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Article *in* International Journal of Primatology · February 1997

DOI: 10.1023/A:1026384922066

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International Journal of Primatology, Vol. 18, No. 1, 1997

Context and Development of Sexual Behavior of Wild Bonobos (*Pan paniscus*) at Wamba, Zaire

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Received February 19, 1996; accepted May 26, 1996

*I studied sexual behavior of immature bonobos (*Pan paniscus*) in a wild group living at Wamba, Zaire, with special reference to its development. Even immature individuals under 1 year old performed sexual behavior. Sexual behavior occurred in almost all age–sex combinations, except between immature and mature females. Based on analyses of behavioral pattern and context, I classified sexual behavior involving immature individuals into three categories. (1) Genital contact between immature individuals was observed during play, and was performed by males more frequently than by females. This sexual behavior shared many traits with that of other great apes. (2) Copulation-like genital contact was observed between immature males and mature females. Its frequency increased with the immature male's age; it developed into copulation in adulthood. (3) Genital contact used to regulate interindividual relationships. This behavior, which is unique to bonobos, was absent among infants. It developed between late juvenile and early adolescent periods in association with changes in social circumstances.*

KEY WORDS: *Pan paniscus*; development; sexual behavior; genital contact; social behavior.

INTRODUCTION

Studies of bonobos (*Pan paniscus*) spanning more than 20 years have revealed various unique aspects of their sexual behavior. One of the most conspicuous features is that the receptive state of female bonobos is greatly extended to include periods with no ovulation. The total proportion of all days on which adult female bonobos are receptive is much more than that of their closest relative, the chimpanzee (*Pan troglodytes*), in which females

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0164-0291/97/0200-0001$12.50/0

are receptive only during limited periods (Furuichi, 1987, 1992; Kano, 1989, 1992; Wrangham, 1993). This prolonged receptive state seems to moderate intermale sexual competition and, thus, has a great influence on social relationships both within and between groups (Idani, 1990; Kano, 1992; Furuichi, 1992).

Bonobos also use sexual behaviors to regulate social relationships between individuals. While chimpanzees have developed many kinds of nonsexual greeting behaviors — pant-grunt, kissing, and embracing — bonobos have employed behaviors involving genital contact for regulating social relationships between individuals of the same or different sexes (de Waal, 1987; Kano, 1992; Wrangham, 1993; Furuichi and Ihobe, 1995). For example, they use noncopulatory mounting, genito-genital (GG) rubbing, and rump–rump contact for the formation or maintenance of intimate interindividual relationships, tension regulation, and reconciliation (Kano, 1980, 1992; Kuroda, 1980; Thompson-Handler *et al.,* 1984; Furuichi, 1987; Kitamura, 1989). Such sexual behaviors probably contribute to the maintenance of a close aggregation of group members and to narrowing status gaps between males and females, both of which are traits unique to bonobos among the great apes (Kuroda, 1980; Kitamura, 1983; White, 1988; Furuichi, 1989; Kano, 1992).

Another unique aspect of bonobo sexual behavior is that it occurs in most age–sex combinations, including immature individuals (Kitamura, 1989; de Waal, 1990; Enomoto, 1990; Kano, 1992). Most studies of sexual behaviors of bonobos have focused on adult behaviors, and there has been no detailed description or discussion of the development of bonobo sexual behaviors.

Concerning the sexual behaviors of immature bonobos, there are two major questions. The first concerns the developmental process of reproductive and social aspects of sexual behaviors. Do these two aspects develop separately from the outset of their appearance, or are they differentiated at a later stage of development? The second concerns the differences in sexual behavior of immature individuals between bonobos and other great apes. While adult bonobos use sexual behaviors in various social contexts, adult chimpanzees and gorillas rarely use sexual behaviors in such ways. It is important to establish how and when such differences appear in the course of development. Answering these questions may give valuable hints for understanding the social development of immature bonobos and the evolution of their unique sexuality.

I observed sexual behaviors of immature bonobos in the wild, with special regard to their behavioral patterns, the age and sex of partners, and the situations in which they occurred. Based on these data, I classify sexual behaviors of immature individuals into three major categories: (1) play-like genital contact, (2) copulation-like genital contact, and (3) genital contact in social contexts. I will discuss the developmental process of each category and its relationship to adult sexual behaviors.

Table I. Age-Sex Composition of E1 Group

	Age class	Age (years)	Number of males	Number of females
Immature	Infant-I	< 2	3	1
	Infant-II	2 < 4	2	1
	Juvenile-I	4 < 6	2	2
	Juvenile-II	6 < 8	0	1
Mature	Adolescent	8 < 15	2	0
	Adult	≥ 15	7	9

MATERIALS AND METHODS

Study Group and Observation

The study subjects were members of a wild group of bonobos — E1 — living at Wamba, Republic of Zaire (Kano, 1982, 1992; Kitamura, 1983; Furuichi, 1989). E-group had been studied since 1974 and artificially provisioned with sugar cane since 1976. E-group split into groups E1 and E2 in 1982–1983. During dry seasons, E1 visited artificial feeding sites and stayed there for a few hours per day.

I call individuals that are 4 to 7 years old juvenile, because they are already weaned and much more independent of their mother than those <4 years old (Table I). This timing of weaning meets the average interbirth interval of 4.5 years (Furuichi *et al.,* 1995).

Bonobos form male-philopatric groups (Furuichi, 1989; Kano, 1992; Hashimoto *et al.,* 1996). Females transfer to nonnatal groups when they are around 8 years old. Therefore, I call individuals ≥8 years old adolescent, though there is no such drastic change separating juvenile and adolescent periods for males. Most researchers have defined adults as individuals ≥15 years old (Kuroda, 1979, 1989; Furuichi, 1989; Kano, 1992), and I accept this definition. However, adulthood might begin earlier: one male in the study group became the alpha when he was 13 years old, and one female in the study group first gave birth when she was about 14 years old.

I divide infant and juvenile classes into two subclasses, each 2 years in length (Table I). Immature describes individuals of all four of these age classes, while mature includes adolescent and adult individuals.

During the study period, between November 1990 and February 1991, E1 consisted of 30 individuals, including 7 adult males, 2 adolescent males, 2 juvenile males, 5 infant males, 9 adult females, 3 juvenile females, and 2 infant females (Table I). Except for one adult male that ranged alone throughout the study period, all members of the group were study subjects. All subjects usually ranged as one mixed party (Furuichi, 1989; Kano, 1992; Elsacker, 1995). They definitely split into two distinct parties on only 1 day.

I observed 12 immature individuals of E1 for 500 min each using a focal-animal sampling method. I collected most of the data at artificial feeding sites. Once I began to observe one individual, I followed it for as long as possible. When I lost sight of the focal individual, I chose another visible individual that had been observed for the least amount of time. I recorded all sexual and social behaviors of focal individuals via a tape recorder, and noted behaviors of all individuals staying ≤ 2 m of the focal animal. A series of continuous sexual behaviors is counted as one bout even if the participants changed posture or position during the series.

During the same observation period, Furuichi and I also collected other data on both immature and mature individuals. For all cases of sexual behavior that occurred at feeding sites, we recorded names of participants and type of behavior as far as possible. Owing to high visibility at the feeding sites and the presence of two observers, our data cover most cases of sexual behaviors. Furthermore, for all members of E1 we checked, presence at the feeding sites by scanning observations at 10-min intervals. These observations provide relative frequencies of sexual behaviors of all members, which were originally used in Hashimoto and Furuichi (1994). To examine developmental changes from immature to mature stages, I reanalyzed these data by grouping individuals into age classes.

Definition of Categories of Behaviors

Sexual behavior includes all types of interindividual interactions in which there was contact between the genitals of participants. Sexual behaviors are subdivided into two categories: copulation and genital contact.

Copulation is mounting with insertion of the penis and ejaculation between a mature male and female. When insertion or ejaculation was not confirmed, but interactions involving normal soliciting behaviors for copulation (Mori, 1984; Kano, 1989; Kitamura, 1989) and thrusting movements were observed, we recorded them as copulations.

Genital contacts between mature individuals included noncopulatory mounting, GG rubbing, and rump–rump contact (Kuroda, 1980; Mori, 1984; Thompson-Handler *et al.,* 1984; Furuichi, 1987, 1992; Kitamura, 1989; Kano, 1989, 1992). Mounting between mature males and females was included in noncopulatory mounting if it lacked one or more behavioral categories including penile erection, insertion, or thrusting movements.

All the sexual behaviors involving immature individuals are classified as genital contact, rather than copulation, even if immature males performed copulation-like behavior with mature females.

Play behavior, which is mentioned in the analysis of play-like genital contact, includes only that involving two or more immature individuals. All the recorded cases consist of wrestling, chasing, carrying, or a combination of these activities. Carrying is a common type of play between immature individuals of different ages, in which the elder carries the younger for a short distance with no apparent destination.

RESULTS

Bonobos in E1 began to show behaviors involving genital contact at <1 year of age. Immature individuals performed genital contact with individuals of all age–sex classes, except that no genital contact occurred between immature and mature females (Table II).

Genital Contact Between Immature Individuals

Genital contact between immature individuals occurred in 43 cases (Table II). The number of cases involving focal animals divided by the total observation time gives a frequency of genital contact between immature individuals of 0.37 time per h (Table III).

Of the 41 cases for which the context was recorded in detail, 32 cases occurred during play. Between individuals of the same age class, genital contact tended to be performed in play with a symmetrical posture, i.e., hugging each other ventroventrally while hanging from branches or lying on the ground or fallen trees. Most cases of genital contact between immature individuals of different ages, however, occurred in less symmetrical play, when the older individuals carried the younger on their bellies while standing or walking.

Table II. Types of Genital Contact of Immature Individuals[a]

Subject individual			With immature individuals				With mature males				With mature females			
				Ventrodorsal				Ventrodorsal				Ventrodorsal		
Age–class	Sex	Number of individuals	Ventroventral	Mounting	Being mounted	Others[b]	Ventroventral	Mounting	Being mounted	Others[b]	Ventroventral	Mounting	Being mounted	Others[b]
Infant-I	Male	3	25				1				10			
	Female	1	3											
Infant-II	Male	2	14	1 (1)[c]	2 (1)	1	3				9	7		1
	Female	1	7				1		1 (1)					
Juvenile-I	Male	2	14	5		1			3	1	15	26 (8)		3
	Female	2	8		2				1 (1)					
Juvenile-II	Female	1	1		2				7	1				

[a] One case of genital contact between immature individuals was counted as two cases in the column "With immature individuals."
[b] Includes cases in which a juvenile brought its genitals into contact with those of another individual which was in sexual interaction with a third individual and cases in which a juvenile presented but was ignored.
[c] Figures in parentheses show cases in which both ventrodorsal and ventroventral genital contact behaviors occurred continuously in one sequence.

Table III. Frequency of Genital Contact Behavior of Immature Individuals[a]

Focal animal	Total observation time of focal animals (min)	Age-sex of partner		
		Immature individuals	Mature males	Mature females
Males (n = 7)	3500	25 (0.43)[b]	8 (0.14)	23 (0.39)
Females (n = 5)	2500	12 (0.29)	9 (0.22)	0 (0)
Both sexes (n = 12)	6000	37 (0.37)	17 (0.17)	23 (0.23)

[a] To obtain frequency per unit time, only cases of genital contact which involved focal animals were dealt with in this analysis.
[b] Figures show number of cases, and figures in parentheses show frequency per hour.

There is a sexual difference in the frequency of genital contact between immature individuals (Fig. 1a). Males performed genital contact more frequently than females did (Mann–Whitney U test, $n_1 = 7, n_2 = 5, U = 3, p < 0.05$). In the different sex combinations, male–male dyads performed genital contact more frequently than male–female dyads did ($n_1 = 21, n_2 = 35, U = 229, p < 0.01$) and more frequently than female–female dyads did ($n_1 = 21, n_2 = 10, U = 44.5, p < 0.01$). However, there is no significant difference between male–female and female–female dyads ($n_1 = 35, n_2 = 10, U = 147.5, p = 0.45$). These sexual differences may reflect the tendency for immature males to engage in play more frequently than immature females do (Fig. 2). The proportion of time spent playing is higher for males than for females in each age class, though the sample size is too small to test for statistical significance.

With regard to kin relations, genital contact occurred more frequently between sibs than between nonsibs (Mann–Whitney U test, $n_1 = 62, n_2 = 4, U = 22.5, p < 0.01$), probably because immature individuals usually stayed with their mothers and therefore had more opportunities to play with their sibs.

As for the posture of genital contact, individuals of the infant-I stage engaged only in ventroventral genital contact (Table II). Ventrodorsal genital contact appeared in the infant-II stage, after which the proportion of ventrodorsal type increased with age. Males mounted others or were mounted by others ventrodorsally, but females never mounted other individuals.

Genital Contact Between Immature Individuals and Mature Males

Genital contact between immature individuals and mature males occurred in 19 cases (Table II) or 0.17 time per h (Table III), which is less than for other age–sex combinations. Although one juvenile-II female showed a very high frequency of genital contact with males, there was no significant difference between the frequencies for immature males and immature females (Fig. 1b; $n_1 = 7, n_2 = 5, U = 16.0, p = 0.81$).

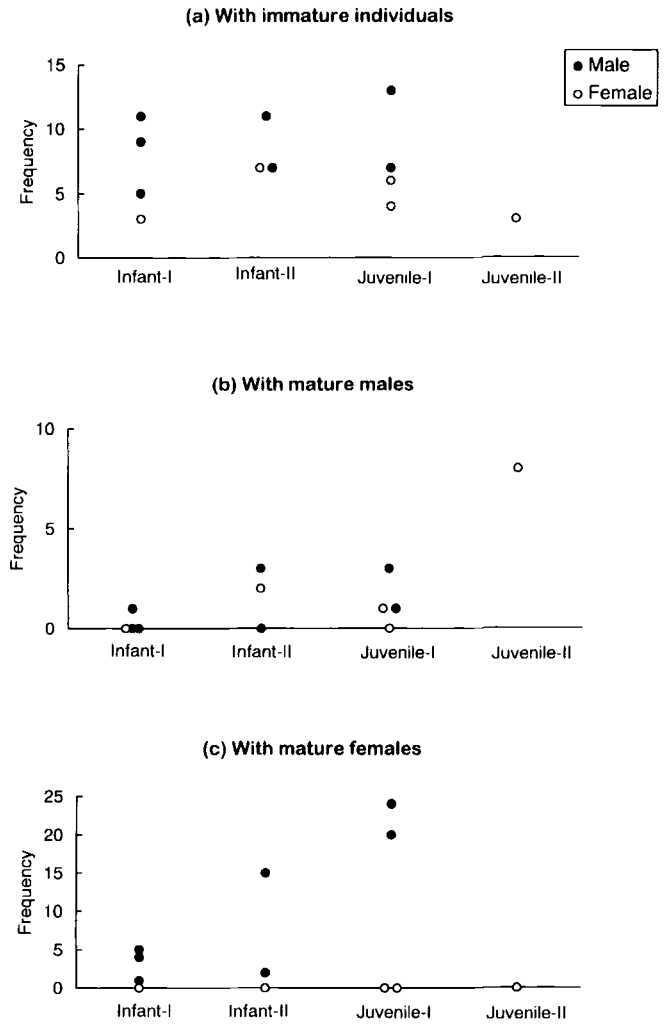

Fig. 1. Frequency of genital contact of immature individuals with (a) other immature individuals, (b) mature males, and (c) mature females.

The type of genital contact between immature individuals and mature males changed with age. In five of six cases involving infants, mature males held infants ventroventrally, and rocked them so that their genitals rubbed together (Table II). This is a unique behavior of bonobos that occurs most frequently between mature males and infants as a part of play. This type of genital contact was absent between mature males and juveniles.

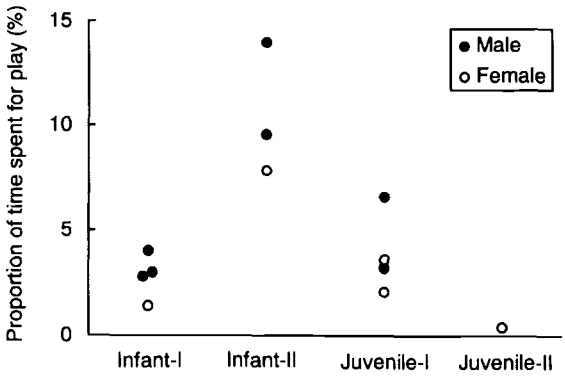

Fig. 2. Proportion of time spent in play by immature individuals. Only the data for focal animals were used for this analysis. Proportion is given as the time spent in play divided by the total time of focal-animal sampling for each individual.

Most genital contacts between juveniles and mature males (10 of 13 cases) occurred during agonistic interactions, or when party members were excited at the beginning of the feeding phase. Such genital contact was performed in the same context as noncopulatory mounting and rump–rump contact, which were performed by mature males apparently to reduce tension. For example, when immature males or females were threatened by a mature male, they presented toward him and he mounted them. However, there was no case in which juvenile males spontaneously attempted to have social interactions involving genital contact with mature males.

One juvenile-II female frequently performed genital contact with adult males (Fig. 1b), all of which were noncopulatory mountings. Although there was no juvenile-II male in E1 during this study period, during other studies I observed that a juvenile-II male performed genital contact more frequently than juvenile-I males did.

Genital Contact Between Immature Individuals and Mature Females

There is a marked sexual difference in genital contact between immature individuals and mature females. Immature males frequently performed genital contact with mature females (71 cases in total, 0.39 time per h; Tables II and III). The frequency increased with the age of the male (Fig. 1c). Contrarily, no genital contact occurred between immature females and mature females during focal-animal sampling. During scan sampling I observed it once (Fig. 4b).

Table IV. Swelling Phase of Mature Females and Frequency of Genital Contact Between Immature Males and Mature Females

Swelling phase of mature females	Number of female-days	Frequency of genital contact between immature males and mature females*	
		Observed	Expected
No swelling	130	3	21.2
Swelling	70	6	11.4
Maximal swelling	155	49	25.3

*$\chi^2 = 40.4$, df = 2, $p < .0.0001$.

In all genital contacts involving infant-I males, mothers held the infant ventrally and rubbed them against their genitals (Table II). This type of behavior appeared to be used by mothers to reduce their own tension. Eight of nine cases for which the context was recorded occurred when mothers seemed to be stressed: for example, just after they appeared at a feeding site (three cases) and when their solicitations for sexual behavior were ignored (two cases).

Genital contact involving infant-II or older males was spontaneous behavior by the immature males. The most frequent pattern was that an immature male approached a female that was copulating or having other genital contact with mature individuals, and performed genital contact with her following that sexual act (16 of 61 cases). Other cases were observed in a large variety of contexts without any prominent pattern.

This category of genital contact of immature males is similar to copulatory behavior between mature males and females. In most cases, immature males showed sexual arousal, with their penes erect. Furthermore, genital contact between immature males and mature females involved females with maximal swelling significantly more frequently than females in other swelling phases (Table IV). This was probably either because immature males selected females with maximal swelling, just as mature males do, or because they frequently had genital contact with mature females that had just finished copulation.

In spite of the high frequency of genital contact with mature females, infant-II or older males were rarely involved in such behavior with their own mothers. Only 2 of the 61 cases involved mother and son. This frequency is significantly lower than expected by chance (binomial test, $n = 61$, $p = 0.11$, $p < 0.01$). This tendency is similar to incest avoidance in copulation between mature individuals (Kano, 1992).

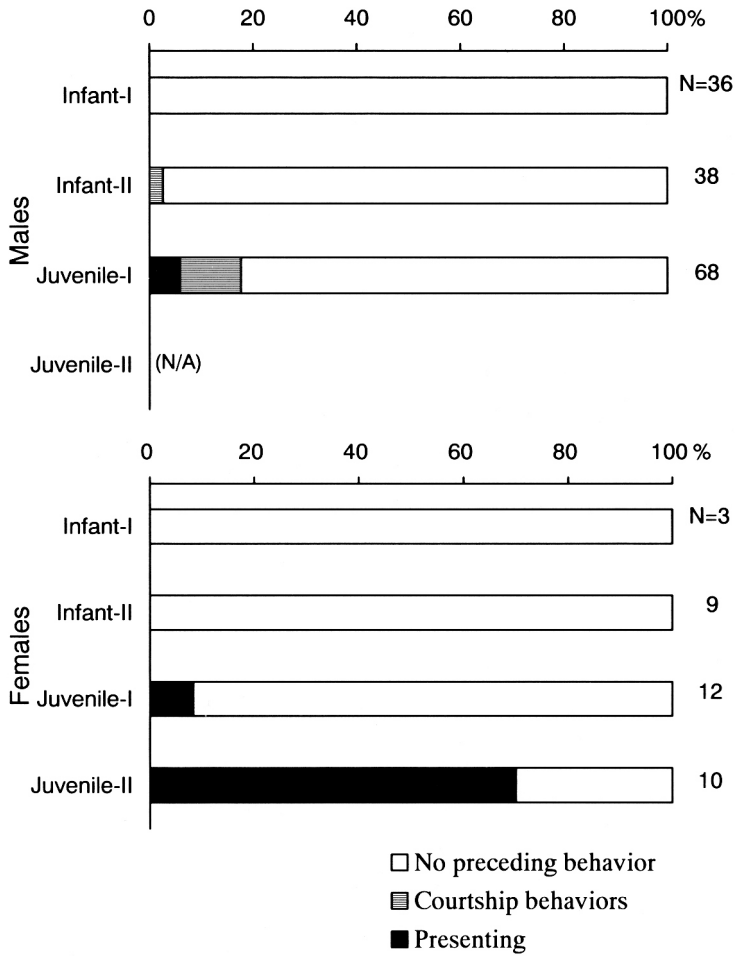

Fig. 3. Proportion of genital contacts of immature individuals that accompanied presenting, courtship behaviors, and no preceding behavior. Figures at the right of each bar show the total number of genital contacts for each age–sex class. N/A, not applicable. There was no individual in this age–sex class.

Age-Related Change of Sexual Behavior

Most cases of copulation and genital contact between mature individuals were preceded by courtship behaviors — bipedal standing, stretching hand, swaying back, displaying penile erection — or presenting

behavior (Mori, 1984) or both. By contrast, most genital contacts involving infants occurred without any such behavior (Fig. 3). For males, both courtship behaviors and presenting were performed initially by infant-II and increased in juvenile-I (between infant-II and juvenile-I, corrected χ^2 test, $V^2 = 5.06$, df = 1, $p < 0.05$). For females, presenting began in juvenile-I and became frequent in juvenile-II (between juvenile-I and juvenile-II, Fisher's exact test, $p = 0.01$, two-tailed). As these preliminary behaviors were included, genital contacts of immature individuals came to resemble typical sexual behavior patterns of mature individuals.

Figure 4a shows age-related changes in the frequency of each category of male sexual behavior. The most drastic change during the immature stages is the increase in the frequency of genital contact with mature females. In adolescence, however, the frequency of sexual behavior with mature females — copulation — dropped. Males in this age class received aggressive behaviors consistently from adult males and tended to stay on the periphery of the party. The frequency of copulation increased somewhat when males reached adulthood but did not reach the high frequency of the juvenile-I stage. Contrarily, genital contact with mature males gradually increased until adolescence, then became very frequent in adulthood.

Age-related changes in female sexual behavior are shown in Fig. 4b. Compared with immature males, immature females up to juvenile-I showed much lower frequencies of sexual behavior because immature females have a lower frequency of genital contact with immature individuals and because they did not develop copulation-like genital contact with adult males. By contrast, one juvenile-II female showed very frequent genital contacts with mature males. Like adolescent males, she frequently received aggressive behavior from adult males, and she showed presenting behavior that solicited them to perform noncopulatory mounting. This might be because her mother died just before the study period. Without any support from her mother, she had to show appeasement behavior in response to frequent aggression from others.

While immature females rarely had genital contact with mature females, adult females showed frequent genital contact with one another. Although there was no adolescent female, newly immigrated adolescent females tend to show genital contact and copulation more frequently than adult females do (Furuichi, 1989; Idani, 1991). Accordingly, copulatory behavior with mature males and genital contact with mature females rapidly increase between juvenile-II and adolescent periods, when females transfer to other groups.

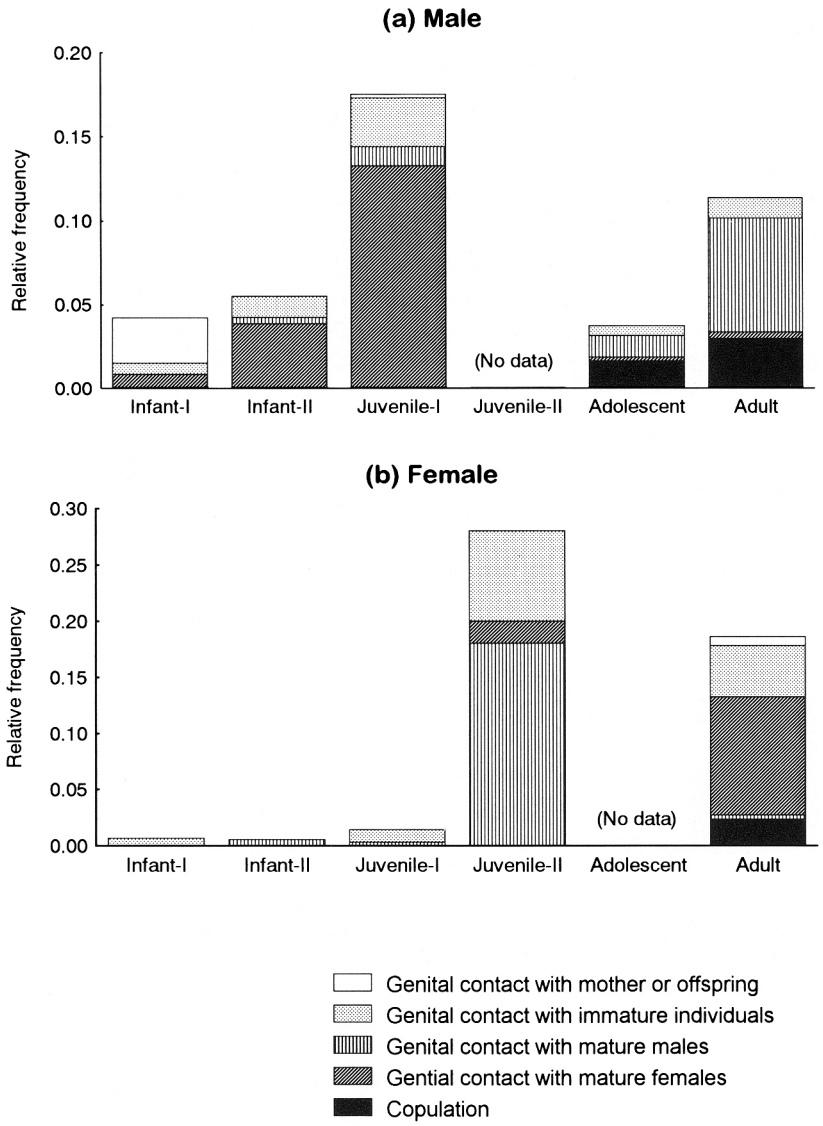

Fig. 4. Age-related change of relative frequencies of copulation and genital contact with individuals of different age–sex classes. Relative frequency is given as the number of cases of sexual behavior divided by the total number of scanning observations in which each individual was present. Values for each age–sex class represent averages for individuals included in the class.

DISCUSSION

Play-like Genital Contact

I observed genital contacts between immature bonobos more frequently than had been reported for other great apes. In Rwandan gorillas (*Gorilla gorilla beringei*), Harcourt *et al.* (1980) observed such behaviors 0.004 time per h, and Nadler (1986) observed them 0.10 time per h. Because these values are for genital contacts in a group, the frequency for one individual must be much lower than the 0.37 time per h per individual that I recorded. For chimpanzees, quantitative data about genital contacts between immature individuals are not available. However, Nishida reported that immature chimpanzees in the Mahale Mountains rarely perform genital contact with each other (personal communication).

By contrast, there are many common traits among these species, regarding the pattern or context of genital contacts between immature individuals. Most genital contacts between immature individuals are performed during the course of play (Goodall, 1968; Tutin and McGinnis, 1981; Plooij, 1984; Nadler, 1986). Genital contacts between mature individuals are mostly performed in tense situations, such as at the beginning of a feeding session, at the end of an agonistic interaction, or when encountering other groups (de Waal, 1987; Kano, 1992; Hashimoto and Furuichi, 1994; Furuichi and Ihobe, 1995). Contrarily, genital contacts between immature individuals are observed in more relaxed situations, such as after settling down at a feeding site or when mature members are resting (Hashimoto and Furuichi, 1994).

The second common trait is that males perform genital contact more frequently than females do (Tutin and McGinnis, 1981; Nadler, 1986). Nadler (1986) suggested that this is because males are involved in play more than females are. Indeed, male bonobos played more frequently than females did, and this seems to be a general tendency of apes and humans [Gorilla (Freeman and Alcock, 1973); Orangutan (Nadler and Braggio, 1974); human (Maccoby, 1966].

Third, there is a common tendency in the posture of genital contact. Adult chimpanzees and gorillas almost exclusively take a ventrodorsal posture in copulation (Harcourt *et al.,* 1981; Nadler, 1986; Hasegawa, 1987). However, genital contact between immature individuals of these species is sometimes performed ventroventrally as well (Goodall, 1968; Nadler, 1986). In bonobos, the ventroventral posture in copulation or genital contact is observed at all stages of life, but it is most common during the earlier immature stages, and more common among adolescents than among adults (Furuichi, 1987; Kano, 1992). Thus the change with age in the proportion

of ventroventral genital contact shows a similar pattern in these three species. It is also a common feature that females rarely mount other individuals, while males serve as both mounter and mountee (Plooij, 1984; Nadler, 1986).

As there appears to be no marked difference other than one of frequency, genital contact between immature individuals may be a common developmental phenomenon among the African apes, as Nadler (1986) suggested.

Copulation-like Genital Contact

Development of genital contact resembling copulation is quite different in males and females. For immature Wamba females, all cases of genital contacts with mature males involved noncopulatory mounting, apparently to reduce tension. Like many other primates, female bonobos begin to show copulatory behaviors after sexual maturity, i.e., after they transfer to nonnatal groups and begin to show swelling of the sexual skin. By contrast, immature males show genital contact with mature females more and more frequently as they grow older, which seems to develop into copulation in adulthood. As immature males prefer females with maximal sexual swelling, and insert their penes in some cases, it is difficult to distinguish such genital contact from copulation between mature individuals (Kitamura, 1989).

Such genital contacts between immature males and mature females occur also in chimpanzees. Although nursing chimpanzee females tend to range alone with their offspring apart from mixed parties, infant males show a strong interest in females and perform genital contact when they encounter estrous females (Hasegawa, 1987). Juvenile males perform genital contact with mature females more frequently than mature males copulate with them (Sugiyama and Koman, 1979; Tutin, 1979; Hasegawa and Hiraiwa-Hasegawa, 1990).

There are two factors that may enable immature males to perform copulation-like genital contact more frequently than mature males perform copulation. First, immature males may attempt "copulation" frequently with short intervals because they do not ejaculate. In wild chimpanzees, noticeable increase in scrotal size and first ejaculation occur between 8 and 10 years (Tutin and McGinnis, 1981; Goodall, 1986). Assuming that bonobos reach sexual maturity at the same age as chimpanzees (Kuroda, 1989) males up to the juvenile-II stage cannot ejaculate. At Wamba, 48.1% of copulation-like genital contacts of immature males were followed by another within 1 h, while only 9.6% of copulations of mature males were followed by another copulation (Furuichi, unpublished data).

Secondly, mature males and females show a high tolerance toward immature male sexual behavior. In both chimpanzees and bonobos, adult females are usually tolerant toward, or even cooperative with, attempts by immature males to perform genital contact with them (Hasegawa, 1987; Kitamura, 1989; Kano, 1992; Wrangham, 1993). Furthermore, in bonobos, immature males are usually with their mothers and are allowed to stay in the central part of the mixed party where all the females usually aggregate (Furuichi, 1987; Kano, 1992; Elsacker, 1995). This provides immature males with frequent opportunities to approach estrous females.

When male bonobos reach the late juvenile or early adolescent stage, however, neither mature males nor females show such a high tolerance toward them. Adult males frequently show aggressive behavior toward them, keeping them on the periphery of the mixed party (Kano, 1992), where they have fewer opportunities for access to estrous females. The attitude of mature females also changes in this period. Although younger immature males are sometimes allowed to insert their penes without any preceding soliciting behaviors, such one-sided sexual behavior is rarely observed for late juvenile or adolescent males (Kano, 1989). These changes of attitude of mature individuals probably explain why the frequency of genital contact with mature females decreases when males reach adolescence.

In chimpanzees, however, copulation-like behavior of immature males does not decrease in early adolescence (Sugiyama and Koman, 1979; Tutin, 1979; Hasegawa and Hiraiwa-Hasegawa, 1990). This may be partly because chimpanzees show a much more dispersed grouping pattern (Wrangham, 1979; Kawanaka, 1984). Under such conditions, adolescent males have more opportunities to gain access to females without disturbance by older males. Another factor may be a tendency for adult females to show a very positive attitude toward copulation with adolescent males (Hasegawa, 1987).

It is a common supposition that copulation-like sexual behavior of immature males is necessary for learning copulatory behavior (Hasegawa, 1987; Wrangham, 1993). In fact, male chimpanzees raised in isolation cannot copulate normally (Rogers and Davenport, 1969; Tutin and McGrew, 1973). However, this learning hypothesis cannot explain the high frequency of sexual behavior of immature male chimpanzees and bonobos. Immature males of other species do not show such frequent sexual behavior, but they can copulate when they reach adulthood (Wrangham, 1993).

Among primates, chimpanzees and bonobos are unique in that infants begin to show copulation-like behaviors before weaning, immature males perform such behaviors with fecund females, and the frequency of copulation-like behavior by immature males is higher than that of copulation by mature males. These two species are also unique in the high frequency of copulation by mature males. The early development and high frequency of

copulation-like behavior while immature might be a normal developmental process of males that will be exposed to severe sperm competition in a multimale group (Hasegawa and Hiraiwa-Hasegawa, 1990).

Genital Contact in Social Context

Although mature female bonobos frequently perform GG rubbing, we did not observe it between immature and mature females (Kitamura, 1989; de Waal, 1990; Kano, 1992). Although Kano (1992) supposed that this was because the external genital organs of immature females are too small to perform GG rubbing, changes in social circumstance may also be important factors in the development of this behavior. Furuichi (1989) and Idani (1991) reported that early adolescent females that have recently immigrated into a strange group perform GG rubbing much more frequently than older resident females do. They employ GG rubbing as greeting behavior when they approach specific senior females with which they are attempting to establish affinitive relationships. When females have established a stable social status in the new group, however, the frequency of GG rubbing decreases to a moderate level. Thus the frequency of GG rubbing and the social status of females correspond to one another.

A similar correspondence with social status is also found for noncopulatory mounting and rump–rump contact with mature males (Furuichi, 1987; Kitamura, 1989; Kano, 1992). Immature males and females begin to show these behaviors in the juvenile-II stage or early adolescence. This is the period when mature males begin to show aggressive behaviors toward them. For females, these genital contacts do not develop so much toward adulthood. This is probably because they use copulation with mature males to regulate social relationships after immigration to a new group (de Waal, 1987). For males, however, these behaviors become the most important social tactics in adulthood to cope with other male members (Kitamura, 1989; Kano, 1992; Furuichi and Ihobe, 1995).

Different Processes of Development of the Three Categories of Genital Contact

In conclusion, the three categories of genital contact including immature bonobos differ in aspects of the developmental process and in the extent of similarities with sexual behaviors of the other African great apes. The play-like genital contact and the copulation-like genital contact of bonobos appear form an early stage of development and have many features in common with those

of the other great apes. Although there was a difference in frequency, these seem to be common behaviors for immature individuals of great apes, rather than unique characteristics of bonobos. Contrarily, the genital contacts performed in social contexts appear in the latest stage of development in bonobos, and are not found among the other great apes.

Chimpanzees have developed many kinds of behaviors for greetings, reassurances, and reconciliation, which rarely involve contact of genital organs (Bygott, 1979; Nishida, 1979; Goodall, 1986). These behaviors gradually develop through all immature stages. Hiraiwa-Hasegawa (1986) reported that infants <2 years old show greeting behaviors when their mother pant-grunts, and they show these behaviors more and more independently as they grow older.

By contrast, most of the behaviors that bonobos use for similar purposes involve contact of the genitals (de Waal, 1990; Ihobe, 1992; Kano, 1992; Furuichi and Ihobe, 1995). These behaviors do not appear in the infant period, but develop rather rapidly in the late juvenile or early adolescent periods. Compared with chimpanzees, it seems as if bonobos have no period for gradual learning of such behaviors.

One feature of bonobos that might be related to this issue is that immature bonobos perform play-like genital contact more frequently than the other great apes do. Provided with many experiences of such sexual play, bonobos might be able to learn or develop genital contacts for social use rather rapidly when the necessity arises. The precise details of developmental changes during this critical period are difficult to assess by comparing different individuals at different ages, as the present study has done. To clarify the process further longitudinal studies of several individuals throughout this crucial period of development will be required.

ACKNOWLEDGMENTS

I thank Prof. T. Kano, Dr. G. Idani, Dr. H. Ihobe, Dr. Ellen Ingmanson, and other researchers of bonobos at Wamba who supported my fieldwork and gave me valuable advice for writing this paper. The staff of the Research Center for Ecology and Forestry (CREF) of Zaire and the staff of the research station at Wamba also supported me. Prof. Y. Sugiyama, Dr. J. Yamagiwa, and other members of the Primate Research Institute, Kyoto University, Dr. Y. Takahata, and Dr. H. Takasaki gave me useful suggestions on early drafts of this paper. Dr. T. Furuichi advised me during the fieldwork and writing of this paper, and allowed me to use his unpublished data. I express deep gratitude to them all. This study was financially supported by grants under the Monbusho International Scientific Research Program to T. Kano (No. 63041078).

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