Changes in Nearest-Neighbor Associations in a Captive Group of Western Lowland Gorillas After the Introduction of Five Hand-Reared Infants

Colleen M. McCann¹* and Jessica M. Rothman²

¹Department of Mammalogy, Wildlife Conservation Society, Bronx, New York
²Department of Animal Science, Cornell University, Ithaca, New York

The successful management of a captive gorilla population often necessitates the hand-rearing of infants and their subsequent re-integration into social groups of conspecifics. In the present study we quantified the changes in nearest-neighbor associations in a group consisting of a silverback male, three adult females, and two sub-adult females after the introduction of five hand-reared infants. Additionally, we examined the associations among kin and non-kin group members to determine whether genetic relatedness was a factor influencing the integration of the infants into the group and the subsequent patterns of association among infants and adults. Results showed that after the introduction, the silverback male spent >60% of his time in close proximity to an infant and 10% of his time within a “cluster” of infants. There was a significant change in a female’s nearest-neighbor associations; however, the change did not include an infant. The most significant finding among infants was a strong bias by each to associate with another infant. When the infants associated with an adult, three of the five associated most with the silverback male ($P < 0.001$), whereas the other two infants distributed their time among all the adults. The most significant change in behavior patterns was exhibited by one of the sub-adult females who displayed parental behaviors 18% of the time compared to <1% for all other females. Adults and one sub-adult female associated significantly more often with related infants compared to unrelated infants ($P < 0.025$), and the infants showed a bias to associate with another related infant ($P < 0.001$). Results of an infant’s association with an adult showed that three of the five infants preferred to associate with a related adult ($P < 0.0001$). An individual’s age, sex, and behavioral profile may have also influenced association patterns among group members. These findings lend strong support to the importance of peer groups and the presence of a silverback male for facilitating the integration of hand-reared infants into established adult groups. Zoo Biol 18:261–278, 1999. © 1999 Wiley-Liss, Inc.

Key words: Gorilla gorilla gorilla; integration; affiliations; kin relatedness

*Correspondence to: Colleen McCann, Department of Mammalogy, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460. E-mail: cmccann@wcs.org

Received for publication May 5, 1998; revision accepted October 12, 1999.

© 1999 Wiley-Liss, Inc.
INTRODUCTION

The western lowland gorilla (*Gorilla gorilla gorilla*) is one of many threatened species in cooperative breeding programs in zoological parks around the world. The wild population is estimated to be at least 100,000, whereas the eastern lowland (*G. g. graueri*) and mountain (*G. g. beringei*) gorilla number 16,000 and 600, respectively [Oates, 1996]. Although the data on wild populations show that they are threatened in most countries where they occur [Stewart and Harcourt, 1987; Harcourt, 1995], the North American captive population of western lowland gorillas has increased significantly in recent years to more than 350 [Wharton et al., 1992; Wharton, 1997]. Successfully reproducing gorillas require an adequate diet, large, stimulating enclosures, and suitable breeding groups [Maple, 1979; Maple and Hoff, 1982]. These requirements are not always easily attained, since the gorilla’s habitat is difficult to reproduce within the confines of a controlled environment [Maple and Finlay, 1986]. However, great strides have been made in the management of captive gorillas that have come about through the American Zoo and Aquarium Association’s (AZA) Western Lowland Gorilla Species Survival Plan (SSP). In particular, the facilitation of appropriate social groupings for captive gorillas is in large part responsible for the success in reproduction and increase in birth rates experienced in this population [Ogden and Wharton, 1997].

Whereas birth rates in captivity have increased substantially over the past 10 years, and the percentage of hand-reared infant gorillas has decreased (e.g., <50% of infants are hand reared today compared to 80% in 1980 [D. Wharton, pers. comm.]), maternal competence still remains a problem [Maple, 1983; Gold, 1992a; Porton, 1997]. Newborn gorillas are often ignored or not cared for properly [Schaller, 1964; Nadler, 1974; Kingsley, 1977; Clift and Martin, 1978; Maple, 1979; Maple and Hoff, 1982]. As a result, there is a dependence on the hand rearing of infants, and their subsequent reintroduction into social groups of adults. However, a corollary of this dependence has been a significant advancement of the techniques used for hand rearing and reintroducing infants into social groups [Olson and Gold, 1985; Gold, 1992b; Porton, 1997]. To date, there have been several studies focusing on the manner in which gorillas are introduced, addressing issues concerning the primary group members used for introductions, the age of introduced infants, adult male-to-infant interactions, and the structure of the hand-reared group from neonate to the age at introduction. Hand-reared infants are often reintroduced to groups that include their mother or other related individuals. The effects of introducing gorilla infants to their relatives have not yet been reported. Only a few studies attempted to identify mechanisms of kin recognition in nonhuman primates [reviewed in Gouzoules, 1984; Walters, 1987; Bernstein, 1991], including gorillas [Tilford and Nadler, 1978; Farrow and Lockard, 1992].

Studies by Meder [1989] and Jendry [1996] showed that older females were often preferred as surrogates. Their calm nature and central role within the group provided a stable environment for the vulnerable infants. When the infants appeared to acclimate to the presence of an adult female, other individuals were then added to the group. Hand-rearing gorillas in peer groups has also proved to be an important factor in introductions, providing an opportunity for tactile contact and the development of normal social behavior [Fossey, 1979; Miller, 1982; Codner and Nadler, 1984; Hamburger, 1988: orangutans (*Pongo pygmaeus*); Tomasello et al., 1990: chimpanzees (*Pan troglodytes*); Jendry, 1996]. Additionally, introducing infants with other
peers provided a means of protection and security among the infants [Schildkraut, 1985]. Meder [1990] suggested that infants be reintroduced at 1–2 years of age to allow adult females to “adopt” them, increasing their acceptance among group members. Beck and Power [1988] argue that the infant’s age at introduction is critical and can significantly affect the development of social and reproductive behaviors.

In a descriptive study of infant introductions, Meder [1990] reported that silverback males had problems adjusting to the newly introduced infants. The infants’ first contacts with the silverback contained mostly sexual or aggressive behav-

### TABLE 1. Composition of gorilla group 1 at the Bronx Zoo/Wildlife Conservation Park

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>House name</th>
<th>Sex, age (yr. mo) (age-class)</th>
<th>No. of offspring</th>
<th>Related group members (r)</th>
<th>No. of previous infant introductions (no. of infants)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Tim</td>
<td>M, 37 (A)</td>
<td>4</td>
<td>I1 (0.50)</td>
<td>1 (2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I4 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I5 (0.50)</td>
<td></td>
</tr>
<tr>
<td>F1</td>
<td>Tunuka</td>
<td>F, 31 (A)</td>
<td>8</td>
<td>I1 (0.25)</td>
<td>3 (2, 3, 4)</td>
</tr>
<tr>
<td>F2</td>
<td>Huerfanita</td>
<td>F, 23 (A)</td>
<td>6</td>
<td>F3 (0.50)</td>
<td>3, (2, 4, 2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S2 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I2 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I3 (0.25)</td>
<td></td>
</tr>
<tr>
<td>F3</td>
<td>Triska</td>
<td>F, 10 (A)</td>
<td>2</td>
<td>F2 (0.50)</td>
<td>1 (4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S2 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I2 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I3 (0.50)</td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>Paki</td>
<td>F, 7 (S)</td>
<td>0</td>
<td>I4 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I5 (0.25)</td>
<td></td>
</tr>
<tr>
<td>S2</td>
<td>Holli</td>
<td>F, 7 (S)</td>
<td>0</td>
<td>F2 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F3 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I2 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I3 (0.25)</td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>Tuti</td>
<td>F, 1.11 (I)</td>
<td>—</td>
<td>M1 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F1 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I4 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I5 (0.25)</td>
<td></td>
</tr>
<tr>
<td>I2</td>
<td>Honi</td>
<td>F, 1.9 (I)</td>
<td>—</td>
<td>F2 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F3 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S2 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I3 (0.25)</td>
<td></td>
</tr>
<tr>
<td>I3</td>
<td>Imani</td>
<td>F, 1.6 (I)</td>
<td>—</td>
<td>F2 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F3 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S2 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I2 (0.25)</td>
<td></td>
</tr>
<tr>
<td>I4</td>
<td>Ngoma</td>
<td>M, 1.10 (I)</td>
<td>—</td>
<td>M1 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I5 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I1 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S1 (0.50)</td>
<td></td>
</tr>
<tr>
<td>I5</td>
<td>Tambo</td>
<td>M, 1.10 (I)</td>
<td>—</td>
<td>M1 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I4 (0.50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I1 (0.25)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S1 (0.25)</td>
<td></td>
</tr>
</tbody>
</table>

M, male; F, female; A, adult; S, sub-adult; I, infant; r, coefficient of relatedness.
iors. This corroborates data from wild populations that reported aggression between silverbacks and unrelated infants [Fossey, 1984; Watts, 1990]. Based on these reports, some authors warn that aggression may occur between the mature males and unrelated infants and should be taken into consideration when forming captive breeding groups [Foster, 1982; Brown and Wagster, 1986; Mitchell, 1989]. However, in a study by Ancrenaz [1993], adolescent males facilitated the introduction of a 4-year-old wild orphan to an established captive group. In wild gorillas, Fossey [1976, 1979] reported two cases of a silverback adopting an infant orphan, although it is not known whether these infants were born into the troop and related to the silverback. Other studies also documented that silverbacks may facilitated the introduction of infants [Van Elsackler et al., 1990], suggesting that paternal ties within the group allow the infant a secure and structured integration among group members [Fossey, 1979].

To date, there have not been any studies on captive gorillas that quantify the effects of recently introduced infants on the established group members. Although previous studies describe initial stages of the introductory process of hand-reared infants to an adult [Schildkraut, 1985; Meder, 1989, 1990; Porton, 1990; Ancrenaz, 1993; Jendry, 1996], the present study, in contrast, focused on the effect of the introduction of infants on association patterns among group members, in addition to changes in general activity patterns. The study group included at least one parent of each infant and one or more siblings, providing an opportunity to investigate further what role kin relationships may have played in the process of integration of the infants. This was a descriptive study, and therefore, no specific hypotheses were tested.

METHODS

Subjects

The study group consisted of 11 captive, western lowland gorillas maintained at the Bronx Zoo/Wildlife Conservation Park (BZ/WCP) (Table 1). The adult group included five females (three adult, two sub-adult) and one silverback male. The 37-year-old silverback male, M1, was transferred from the Cleveland MetroParks Zoo to the BZ/WCP in 1991 as the result of an SSP recommendation. Approximately 10 months before the study, the silverback male M1 was introduced to Group 1, which consisted of five female gorillas (F1, F2, F3, S1, and S2). F1 is a wild-caught female, F2 was transferred from the Rio Grande Zoo in 1978, and females F3, S1, and S2 were born at the BZ/WCP. F2 is the mother of F3 and S2; however, parental bonds were not continuous. At the time of the study, three of the females were multiparous (F1, F2, and F3) and two were nulliparous (S1 and S2). However, F3 and S2 were pregnant during the observational stage of the study.

The group of infant gorillas was composed of three females (I1, I2, and I3) and two males (I4 and I5) that were hand reared as a group from birth. Each infant had a single parent in the group to which they were introduced after separations lasting 13–18 months. Infant I2 is the offspring of F2, I3 is the offspring of F3, and I1, I4, and I5 are the offspring of silverback male M1. Females S2 and I2 are full siblings, and males I4 and I5 are fraternal twins and half-siblings to sub-adult female S1.

Introduction History

Due to maternal incompetence, each infant was taken to a nursery within 48 h of birth, where they were cared for during the first year of life. While at the nursery,
each infant received the same diet and care until their subsequent transfer to the adult group (C. Atkinson, pers. comm.). Each day all five infants interacted freely with one another. At night male twins I4 and I5 were placed in the same sleeping enclosure, females I1 and I2 slept together, and I3 slept alone.

At the BZ/WCP, hand rearing infants is a primary husbandry technique that is used for the management of gorillas. As a result, several infant reintroductions were conducted in the past and included the majority of adult gorillas currently in the BZ collection (Table 1). Thus, many of our gorillas were familiar with the process of reintroducing infants to the group and typically accept them without incident.

The introduction of the five hand-reared infants in the present study began in January 1996, when they ranged in age from 1.1 to 1.6 years old. Like all infant introductions at the BZ/WCP, this one was a slow, steady process. The infants were first introduced to one adult female (F2). Additional adult females were gradually introduced, and eventually the silverback male and sub-adult females rejoined the group. The duration of the integration process lasted approximately 5 months.

**Gorilla Exhibit**

The gorilla exhibit at the BZ/WCP was a semi-circular shaped outdoor exhibit approximately 40 × 20 m. The gorillas were separated from the public by a dry moat, concrete wall, vegetation, and a perimeter fence. The exhibit contained one large fallen tree in its center, along with two hollow logs for climbing. The surface substrate of the exhibit was grass. The exhibit also included various plants and trees that, although protected from active climbing, allowed some opportunistic foraging.

**Behavioral Collection**

The study began June 6 and ended on August 30, 1996. Data on the patterns of association and behavior among adults and newly introduced infants were obtained using instantaneous scan sampling conducted at 10-min intervals [Altmann, 1974]. Observations were made between 1000 and 1700 hours, 5 days a week, for 2–4 h a day, for a total of 190 h of observation (n = 390 scan samples). Data were obtained on the adult group before the introduction of the infants from June 6 to July 30, 1996 (n = 164 scan samples). After the complete integration of the infants, data were collected on all individuals from July 4 to August 30, 1996 (n = 226 scan samples).

During each scan sample, the following data were recorded for each gorilla: 1) nearest neighbor, 2) distance to nearest neighbor (estimated meters), 3) proximity to the silverback male (estimated meters), and 4) behavior. A nearest neighbor was defined as the individual that was closest in proximity to the scanned individual. Nearest-neighbor indices and proximity to the silverback were used as measures of spatial associations among group members. The high frequency of a particular individual as another’s nearest neighbor was considered a measure of the relative strength of the association between those individuals, regardless of who initiated the close proximity. An individual’s tolerance of close proximity to another was viewed as that individual’s acceptance of the spatial proximity of those individuals.

In some instances, however, an individual’s nearest neighbor could not be determined. This specifically occurred when adults and infants were huddled together forming a uniform mass. It was always known who was in the mass, but individual nearest neighbors could not be determined because most or all members were touching; this was noted as a “cluster.” It almost always (99.5% of observations) included at least one infant and one adult.
In addition to proximity data, the behavior of each individual was recorded to determine whether the infant introductions had an effect on overall activity patterns of the adults and sub-adults. Individual behaviors were recorded and later grouped into the general categories listed in Table 2. Although the frequencies of specific individual behaviors are not easily detected in this way, notable shifts in the rate of general behavior categories can be detected. Thus, significant changes in an individual’s activity pattern can be surmised.

Data Analyses

All observations were recorded and analyzed using Microsoft Excel 7.0 and the statistical computer package Minitab (version 11.12). Determination of the method of statistical examination was obtained from Sokal and Rohlf [1981]. Percentage of nearest neighbors and distribution of behavior was calculated for each gorilla. When the gorilla was an adult, these values were compared before and after the infants were introduced into the group using the Student t-test and the Mann-Whitney U-test. When the gorilla was an infant, these values were compared before and after they were introduced using the Mann-Whitney U-test. The data associated with the cluster and the amount of time spent with infants were calculated into a percentage and a 95% confidence test was used to determine significance. Nearest-neighbor indices were correlated to behavior using the G-test. All comparisons involving distance were analyzed using the Student t-test. The frequency of behaviors before and after infants were introduced was analyzed using the G-statistical test. Comparisons of nearest neighbor and behavior between non-kin and kin were determined by the Student t-test. The \( \chi^2 \) test was performed to determine the probability of an infant’s affiliation with each adult. The degree of relatedness of each group member was calculated according to the coefficient of relatedness (r) [Hamilton, 1964]. An alpha level of significance of 0.05 was used in all statistical tests.

RESULTS

Changes in Behavior After the Infant Introduction

Overall behavior patterns in the group did not change significantly after the infants were added except for sub-adult female S1. S1 spent more time displaying locomotor behaviors after the infants were added and less time resting (\( P \leq 0.05, G = 39.56, df = 8 \)). Additionally, S1 spent >18% of her time exhibiting parental behav-

<table>
<thead>
<tr>
<th>Category</th>
<th>List of behaviors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>Eating, foraging, drinking, regurgitating, and re-ingesting.</td>
</tr>
<tr>
<td>Locomoting</td>
<td>Standing, standing bipedal, walking, running, and climbing.</td>
</tr>
<tr>
<td>Resting</td>
<td>Sitting, resting, lying down, sleeping, and nesting.</td>
</tr>
<tr>
<td>Self-care</td>
<td>Picking nose, auto-grooming, urinating, and defecating.</td>
</tr>
<tr>
<td>Sexual</td>
<td>Soliciting, copulating, and masturbating.</td>
</tr>
<tr>
<td>Parental</td>
<td>Carrying/being carried and holding/being held.</td>
</tr>
<tr>
<td>Affiliative</td>
<td>Touching, grooming, playing, and play face.</td>
</tr>
<tr>
<td>Agonistic-passive</td>
<td>Avoiding, cowering, mouthing, chest beating, and staring.</td>
</tr>
<tr>
<td>Agonistic-active</td>
<td>Approaching, charging, chasing, pushing, throwing at, bluff charge, screaming, pig grunt, and belch vocalization.</td>
</tr>
</tbody>
</table>
iors after the addition of the infants to the group, whereas all the other gorillas spent <1% of their time displaying parental behaviors.

Analyses were also conducted on whether there were more or less aggressive behaviors observed in the group before or after the introduction of the infants. The results of these analyses revealed that aggression levels in the group remained the same ($P > 0.05$). Although these values were extremely low, the highest amount of aggression was displayed by sub-adult female S1 but only represented 6% of the total number of scans recorded. Silverback male M1, adult female F3, and sub-adult female S2 showed less aggression toward another adult when the infant gorillas were present in the group, whereas adult females F1 and F2 and sub-adult female S1 showed more aggression toward another adult after the introduction, yet this increase was extremely small ($≤2\%$).

Additional analyses were made with regard to whether an individual’s nearest neighbor influenced their behavior. A comparison of adult gorilla behavior was made looking at the differences when the nearest neighbor was 1) the silverback M1, 2) an adult or sub-adult female, or 3) an infant gorilla. Silverback M1 and sub-adult female S2 spent more time exhibiting resting behaviors when the infants were their nearest neighbor compared to when other adult gorillas were their nearest neighbors ($G = 13.49, df = 5, P ≤ 0.05; G = 18.31, df = 10, P ≤ 0.05$). No significant differences were found in behavior for adult females F1, F2, and F3 or sub-adult female S1.

**Adult Nearest-Neighbor Associations Before the Infant Introduction**

Before the introduction of the infants, the association patterns of the adult and sub-adult group members showed biases (>20%) for particular individuals. Silverback male M1’s association patterns showed he spent most of his time in close proximity to adult female F3, followed by sub-adult female S1. Adult female F1 associated most often with sub-adult females S2 and S1, and adult female F2 associated with sub-adult female S1 and adult female F1. Adult female F3 spent a significant amount of time associating with the silverback M1 but equal amounts of time with adult female F1 and sub-adult females S1 and S2. Sub-adult female S1 associated equally with all group members, and sub-adult female S2 associated most with sub-adult female S1 and adult female F1.

**Adult Nearest-Neighbor Associations After the Infant Introduction**

Introducing the five hand-reared infants affected the pattern of spatial associations among the adult and sub-adult females (Fig. 1). After the introduction of the infants, sub-adult female S1 was nearest neighbor to adult female F1 less frequently ($t = 3.94, df = 26, P = 0.0005$), whereas adult female F2 associated less often with adult female F1 and sub-adult female S1 ($t = 2.18, df = 25, P = 0.039; t = 2.89, P = 0.011, df = 15$, respectively). Adult female F3 and sub-adult female S2 had no significant change in female nearest neighbors. F3 did, however, have the silverback male M1 as her nearest neighbor less frequently after the infants were in the group ($t = 2.89, df = 20, P = 0.01$). Sub-adult female S1 spent less time with silverback male M1 ($t = 2.89, df = 20, P = 0.009$), but there were no changes in her female nearest neighbor associations.

The silverback male M1’s nearest-neighbor associations were clearly affected by the introduction. There was a significant decline in the percentage of time that adult females F2 ($t = 2.68, df = 9, P = 0.025$) and F3 ($t = 3.99, df = 15, P = 0.0012$)
Fig. 1. Mean percentage of sub-adult and adult gorillas' nearest neighbor before (n = 164 scans) and after (n = 226 scans) infants were introduced into the group. Hatched bars, before introduction; filled bars, after introduction; C, cluster as defined in Methods section. ++, an adult-infant genetic relationship of $r = 0.50$; +, an adult-infant genetic relationship of $r = 0.25$. Significant differences ($P \leq 0.05$) between before and after were determined by the Student $t$-test and the Mann-Whitney $U$-test and are indicated by an asterisk.
Nearest-Neighbor Changes After Introductions

and sub-adult females S1 ($t = 2.81$, $df = 9$, $P = 0.012$) and S2 ($t = 2.42$, $df = 15$, $P = 0.02$) were his nearest neighbors as a result of the infants being introduced. M1’s nearest-neighbor status with adult female F1 did not result in a change ($t = 0.09$, $df = 28$, $P = 0.93$) due to the newly introduced infants. In addition, both the adult and sub-adult females were not in or near the cluster as often as M1 ($P \leq 0.05$), who spent 10% of his time in the cluster.

Figure 2 shows the percentage of time that an adult had an infant as its nearest neighbor. For silverback M1, 67.8% of the time an infant was his nearest neighbor. The adult and sub-adult females did not have an infant as their nearest neighbor as often, e.g., S1 = 37.8%, F2 = 25.2%, F1 = 20.7%, F3 = 20.7%, and S2 = 19.2%. There is 99.9% confidence that M1 had an infant as a nearest neighbor more often than any adult or sub-adult gorilla. No significant results were found among the adult and sub-adult female gorillas in this regard.

Infant Nearest-Neighbor Associations

When the association patterns of the infant gorillas are compared, the results are striking. As illustrated in Fig. 3, the most frequent nearest neighbor of each infant was another infant. Infant I1’s most frequent nearest neighbor was I4, whereas I4 and I5 were each other’s nearest neighbor. When an adult was the nearest neighbor of an infant, the nearest neighbor of I1, I4, and I5 was most often M1 ($P = 0.001$). Infant I2 spent most of her time with I3 and equal amounts of time (within 2%) with each adult and sub-adult female. Infant I3 spent the majority of her time with infant I2. Both infants I2 and I3 spent equal or greater amounts of time associating with an adult as they did to infants I1, I4, or I5. The infants’ strong association with each other was also reflected in the values associated with the cluster. The

---

**Fig. 2.** The percentage of time an infant was the nearest neighbor of each sub-adult and adult gorilla ($n = 226$ scans). Values were determined by calculating the total number of scans an infant was the nearest neighbor to an adult. The values were then converted into a percentage. A 95% confidence test was performed to determine statistical significance. Significant differences of $P \leq 0.05$ are indicated by an asterisk.
Fig. 3. Mean percentage of infant gorillas’ nearest neighbors (n = 226 scans). C, cluster as defined in Methods section. ++, an infant-infant genetic relatedness of r = 0.50; +, an infant-infant genetic relatedness of r = 0.25.
frequency that the cluster was an infant’s nearest neighbor, or an infant was included in the cluster, ranged from 7 to 21%.

**Distance to Nearest Neighbors Before and After Infant Introduction**

There were no significant results in terms of the distance of each adult gorilla’s nearest neighbor before and after the introduction. Significant results were found between infants I1 (t = 3.62, df = 3, P = 0.036) and I2 (t = 3.50, df = 6, P = 0.013); when another infant was their nearest neighbor, the distance was smaller between them compared to when an adult was their nearest neighbor. Infant I3 did not display any significant difference in the proximity of her nearest neighbor. Moreover, comparisons for infants I4 and I5 could not be made because the number of scans that a sub-adult was observed as their nearest neighbor was too small for statistical analysis. This fact alone may be important.

**Proximity to the Silverback Male Before and After the Infant Introduction**

In addition to nearest-neighbor indices, significance was found with regard to an individual’s proximity to the silverback male. The infant gorillas were closer in proximity to M1 compared to the adult females (t = 12.03, df = 165, P = 0.00001) (Fig. 4a). Figure 4b displays the effects of introducing the infants to the group on adult female proximity to the silverback male. Adult female F1 and sub-adult female S1 were significantly closer to the male after the infants were added (t = 2.06, df = 41, P = 0.046 and t = 3.41, df = 55, P = 0.0012, respectively), but adult females F2 and F3, and sub-adult S2 showed no significant changes in this regard. Thus, the introduction of the infants did not adversely affect the female’s spatial relationship with the silverback male. In all instances, the distance between the females and the silverback M1 decreased or remained the same.

**Influence of Kinship on Association Patterns**

In addition to the general associations among group members, analyses were performed that compared the effect of kin relatedness on an individual’s nearest neighbor (Fig. 1). With the exception of females F1 and S1, the results showed that adults and sub-adults associated more with infants to which they were related compared to those that were unrelated (M1: t = 4.11, df = 107, P = 0.0001; F2: t = 4.13, df = 26, P = 0.0001; F3: t = 3.14, df = 65, P = 0.0025; S2: t = 4.40, df = 62, P = 0.00001).

When the reverse was explored—an infant’s association with kin and non-kin adults—results were divided. Infants I2 and I3 did not spend more time associating with related adults than with unrelated; however, significant differences were found with regard to relatedness for infants I1, I4, and I5 (P ≤ 0.05).

Nearest-neighbor indices for infants indicated that their primary nearest neighbor was correlated with relatedness (Fig. 3). Related infants I2 and I3 were most often each other’s nearest neighbor (I2: t = 4.66, df = 25, P = 0.0001; I3: t = 5.05, df = 25, P=0.00001), whereas related infants I1, I4, and I5 were most often the nearest neighbor to each other (I1: t = 8.82, df = 55, P = 0.00001; I4: t = 8.19, df = 53, P = 0.00001; I5: t = 9.81, df = 51, P = 0.00001).

**Influence of Sex and Age on Association Patterns**

An analysis was performed to determine whether an infant’s adult nearest neighbor was influenced by the sex of the adult. For this analysis, the number of scans an
infant was nearest neighbor to an adult or sub-adult was calculated. Based on this value, it was expected that if sex were a factor, it would be biased toward the same-sex adult. It was found that the nearest neighbor of female I1 and the male twins (I4 and I5) was most frequently silverback male M1 ($\chi^2 = 21.2$, $P = 0.001$; $\chi^2 = 29.6$, $P = 0.001$; $\chi^2 = 29.5$, $P = 0.001$, respectively). This result was found to be non-random. Female I3’s nearest neighbor was also non-random; she frequently associated with sub-adult female S1 ($\chi^2 = 43.2$, $P = 0.001$). Female I2’s adult nearest neighbor, however, was random ($\chi^2 = 4.75$, $P = 0.001$).
Analyses were attempted with regard to the sex and age of the infants to determine whether there were significant associations among infants with regard to these parameters. Four of the five infants (I2, I3, I4, I5) associated most with an infant of the same sex and four of the five infants (I1, I3, I4, I5) associated most with another infant that was closest in age to them. However, the sample size (which included a set of twins) was too small to determine the effects that these variables may have had on infant-infant relationships.

DISCUSSION

Behavior Changes After the Infant Introduction

Changes in behavior before and after the infants were introduced revealed no significant differences. Overall, silverback male M1’s behavior patterns did not change as a result of the infants being added to the group; however, there was a noticeable difference in his resting behaviors when his nearest neighbor was an infant. The adult females and sub-adult female S2 did not show a change in behavior whether an infant, sub-adult, or adult female was their nearest neighbor. Although there were no noticeable effects on the adult females’ behavior as a result of the infant introduction, this may be an indication of their general indifference to the presence of the infants in the group. However, given that the adult females in this study were experienced with infant introductions (Table 1), it is likely that what appeared to be indifference was, in part, the result of their familiarity with having infants introduced to them. Thus, the infants were not a novel social stimulus for these particular females, and therefore their response to them may be a reflection of their experience at accepting the addition of infants into their social group [Porton, 1997].

Adult Nearest-Neighbor Associations After the Infant Introduction

With regard to the adult females, significant differences were found in their nearest-neighbor association patterns before and after the introduction. However, the change in associations almost always included another female or the silverback (Fig. 1). Thus, although their primary nearest neighbors did change, it did not include the infants.

Among all the females, sub-adult S1, a young nulliparous female in the group, displayed the most significant change in her association patterns. Her most frequent nearest neighbor was I3, the youngest infant in the group, and appeared to be the main focus of her attention (Fig. 1). This behavior in young females has been reported in many other primate species, in which infants become the focal point for the younger female members of the natal group [Lancaster, 1971; Hrdy, 1976; Quiatt, 1979; McKenna, 1981; Nicolson, 1987]. However, the other young female in the group, sub-adult S2, did not display the same enthusiasm toward the infants as did female S1. This may be explained in part by the fact that she was in her third trimester of pregnancy during this phase of the study. Thus, her reproductive state may have been a contributing factor in her overall behavior patterns, and therefore direct comparisons between these two females could not be made.

The silverback male M1 in the group exhibited a noticeable change in his association patterns after the introduction of the infants. Most often he associated with an infant, as indicated by their close proximity. This was usually a passive association since the infants appeared to choose to stay near the silverback male, and he ac-
cepted their close proximity, although this was not systematically determined. These findings are similar to those reported by Kirkevold and Lockard [1992] that show silverback males rarely initiate contact with infants. Despite his lack of initiating close proximity to the infants, M1 spent the most time (67.8%) near the infants compared to any other female (19.2–37.8%), and the cluster most often included him than any of the females. For the infants, it appeared that M1 provided protection and a sense of security for them. Their closeness to him allowed them protection from other group members’ more aggressive approaches. For example, whenever any of the infants were distressed, usually due to the persistent approaches of the sub-adult females, M1 would come to their aid and intervene in the encounter. This is in accordance with data reported from wild populations of gorillas that showed that infants are often attracted to the silverback because of his role as protector [Schaller, 1963; Stewart and Harcourt, 1987]. As a result, the silverback can play a pivotal role in the assimilation of infants into established groups [Fossey 1976, 1979; Van Elsackler et al., 1990).

Infant Nearest-Neighbor Associations

The most significant result regarding the infants’ introduction into the group was their strong dependence on each other for support and reassurance. For an overwhelming amount of the time observed, another infant was the nearest neighbor of each of the infants (Fig. 3), and when an infant was the nearest neighbor to another infant, the distance was smaller compared to when that infant was nearest neighbor to an adult. M1’s offspring (I1, I4, and I5) spent so little time with other adults (<4%) that the sample size was insufficient to perform any statistical measures. This becomes even more evident when looking at data associated with the cluster. The infants spent 7–21% of their time in a cluster immersed in tactile contact with each other, indicating their dependence on one another. Most of their other associations were through resting, usually locked in an embrace with one another, and playing. These results suggest that infants depend on each other for support and comfort and lend credence to the view that hand-rearing infants in peer groups facilitates their introduction into adult groups [Miller, 1982; Codner and Nadler, 1984; Schildkraut, 1985; Hamburger, 1988; Tomasello et al., 1990].

Influence of Kinship on Association Patterns

When the silverback’s spatial relationship with the newly introduced infants was explored, the results indicated that related infants were his nearest neighbor more often, despite the fact that all of them were initially unfamiliar. Thus, in this case, familiarity was not a factor influencing the spatial patterns of association. However, in this study M1 was introduced to all five infants simultaneously, and it is difficult to determine by what mechanism he may have discriminated his own offspring from the others in the absence of prior associational cues.

Female-infant associations revealed a bias toward kin; however, the degree of the association varied with the degree of relatedness. Adult females F2 and F3 were nearest neighbor to an infant very infrequently (<20%), but when they did come into contact with an infant, it was most often with a related infant (90 and 67%, respectively). Similarly, sub-adult female S2’s most frequent nearest-neighbor infant were the two that were related to her (71%).

Adult female F1 and sub-adult female S1 did not associate more often with
related infants; however, they did significantly increase their spatial proximity to the
silverback male after the introduction of the infants, possibly attempting to associate
more closely with infants by keeping close proximity to M1.

As previously noted, the infants were introduced to the adults as a peer group.
Among this peer group, two of the infants are full-siblings (fraternal twins I4 and I5)
and I1 is a half-sibling to them, whereas the remaining two infants (I2 and I3) are
half-siblings to each other. The results of the analyses on kin interactions revealed
that related infants were nearest neighbors significantly more often than were unre-
lated infants, even though all infants had prior association with each other and thus
were equally familiar with each other. However, further investigations into twin dy-
namics were not undertaken for this study.

**Influence of Age and Sex on Association Patterns**

When investigating an infant’s association with an adult, it was inconclusive
whether kin recognition was a factor in their patterns of association. For example,
with regard to the infants’ proximity to adults, male M1 was the nearest neighbor of
I1, I4, and I5 (his offspring) more often than any of the unrelated females. However,
this may be due more to the fact that their father was the silverback and provided the
infants with security and protection. It was documented in some primates that young
males are often attracted to adult males [reviewed in Taub, 1984; Whitten, 1987]. In
this study, male twins I4 and I5 associated more with M1 over any of the females;
however, female I1 also associated most with M1, and all three of these infants were
his offspring.

There were no significant differences in the associations of infants I2 and I3
with adult kin versus non-kin. In fact, they associated as often with unrelated adults
as they did with related adults. After being separated from their mothers, Codner and
Nadler [1984] described a brief detachment phase by infant great apes after being re-
introduced to their mothers. Although the connection is usually re-established within
a short period of time, if the mother has no interest in the offspring, a behaviorally
compatible surrogate may initiate contact. The infants in the present study seemed
responsive to adults that initiated contact by providing parental care and exhibiting
behaviors that were comforting. This may explain the high frequency of interactions
observed between unrelated females and infants, especially the high number of inter-
actions between sub-adult female S1 and unrelated infant I3. In any case, given that
female gorillas commonly transfer out of their natal groups as juveniles or adults,
female-female bonds are not likely to develop [Stewart et al., 1987].

Age may have been a factor influencing the patterns of associations observed
among infants. For example, I1, I3, I4, and I5 associated most with infants that were
closest in age to them and therefore may have chosen their nearest neighbor based
on age. Although I2 was closer in age to I1, I4, and I5, she associated more fre-
quently with I3, the youngest of the five infants. Data on peer interactions in chim-
panzees suggest that individuals prefer to associate with the youngest individual in
the group [Tomasello et al., 1990]. Female I2 was the only infant who displayed this
association.

Another possible factor that could be influencing association patterns is the sex
of the infants [Pereira and Fairbanks, 1993]. Male infants I4 and I5 and female in-
fants I2 and I3 may have associated more with one another based on their similar
sex. It is not known whether male infants I4 and I5 associated more with each other
based on the fact that they are twins or the fact that they are the same sex. Female I1’s nearest neighbors were related males I4 and I5 overwhelmingly more than female infants I2 and I3. Moreover, I1 was placed in the same sleeping enclosure with I2 every night for their first year of life; therefore, based on familiarity, it was expected that they would associate more with each other but that was not the case.

**Influence of Behavioral Profiles on Association Patterns**

It is likely that similar behavioral profiles of adults and infants may have been as important in producing the association patterns observed as were age, sex, or kin relationships. It is noteworthy that the silverback and his offspring exhibited the same behavioral indices (cautious, apprehensive, and protective) as did females F2 and F3 and their offspring (sociable, playful, and permissible) and therefore had a greater affinity toward one another [behavioral indices per Gold and Maple, 1994]. Infants I2 and I3 displayed independence and integrated well within the group, possibly causing a higher probability of interaction with all group members. The similarities in behavioral profiles may be a major factor influencing the association patterns described in this study. However, it is also important to note that behavioral traits have a genetic component [Wilson, 1975], and therefore, the similar traits seen in related individuals may provide a basis for kin recognition.

In sum, it is difficult to determine whether it was solely the genetic relatedness between adults and infants or the similar behavioral profiles exhibited by related individuals that primarily drove the patterns of associations observed. Likewise, the age and sex of individual’s may have also influenced the outcome of behaviors. The results of this study support that kin relatedness and similar behavioral profiles are important variables influencing patterns of association in gorillas. Nevertheless, although the sample size and conditions of this study cannot unequivocally confirm that kin recognition was an important factor operating in this case, the results do lend strong support to the success of using related individuals in infant gorilla introductions.

**CONCLUSION**

The integration of the five hand-reared infants into the group of adults described in this study was successful and without incident. Additionally, it was the first introduction at the BZ/WCP that included infants younger than 1.6 years old. Based on the results in this study, the following main conclusions can be made:

The silverback male played a pivotal role in the successful integration of the five infants into the established group of adults. Although some studies reported that adult males can respond aggressively toward hand-reared infants, in this study, the male facilitated the introduction process by providing protection to the infants and cohesiveness among the group.

Adult females showed no change in behavior patterns, suggesting their general acceptance of the addition of infants into the group. Sub-adult female S1 benefited from the addition of infants into the group by gaining parental experience, increasing her chances of becoming a competent mother.

The five infants associated with one another significantly more often than with an adult. Infant gorillas in peer groups when introduced to adults proved successful. Being raised in a peer group appeared to give the infants a strong sense of security and companionship.
In this study, infant gorillas interacted with related infants over unrelated infants. When adults interacted with an infant, it was usually a related infant. An individual’s age, sex, kin relatedness, and similarities in behavioral profiles are important variables influencing patterns of association in gorillas and should, therefore, be taken into consideration when introducing infants into groups of conspecifics.

ACKNOWLEDGMENTS

This study was funded in part by the Robert G. Engel Wildlife Conservation Park Mammal Intern Program. We thank James Doherty, Patrick Thomas, Dan Wharton, Ellen Dierenfeld, and particularly three anonymous reviewers for their useful comments and suggestions. Special thanks to Thomas Seeley (Cornell University) for providing invaluable assistance in the statistical analyses and earlier drafts of this manuscript. We are grateful to Caroline Atkinson, Louisa Gillespie, and the BZ/WCP Animal Keeper Staff for the great care and attention they provided to the gorillas in this study.

REFERENCES

Farrow RA, Lockard JS. 1992. Play type and rate across the first seven years of development in captive western lowland gorillas (Gorilla g. g.). Am Zoo 32:10a.
Kirkevold BC, Lockard JS. 1992. Play type and rate across the first seven years of development in captive western lowland gorillas (Gorilla g. g.). Am Zoo 32:10a.


