Ray (juvenile male)		
	? (new born)		
11	Dick (adult male)	M	10
	Saba (adult female)		
	Thomas-O (infant male)		

Table 5. Various behaviors observed and references to previous captive and wild studies.

+ = has been observed, - = rare or has not been observed.

Behavior	Orang-utan in the wild	Orang-utan in captivity	Gorilla in the wild	Gorilla in captivity
adult male/infant contact	-(MacKinnon, 1974)	+(present study)	-(Schaller, 1963) initiation by male +(Schaller, 1963) initiation by infant	-(present study) +(Tilford and Nadler, 1978) initiation by male
adult male/infant and juvenile social play	-(MacKinnon, 1974) -(Rijksen, 1978)	+(Zucker, et al., 1978) +(present study) when adult female also participated	-(Schaller, 1963)	+(present study)

Table 5 (cont'd)

Behavior	Orang-utan in the wild	Orang-utan in captivity	Gorilla in the wild	Gorilla in captivity
adult male/adult female contact and social play	+(MacKinnon, 1974) pre-copulatory chase resembles behaviors that occur in social play	+(present study) +(Maple, 1980) +(Zucker, et al., 1986)	-(Schaller, 1963)	+(present study) social play
adult female/adult female contact and close proximity	-(MacKinnon, 1974)	+(present study)	+(Schaller, 1963) closely and continuously associated -(Schaller, 1963) contact -(Harcourt, 1979) +(Harcourt, 1979) related females more closely associated	-(present study) contact +(present study) related females closely associated

Table 5 (cont'd)

Behavior	Orang-utan in the wild	Orang-utan in captivity	Gorilla in the wild	Gorilla in captivity
adult female/adult female social play	-(MacKinnon, 1974)	-(present study)	-(Schaller, 1963)	+(present study) related females
related adult female/ infant and juvenile social play	+(Rijksen, 1978)	-(present study) with the exception of Donna, a young adult female	-(Schaller, 1963)	+(present study)
unrelated adult female/infant and juvenile contact and close proximity	-(MacKinnon, 1974)	+(present study) adult females are willing to adopt unrelated infants	+(Harcourt, 1979) adult females take an interest in newborns	+(present study)
adolescent/adolescent social play	+(Rijksen, 1978)	+(present study)		

Table 6. Adult male/infant interactions. Number of times behavior was observed to occur with an infant. Total number of observations include only those times when both individuals were in sight. R=relationship (F=father, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, ?=unknown information, *=not a focal individual.

Adult Male	Infant	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Dick	Tommy (m)	F	M	O	86	122	1	1194
Sam	Pongo (m)	F	B	O	296	62	0	731
Sam	Herbie(m)*	-	B	O	0	0	0	237
Stanton	?*	F	L	O	0	0	0	61
Samson	Becky (m)	F	B	G	3	86	15	1220
Samson	Aqualina(f)	F	B	G	0	20	13	1220
Frank	Brook (m)*	F	L	G	0	74	0	484

Table 7. Adult male/juvenile interactions. Number of times behavior was observed to occur with a juvenile. Total number of observations include only those times when both individuals were in sight. R=relationship (F=father, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Adult Male	Juvenile	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Sam	Pepper (f)	-	B	O	1	1	0	587
Stanton	Ray (m)	F	L	O	4	8	22	1067
Frank	Kowali (f)	F	L	G	2	7	2	599
Frank	Kivu (f)	-	L	G	1	22	6	609
Frank	Gino (m)	-	L	G	0	1	0	732

Table 8. Adult male/adult female interactions. Number of times behavior was observed to occur with an adult female. Total number of observations include only those times when both individuals were in sight. R=relationship (F=father, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Adult Male	Adult Female	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Dick	Saba	-	M	O	7	34	0	1192
Sam	Hahna	-	B	O	0	10	0	216
Sam	Katy	-	B	O	1	0	0	775
Stanton	Donna	F	L	O	146	111	43	1116
Stanton	Erica	-	L	O	0	9	0	1187
Stanton	Tanga	-	L	O	0	3	0	1067
Frank	Debbie	-	L	G	0	6	0	1178
Frank	Kumba	-	L	G	2	47	5	1216
Frank	Terra	-	L	G	0	7	3	1193
Samson	Alpha	-	B	G	0	12	0	1220
Samson	Babs	-	B	G	14	44	29	1220
Tanga	Diane	-	M	G	0	3	0	610

Table 9. Adult female/infant interactions. Number of times behavior was observed to occur with an infant. Total number of observations include only those times when both individuals were in sight. R=relationship (M=mother, FM=foster mother, GM=grandmother, S=sibling, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, ?=unknown information, *=not a focal individual.

Adult Female	Infant	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Saba	Thomas-O(m)	M	M	O	333	108	0	1136
Hahna	Pongo (m)	M	B	O	163	40	0	404
Katy	Herbie* (m)	FM	B	O	91	54	0	340
Katy	Pongo (m)	-	B	O	4	0	0	619
Erica	?*	M	L	O	61	0	0	61
Tanga	?*	-	L	O	1	13	0	122
Donna	?*	-	L	O	0	0	0	61
Alpha	Aqualina(f)	M	B	G	661	298	16	1220
Alpha	Becky (m)	GM	B	G	8	22	0	1220
Babs	Becky (m)	M	B	G	591	276	2	1220
Babs	Aqualina(f)	S	B	G	13	53	20	1220
Kumba	Brook* (m)	M	L	G	176	76	0	488
Terra	Brook* (m)	-	L	G	55	24	0	484
Debbie	Brook* (m)	--	L	G	31	63	0	452

Table 10. Adult female/juvenile interactions. Number of times behavior was observed to occur with a juvenile. Total number of observations include only those times when both individuals were in sight. R=relationship (M=mother, FM=foster mother, S=sibling, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Adult Female	Juvenile	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Katy	Pepper (f)	FM	B	O	179	77	2	930
Tanga	Ray (m)	M	L	O	207	173	1	1207
Erica	Ray (m)	-	L	O	8	36	8	1084
Donna	Ray (m)	S	L	O	43	32	63	1074
Kumba	Kowali (f)	M	L	G	0	21	0	600
Kumba	Kivu (f)	-	L	G	0	42	0	610
Kumba	Gino (m)	-	L	G	1	28	1	732
Debbie	Gino (m)	FM	L	G	4	143	16	724
Debbie	Kowali (f)	-	L	G	0	2	1	592
Debbie	Kivu (f)	-	L	G	0	30	0	602
Terra	Kowali (f)	-	L	G	0	1	0	581
Terra	Kivu (f)	-	L	G	0	6	0	591
Terra	Gino (m)	-	L	G	0	0	0	713

Table 11. Adult female/adult female interactions. Number of times behavior was observed to occur with another adult female. Total number of observations include only those times when both individuals were in sight. R=relationship (M/D=mother/daughter, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Adult Female	Adult Female	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Donna	Erica	-	L	O	0	13	0	1206
Donna	Tanga	M/D	L	O	25	58	0	1085
Erica	Tanga	-	L	O	49	155	0	1095
Alpha	Babs	M/D	B	G	17	22	19	1220
Kumba	Debbie	-	L	G	0	53	0	1182
Kumba	Terra	-	L	G	0	18	0	1197
Debbie	Terra	-	L	G	0	1	0	1159

Table 12. Juvenile/juvenile interactions. Number of times behavior was observed to occur with another juvenile. Total number of observations include only those times when both individuals were in sight. R=relationship (- = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Juvenile	Juvenile	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Kivu (f)	Kowali (f)	-	L	G	1	31	14	1200
Kivu (f)	Gino (m)	-	L	G	4	28	39	1089
Kowali (f)	Gino (m)	-	L	G	19	19	48	1087

Table 13. Juvenile/infant interactions. Number of times behavior was observed to occur with an infant. Total number of observations include only those times when both individuals were in sight. R=relationship (S=sibling, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orang-utan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, ?=unknown information, *=not a focal individual.

Juvenile	Infant	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Pepper (f)	Pongo (m)	-	B	O	4	2	37	728
Pepper (f)	Herbie (m)	-	B	O	10	6	61	350
Ray (m)	?*	-	L	O	3	15	8	181
Kivu (f)	Brook* (m)	-	L	G	0	0	0	183
Kowali (f)	Brook* (m)	S	L	G	54	12	0	183
Gino (m)	Brook* (m)	-	L	G	1	6	17	244

Table 14. Infant/infant interactions. Number of times behavior was observed to occur with another infant. Total number of observations include only those times when both individuals were in sight. R=relationship (C=cousins, - = no relationship), Z=zoo (B=Brookfield Zoo, L=Lincoln Park Zoo, M=Milwaukee County Zoo), S=species (G=gorilla, O=orangutan), Close proximity = within 3 feet of another individual, (m)=male, (f)=female, *=not a focal individual.

Infant	Infant	R	Z	S	Contact	Close Proximity	Social Play	Total Number of Observations
Becky (m)	Aqualina(f)	C	B	G	5	67	66	1220
Pongo (m)	Herbie* (m)	-	B	O	0	0	5	279

REFERENCES CITED

Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. Behavior. 49: 227-265.

Beach, F.A 1976. Sexual Attractivity, Proceptivity, and Receptivity in Female Mammals. Hormones and Behavior. 7: 105-138.

Clutton-Brock, T.H. 1974. Primate Social Organization and Ecology. Nature. 250: 539-542.

Devore, I. and S.L. Washburn 1963. Baboon Ecology and Human Evolution. pp. 335-367. In: F.C. Howell and F. Bourliere (eds.) African Ecology and Human Evolution. Aldine, Chicago.

Eisenberg, J.F., N.A. Muckenhirn, and R. Rudran 1979. The Relation Between Ecology and Social Structure in Primates. pp. 455. In: W. Sussman (ed.) Primate Ecology. John Wiley and Sons, Inc., New York.

Erwin, J. and R. Deni 1979. Strangers in a Strange Land: Abnormal Behaviors or Abnormal Environments? pp. 1-28. In: J. Erwin, T.L. Maple and G. Mitchell (eds.) Captivity and Behavior. Van Nostrand Reinhold, New York.

Fossey, D. 1971. More Years with Mountain Gorillas. National Geographic Magazine. 140: 574-585.

Fossey, D. 1979 Development of the Mountain Gorilla (Gorilla gorilla beringei): The First Thirty-six Months. pp. 139-186. In: D.A. Hamburg and E.R. McCown (eds.) The Great Apes. Benjamin/Cummings, California.

Fox, H. 1929. The Birth of Two Anthropoid Apes. Journal Mammal. 10: 37-51.

Freeman, H.E. and J. Alcock 1973. Play Behavior of a Mixed Group of Juvenile Gorillas and Orang-utans. International Zoo Yearbook. 13: 189-194.

Galdikas, B.M.F. 1984 Adult Female Sociality Among Wild Orang-utans at Tanjung Puting Reserve Indonesia. pp. 217-236. In: M.F. Small (ed.) Monographs in Primatology, Vol. 4. Female Primates: Studies by Women Primatologists, Alan R. Liss, Inc., New York.

Harcourt, A.H. 1979. Social Relationships Among Adult Female Mountain Gorillas. Anim. Behav. 27: 251-264

Harcourt, A.H., K.J. Steward, and D. Fossey 1976. Male Emigration and Female Transfer in Wild Mountain Gorillas. Nature. 263: 226-227.

Harding, R.S.O. 1977. Patterns of Movement in Open Country Baboons. Amer. J. of Phys. Anthr. 47: 349-354.

Harlow, H.F. 1971. Learning to Love. Albion Publishing Co., San Francisco.

Harlow, H.F. 1962. The Heterosexual Affectional System in Monkeys. Amer. Psych. 17: 1-9.

Hoff, M.P., R.D. Nadler, and T.L. Maple 1977. The Development of Infant Play in a Captive Group of Gorillas. Paper presented at the meeting of the American Society of Primatologists, Seattle, Washington.

Hoff, M.P., R.D. Nadler, and T.L. Maple 1982. Control Role of an Adult Male in a Captive Group of Lowland Gorillas. Folio Primatol. 38: 72-85

Hooijer, D.A. 1949. Mammalian Evolution in the Quarternary of Southern and Eastern Asia. Evolution. 3: 125-128.

Kavanagh, M. 1983. A Complete Guide to Monkeys, Apes and Other Primates. The Viking Press, New York.

MacKinnon, J. 1974. In Search of the Red Ape. Holt, Rinehart, Winston, New York.

MacKinnon, J. 1974. The Behavior and Ecology of Wild Orang-utans (Pongo pygmaeus). Anim. Behav. 22: 3-74.

Maple, T.L. 1977. Unusual Sexual Behavior of Nonhuman Primates. pp. 1167-1186. In: J. Money and M. Musaph (eds.) Handbook of Sexology. North Holland Biomedical Press, Amsterdam, Elsevier.

Maple, T.L. 1980. Orang-utan Behavior. Van Nostrand Reinhold Co., New York.

Maple, T.L. and E.L. Zucker 1978. Ethological Studies of Play Behavior in Captive Great Apes. pp. 113-142. In: E.O. Smith (ed.) Social Play in Primates. Academic Press, New York.

Maple, T.L., E.L. Zucker, and M.B. Dennon 1979. Cyclic Proceptivity in a Captive Female Orang-utan. Behav. Proc. 4: 53-59.

Mitani, J.C. 1985. Mating Behavior of Male Orang-utans in the Kutai Game Reserve, Indonesia. Anim. Behav. 33: 392-402

Nadler, R.D. 1974. Determinants of Variability in Maternal Behavior of Captive Female Gorillas. Symp. 5th Congr. Int. Primat. Soc., 207-215.

Nadler, R.D. 1980. Child Abuse: Evidence from Nonhuman Primates. Developmental Psychobiology. 13(5): 507-512.

Nadler, R.D. 1986 Sex-Related Behavior of Immature Wild Mountain Gorillas. Developmental Psychobiology. 19(2): 125-137.

Poirier, F.E., A. Bellisari, and L. Haines 1978. Functions of Primate Play Behavior. pp. 143-168. In: E.O. Smith (ed.) Social Play in Primates. Academic Press, New York.

Rijksen, H.D. 1978. A Field Study on Sumatran Orang-utans (Pongo pygmaeus abelii Lesson 1827) Wageningen, H. Veenman and Zonen B.V., 420 pp.

Rumbaugh, D.M. 1965. The Birth of a Lowland Gorilla at San Diego Zoo. Zoonooz, 38: 12-17.

Schaller, G.B. 1963. The Mountain Gorilla. University of Chicago Press, Chicago.

Stewart, K.J. 1977. The Birth of a Wild Mountain Gorilla (Gorilla gorilla beringei). Primates 18(4): 965-976.

Struhsaker, T.T. and J.F. Oates 1975. Comparisons of the Behavior and Ecology of Red Colobus and Black and White Colobus Monkeys in Uganda: A Summary. pp. 103-123. In: R.H. Tuttle (ed.) Socioecology and Psychology of Primates. Aldine, Chicago.

Tilford, B.L. and R.D. Nadler 1978. Male Parental Behavior in a Captive Group of Lowland Gorillas. Folia Primat. 29: 218-228.

Watts, D.P. 1985. Relations Between Group Size and Composition and Feeding Competition in Mountain Gorilla Groups. Anim. Behav. 33: 72-85.

Zucker. E.L., L. Brogdor, and T.L. Maple 1976. Social Behavior of Captive Orang-utans. Paper presented at conference of Southeastern Psychological Association, New Orleans, Louisiana.

Zucker. E.L., G. Mitchell, and T.L. Maple 1978. Adult Male Offspring Play Interactions Within a Captive Group of Orang-utans (Pongo pygmaeus). Primates. 19(2): 379-384.

Zucker. E.L., M.B. Dennon, S.G. Puleo, and T.L. Maple 1986. Play Profiles of Captive Adult Orang-utans: A Developmental Perspective. Developmental Psychobiology. 19(4): 315-326.

APPROVAL SHEET

The thesis submitted by Coquette Elliott has been read and approved by the following committee:

Dr. John Janssen, Director
Associate Professor,
Biology
Loyola University of Chicago

Dr. Jan Savitz
Professor,
Biology
Loyola University of Chicago

Dr. Sheryl Coombs
Research Associate,
Parmly Hearing Institute,
Adjunct Faculty Biology
Loyola University of Chicago

The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

Sept 18 1986
Date

Director's Signature