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THE SOCIAL NEXUS OF IMMATURE WILD MOUNTAIN GORILLAS (GORILLA GORILLA BERINGEI)

ABSTRACT: A commonly held hypothesis regarding the "function" of the relatively prolonged stage of early development in primates is that it prepares the young animal for the challenges of adulthood. The early period of behavioral development in primates is a time of learning; it is, presumably, their relatively large brains which enable them to acquire essential social and survival skills through experience. A study was conducted on the social nexus of immature wild gorillas in order to gain some insight into the process by which these animals learn species-appropriate social behavior. The assumption was made that the importance of social contacts for learning species-appropriate behavior is related to the percentage of time spent in association with various age/sex classes of individuals. Nine immature wild mountain gorillas were studied over a period of five months; the animals ranged in age from newborn to 3.3 years and lived in two social groups. The percentage of time spent in physical contact and proximity with another animal varied with group activity, namely, rest periods and travel/feed periods. With the exception of the newborn, all of the immature animals were in physical contact and proximity with another animal for a lesser percentage of time during feeding than during rest periods. The difference, not surprisingly, was reflected primarily in the time spent in contact with the mother during feeding. The age/sex classes with which the immature animals were in contact the greatest percentage of time, apart from the mother, were other infants and juveniles. The silverbacked males were also attractive to the immature animals, but less so than infants and juveniles. The data suggest, therefore, that the most important extra-maternal social contacts of immature mountain gorillas during the first several years of life are other infant and juvenile members of their group. If this is the case, it is likely that what is learned during this early phase of development is a general social competence rather than specific types of behavior.

KEY WORDS: Development – Ontogeny – Socialization – Social behavior – Great apes

INTRODUCTION

It is generally maintained that early social experience is crucial to the development of social competence in primates (e.g., Mason, Davenport and Menzel, 1968). The most compelling evidence for the importance of early social experience in the great apes was obtained in studies of early social deprivation in chimpanzees (Davenport and Rogers, 1970). Chimpanzees that were separated from their mothers shortly after birth and reared in a nursery under various types of social deprivation were socially incompetent as adults, inadequate sexually (Rogers and Davenport, 1969) and, for those females that were eventually impregnated by sexually assertive males, maternally in-

adequate (Rogers and Davenport, 1970). One question that has not been adequately addressed, however, is the nature of the social learning process that takes place during early development and the specificity of the behavior that is learned. Schaller (1963) described social interactions of immature wild mountain gorillas with various other members of the group, but he did not present data on the relative contributions of various age/sex classes to those interactions. Fossey (1979) presented much more quantitative data on the proximity (within 10 feet) of immature gorillas to others, but she did not differentiate between rest and feeding periods and she did not specifically address the issue of social learning. Do young primates learn a general social competence that then enables them to learn

more specific forms of behavior at a later age, or do they learn specific types of behavior, such as sexual and maternal behavior *per se*? The evidence suggests that the former is the case during infancy. A certain percentage of wild-born chimpanzees and gorillas that were separated from their mothers as infants and reared in captivity with only comparably young conspecifics mated adequately as adults, and the females reared their offspring in an acceptable manner (Nadler, 1975, 1981).

A second question relates to the source(s) of social competence from which the infants acquire the basic substrate for learning species-appropriate behavior. The mother is an obvious source of early learning experience, but experimental data on rhesus monkeys suggest that the mother is not a completely sufficient source (Goy, Wallen and Goldfoot, 1974; Wallen, Goldfoot and Goy, 1981; Bercovitch, Roy, Sladky and Goy, 1988). A study was conducted on immature wild mountain gorillas to determine the source(s) of early social experience in this species. Since the mother is always present during early development in the wild, and since other infant primates reared by the mother alone develop some degree of social facility, it was assumed that the mother provided a major portion of the experience required for learning social behavior. It was further assumed that the significance of various other age/sex classes of gorillas to the acquisition of social competence was directly related to the percentage of time the immature animals spent in contact and proximity with those classes. The data from rest and travel/feed periods were analyzed separately because the pattern and frequency of social interactions can vary considerably between these times (Harcourt, 1978). Although the study was conducted some time ago and other aspects published (Nadler, 1986, 1989), the data in this paper have never been presented before.

METHODS

Study Area

The study was conducted during a 5-month period (July–December 1981) at the Karisoke Research Center, Rwanda. The study area included Mt. Visoke and adjacent areas of the Virunga Volcanoes at approximately 1° south latitude, 30° east longitude, between altitudes of approximately 3000 and 4000 m (Fossey, 1974; Fossey and Harcourt, 1977; Watts, 1984). The dense vegetation limited visibility to approximately 5 m in most undisturbed areas.

Subjects

The subjects were 9 immature mountain gorillas ranging in age from 0.2–3.3 years. The ages of the subjects at the midpoint of the study were calculated from birth dates in the long-term records of the Center, obtained primarily by Dian Fossey (1983). Age and sex were confounded in this study; the 4 older animals were male, the 5 younger female. Three of the subjects were members of Group 5

and 6 were members of Nunkie's group, as previously described in other publications of the Karisoke Research Center. The classification of the gorillas as infant, juvenile, subadult, etc. by age follows Harcourt, Stewart and Fossey (1981). Each group consisted of 14 individuals. There were two silverbacked males in Group 5 and one in Nunkie's group. Group 5 contained, in addition, 3 parous adult females, 1 nulliparous adult female, 1 blackbacked male (8–11 years), 1 subadult male (6–8 years), three juveniles (3–6 years) and 3 infants (less than 3 years). Nunkie's group contained 6 parous adult females, 1 nulliparous adult female, 1 juvenile and 5 infants. Not all age/sex classes were represented in either group, therefore, and there were no subadult females in either group.

Data Collection and Analysis

The data were collected as 15 min focal animal samples with 4 group scans at 5 min intervals during each focal animal sample (Altman, 1974). During the group scans, all animals within 2 m and 5 m of the focal animal were noted. There were 98 hr of observation (2.0–6.3 hr/day) collected during 26 days for Group 5 and 122 hr of observation (0.7–6.3 hr/day) collected during 30 days for Nunkie's group. Approximately half of the focal samples for each immature animal were obtained during rest periods and half during travel/feed periods. The two activity periods were defined by the activity of the majority of the animals in the group that could be observed. Social contact scores were defined as the percentage of observation time the immature gorillas were in physical contact with another gorilla. Proximity scores were defined as the percentage of observations at 5 min intervals that the immature gorillas were less than 2 m from another gorilla. The group data are presented as mean and standard error of the mean. T-tests were used to test the statistical significance of the difference between means, and correlation coefficients were calculated to test the significance of linear associations between the behavioral data and the age of the immature animals. Unless otherwise noted, two-tailed tests of significance were used.

RESULTS

Social contact with others

There was a significant difference between the rest (80.3 ± 5.9) and travel/feed (46.3 ± 8.9) periods in the social contact scores of the immature animals, i.e., the percentage of observation time that the immature animals of different age spent in contact with other members of the group. The social contact scores were lower during feeding than during rest periods ($t = 4.5$, $df = 8$, $p = 0.002$). There was no significant correlation between the age of the immature animals and the percentage of time they spent in social contact during the rest periods, but there was decreased social contact with age during feeding ($r = -0.85$, $df = 7$, $p < 0.01$).

Figure 1 presents the relationship between the contact

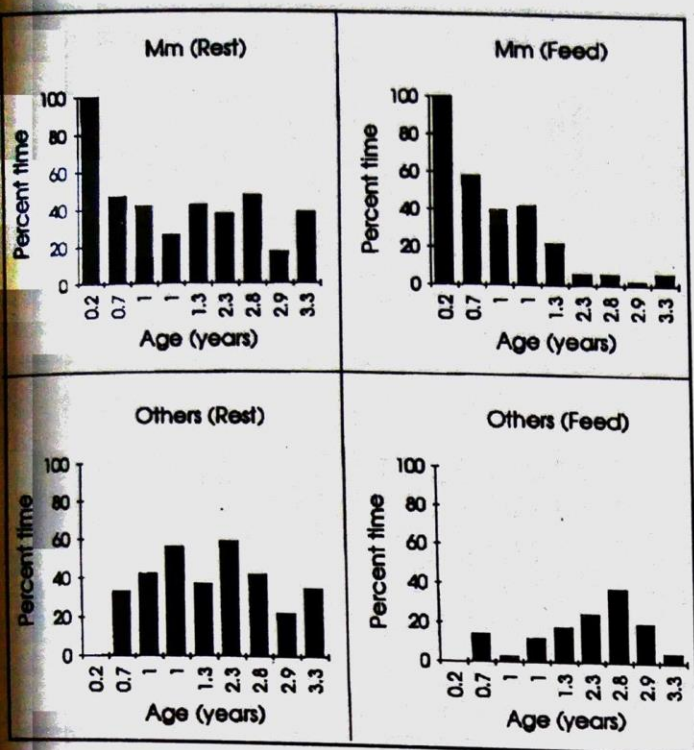


FIGURE 1. The percentage of observation time immature gorillas of different age spent in contact with the mother (Mm) and all other members of the group (Others) during rest (Rest) and travel/feed (Feed) periods.

score with the mother and the sum of the contact scores for all of the other age/sex classes. There was an inverse relationship between the percentage of time spent in contact with the mother and with the other age/sex classes during both the rest ($r = -0.66$, $df = 7$, $p < 0.05$, one-tailed) and feeding ($r = -0.63$, $df = 7$, $p < 0.05$, one-tailed) periods. Figure 2 summarizes the data on the percentage of time the immature animals spent in contact with each of the age/sex classes during rest periods. All of the immature animals spent the greatest percentage of social contact time with the mother (44.0 ± 7.7), little time with other adult females (2.9 ± 1.3), blackbacked and subadult males (3.7 ± 1.3) and silverbacked males (5.3 ± 2.2), but more time with juvenile and infant males (14.0 ± 3.3) and females (12.3 ± 3.2). Figure 3 summarizes the comparable data on social contact time during feeding periods. On average, the greatest percentage of time was spent in contact with the mother (31 ± 10.9), little with other adult females (0.3 ± 0.2), blackbacked and subadult males (1.7 ± 1.2) and silverbacked males (0.2 ± 0.2), and more time with juvenile and infant males (9.0 ± 2.1) and females (4.7 ± 2.0). The younger immature animals (0.2–1.3 years) spent the greatest percentage of time in contact with the mother, but the older ones (2.3–3.3 years) spent the greatest percentage of time in contact with juvenile and infant animals (Figure 4).

Proximity with others

There was a significant difference between the data on the proximity of the immature animals with all other animals during the rest (54.1 ± 5.1) and feeding (26.9 ± 2.2) periods. Since the sum of the proximity scores exceeded

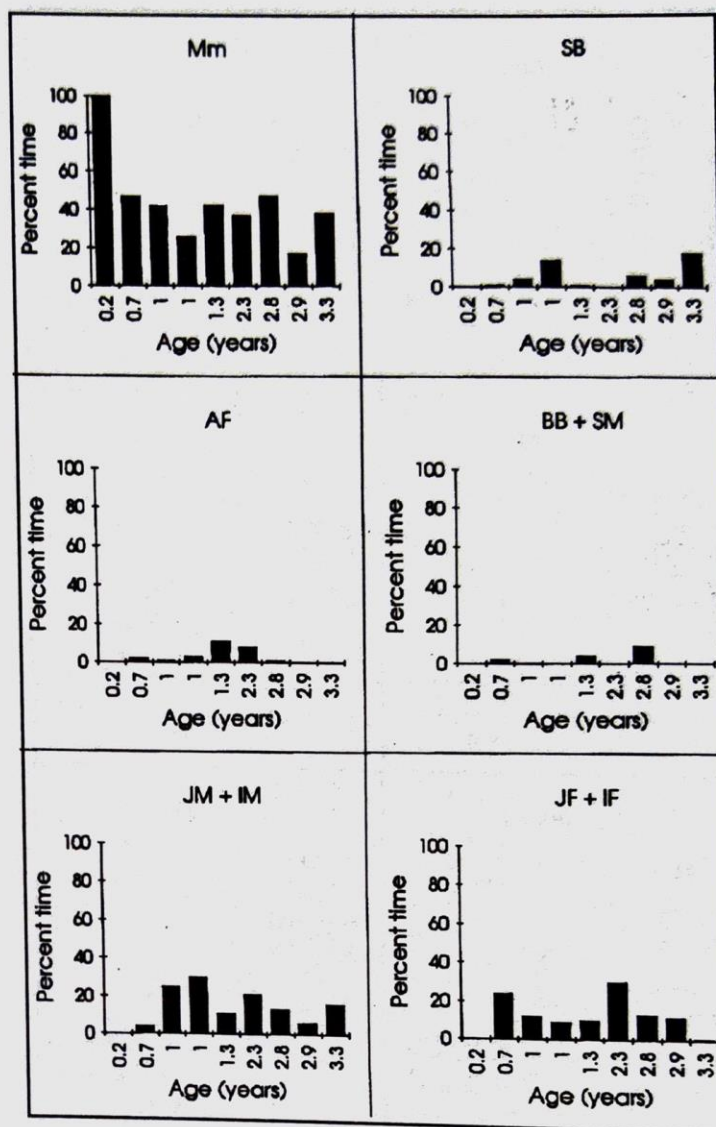


FIGURE 2. The percentage of observation time immature gorillas of different age spent in contact with animals of different age/sex classes during rest periods. Mm = mother, SB = silverback, AF = adult female, BB + SM = blackbacked male and subadult male, JM + IM = juvenile male and infant male, JF + IF = juvenile female and infant female.

100% for most of the animals, the mean proximity score was used in this analysis. All the immature animals had smaller mean proximity scores during the feeding periods ($t = 6.9$, $df = 8$, $p = 0.00$). Figure 5 presents the relationship between the proximity score with the mother and sum of the proximity scores with all the other age/sex classes. Where the sums of the proximity scores exceeded 100%, they were rounded down to 100%. There was an inverse relationship between age and proximity with the mother during both rest ($r = -0.69$, $df = 7$, $p < 0.05$) and feeding periods ($r = -0.96$, $df = 7$, $p < 0.001$), but it was most pronounced during the latter. The immature animals were always in proximity to some other animal during rest and, for 6 of the 9 animals, also during feeding. Figure 6 presents the proximity scores of the immature animals during rest periods. There was no differential relationship to age/sex class or to the age of the immature animals. Figure 7 presents the proximity scores of the immature animals during feeding periods. In addition to the

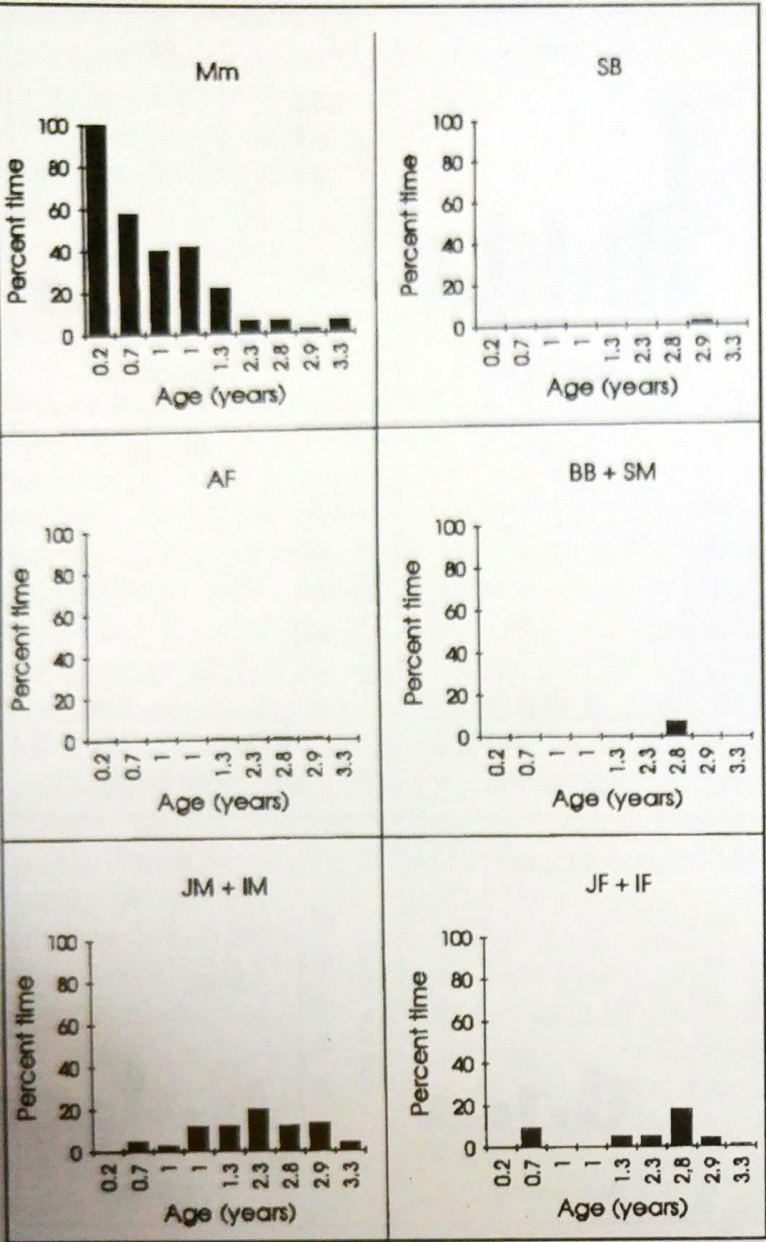


FIGURE 3. The percentage of observation time immature gorillas of different age spent in contact with animals of different age/sex classes during travel/feed periods. Same abbreviations as Figure 2.



FIGURE 4. The mother of a 1.3-year-old female infant watches a play-bout initiated with her infant by a 2.8-year-old male infant.

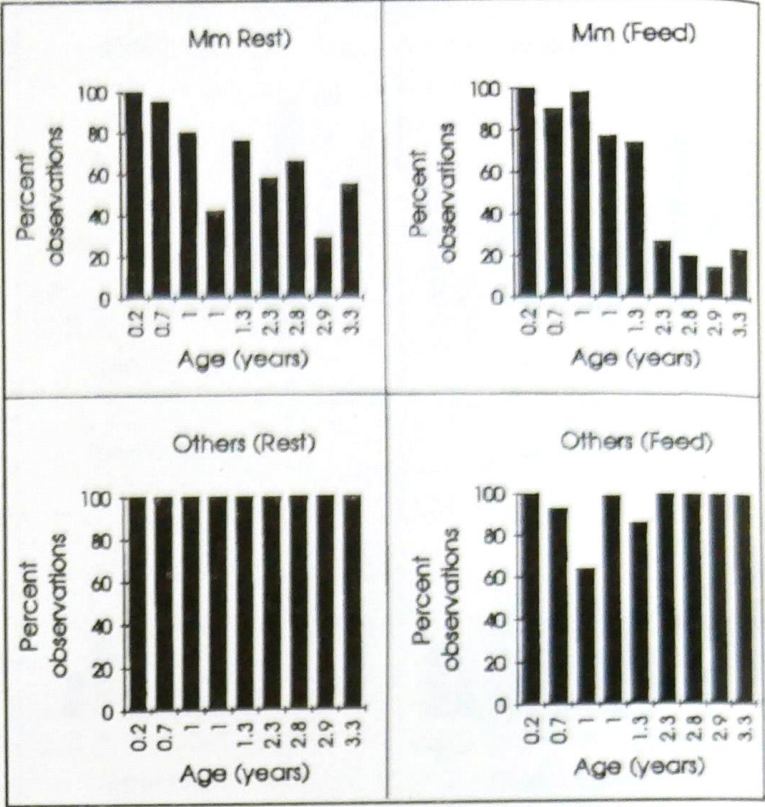


FIGURE 5. The percentage of instantaneous observations at 5 min intervals that immature gorillas of different age were in proximity with the mother (Mm) and all other members of the group (Others) during rest (Rest) and travel/feed (Feed) periods.

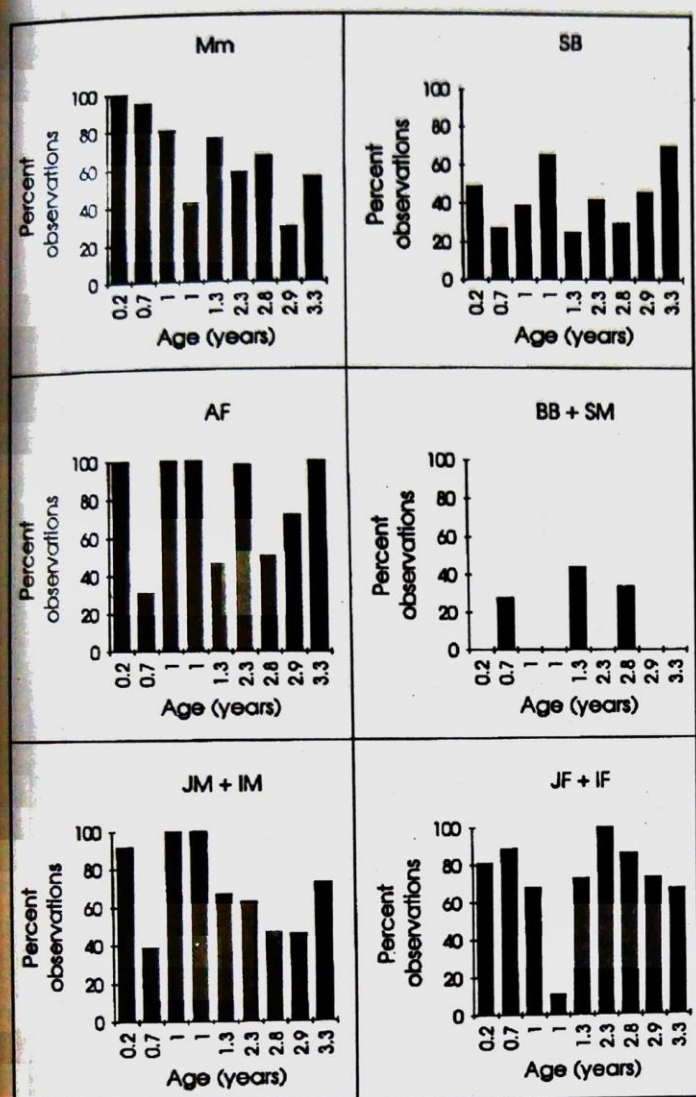


FIGURE 6. The percentage of instantaneous observations at 5 min intervals that immature gorillas of different age were in proximity to animals of different age/sex classes during rest periods. Same abbreviations as Figure 2.

negative correlation between age and proximity to the mother noted above, there was a positive correlation between age and proximity to the silverbacks ($r = 0.63$, $df = 7$, $p < 0.05$). The proximity scores with the mother, moreover, were inversely related to the proximity scores with the silverbacks ($r = -0.70$, $df = 7$, $p < 0.05$). The lesser the percentage of observations in proximity with the mother, the greater the percentage in proximity with the silverbacks.

DISCUSSION

Gorilla groups are closely associated spatially during rest periods, whereas they are relatively dispersed during travel/feed periods (Schaller, 1963; Harcourt, 1978; Fossey, 1983). As anticipated, contact and proximity of the immature animals with others were greater during rest than during feeding. The difference was greatest for the older immature animals (over 2 years of age) because of the age-related decline in social contact scores during the feed-

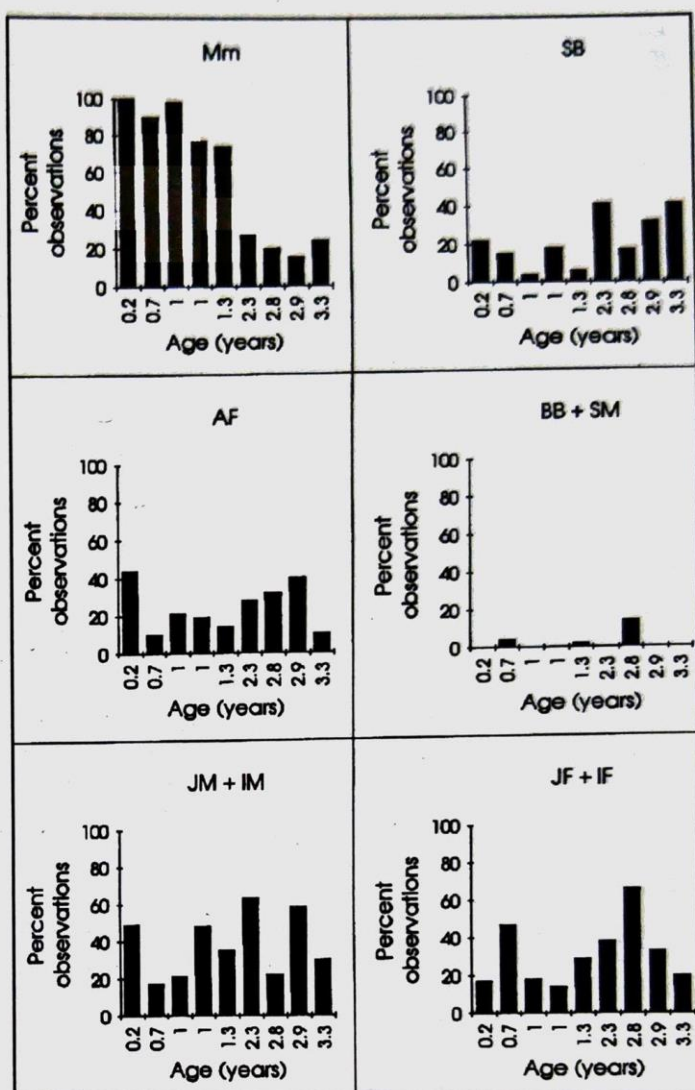


FIGURE 7. The percentage of instantaneous observations at 5 min intervals that immature gorillas of different age were in proximity to animals of different age/sex classes during travel/feed periods. Same abbreviations as Figure 2.

ing periods. The older immature animals had begun feeding on their own. This result suggests that the opportunities for social learning by immature mountain gorillas of this age range, essentially infants, are greater during rest periods than during feeding periods.

Clearly, the most significant social influence on the young gorilla is its mother (Schaller, 1963; Fossey, 1979; Hoff, Nadler and Maple, 1981a). Contact and proximity of the immature animals with the mother, however, declined with age; the decline was most pronounced during feeding periods (Figures 1 and 5). During feeding, the older immature animals spent less time in contact with the mother and less time in proximity to the mother than the younger ones. This difference apparently reflects the greater development of independence from the mother by the older immature animals. Although all these older immature animals were males, the difference in independence is more likely related to age than to sex (Fossey, 1979; Hoff, et al., 1981a, b). These results suggest that maternal interaction has its greatest influence during the first year or so of life, after which the immature gorilla begins to



FIGURE 8. A 3.3-year-old juvenile male gorilla associates closely with the silverback while its mother (in estrus) watches a short distance away (right).

associate with and, presumably, to learn social skills from, animals other than the mother.

The opportunities for social learning by immature animals from animals of different age/sex classes varied as a function of the particular measure of association which was used and the activity period which was selected, in addition to the age of the infant. The data on social contacts during rest periods indicate that the most common extra-maternal conspecifics with which the immature gorillas interacted were juveniles and other infants (*Figure 2*). This finding is consistent with other data on wild (Schaller, 1963; Fossey, 1979) and captive (Hoff, et al., 1981b) infant gorillas. This result, therefore, supports the hypothesis that immature gorillas learn primarily basic social skills during this early period of development rather than specific skills.

The data on proximity of the immature animals to others suggest that the silverbacked males also contributed to the social development of these animals, consistent with previous observations (Schaller, 1963; Fossey, 1979). There was little evidence of the silverbacks' contribution when only the data on contact were examined, or when only the data on proximity during rest periods were considered. The finding of an inverse relationship between proximity with the mother and with the silverbacks during *feeding periods*, however, is consistent with, and supports, prior data (Harcourt, 1978, *Figure 6*). That it was

the older immature gorillas which maintained greater proximity to the silverbacks also supports the earlier findings. Harcourt, for example, failed to find this relationship during the first year of his study, but did so during the second year when the same animals were one year older.

The relationship of the immature animals to the silverbacks may have been underestimated in the current study, because whenever adult females were in estrus data collection was focused on the mating pairs (Nadler, 1989). Observation of the mating pairs revealed that immature animals were especially attracted to the silverbacks during such times (*Figures 8 and 9*; also see Hess, 1973; Fossey, 1979; Nadler, 1986). Those observations were not included in the data analyses because they were not recorded as focal animal data. Those observations, however, were interesting for yet another reason. There was no indication that the infants paid attention to the mating behavior *per se*. They congregated around the silverback, they established contact with the silverback, but they did not attempt to interfere with the mating or to direct their attention toward it in any way that was apparent to the author. The infant that was observed most in contact with the silverback was the offspring of an estrus female. Other infants generally joined that infant, but the only activity in which they were observed to engage was play with each other.



FIGURE 9. Two immature gorillas associate closely with the silverback during copulation. The 3.3-year-old male in contact with the silverback is the offspring of the estrus female.

The present results support earlier proposals regarding the social interactions of immature wild mountain gorillas, primarily those of Fossey (1979). The most important social interactions of infants, based on the percentage of time in contact with and proximity to others, were the mother, other immature gorillas and the silverbacks. The social nexus of the infants changes as the infant matures, becoming "gradually more complex, in that it involved more interactions with a wider range of individuals..." (Fossey, 1979, p. 184). It is apparent that the present results reflect the complex interactions of numerous factors, one of the most significant being the composition of the group. The presence of siblings, the number and proportion of animals of various age/sex classes and the kinship of the mother to others in the group are only a few of the variables that influence the range of opportunities for social interaction of immature gorillas. The absence of any subadult females in the present study is relevant, since this age/sex class was reported to interact frequently with immature animals in a sexual context (Watts, 1990). The data are consistent in most respects with other data on wild and captive gorillas, however, suggesting that the relationships presented here between infants and other age/sex classes of gorillas reflect, in general, the pattern of social interactions that is typical of the species.

Most of the gorillas in the world's zoos are western lowland gorillas (*Gorilla gorilla gorilla*) (Nadler, 1975). The wild-born animals that constitute the original zoo population were all captured at a young age, most likely during infancy. If their opportunities for early learning were comparable to those of the infant mountain gorillas in this study, then it is unlikely that they learned specific patterns of behavior, such as sexual and maternal behavior, prior to being captured. That they learned these specific forms of behavior in the absence of experienced adults suggests that they learned specific skills closer to the age at which those skills were required. It was proposed, for example, that captive chimpanzees (Rogers and Davenport, 1970) and lowland gorillas (Nadler, 1974) learn maternal behavior following the birth of their first infant in a manner which is consistent with a drive reduction theory of learning. Experience during infancy appears to prepare the animal for social interaction with conspecifics, perhaps by reducing the fear of, and/or aggression towards, unfamiliar others.

All but one of the immature mountain gorillas in this study were infants; the data, therefore, reflect the earliest opportunities for socialization and learning. Learning at this early stage of development applies to the acquisition of basic, relatively simple social skills, the rudiments of species-typical social behavior acquired through interactions with the mother and other infants. While such

limited experience under special circumstances is itself apparently sufficient to prepare the infant for learning more complex skills as an adult, there are numerous additional opportunities for learning life's important lessons when the animal matures in its natal group. Further research on young mountain gorillas at later stages of immaturity should reveal further development of more complex and specific skills acquired through practice and further interaction with other members of the social group.

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