

GENITO-GENITAL CONTACTS IN THE PYGMY CHIMPANZEE (*PAN PANISCUS*)

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ABSTRACT This report deals with the pygmy chimpanzee's interactions involving mutual contacts of the ano-genital regions between two individuals, referred to as genito-genital (GG) contacts. Pygmy chimpanzees have unique forms of GG contacts: ventro-ventral copulation, GG rubbing between females, rump-rump contact between males. Moreover, various kinds of GG contacts occur in various combinations of participants, including all age-sex classes. What kinds of GG contact interactions occur in what sorts of dyads is presented. Most of the contacts have a typical pattern for each age-sex class combination. However, the role distribution in these interactions occurring in arbitrary dyads of each combination cannot be explained on the level of behavior patterns exhibited by each participant according to its biological attributes. The regularities seen in how GG contacts occur appear on the level of interaction patterns determined by whether the interactions are intra-set or inter-set. Possibility of a "syntax" analysis of interactions in a certain social system is discussed.

Key Words: Genito-genital contacts; Copulation; Interaction pattern; Pygmy chimpanzee; *Pan paniscus*.

INTRODUCTION

Until recently, pygmy chimpanzees (*Pan paniscus*) have been left in obscurity. Takayoshi Kano and his co-workers formed the research set-up to make long-term field research possible. The characteristics of the society and ecology of the pygmy chimpanzee have been brought to light. One of the most interesting phenomena is the diversity of copulation and copulation like contacts.

Both ventro-dorsal and ventro-ventral copulations are commonly observed among pygmy chimpanzees. Also, the females exhibit a particularly unique form of contact, in which they embrace ventro-ventrally, swing their pelvis sideways, and rub each other's genitals. Among males another unique form of contact occurs when one male presents to another. Instead of mounting, the partner male places his own anal region in contact with the presenting individual's. These facts have been reported not only in the field (Kuroda, 1980; Kano, 1980) but also in the laboratory (Savage-Rumbaugh et al., 1977; Patterson, 1979).

The focus of this report is on the copulation and copulation like contacts among pygmy chimpanzees, not only because of the unique forms of interactions, but also because of the diversity of the combinations of participants, comprising all age-sex classes.

This report deals with the interactions involving mutual contacts of the ano-genital

regions between two individuals, referred to as genito-genital (GG) contacts. What kinds of GG contact interactions occur in what sorts of dyads will be presented. The interactions will be classified according to a clear criterion, for the purpose of understanding what the interactions reveal about inter-individual relationships within the social system of the pygmy chimpanzee.

MATERIALS AND METHODS

The present study was conducted for five months, between September 1978 and February 1979, in the vicinity of Wamba village, Zone de Djolu, Region de l'Equateur, Republique du Zaïre. The main object of study was E group, provisioned by Kano in 1976. Adjacent troops, P group to the south, B and K groups to the east, were also observed (Kitamura, 1983).

One of the main topics of study was the spatial displacement of E group, and the group's ranging pattern was investigated (Kitamura, 1983). While tracing E group's movements many of the chimpanzees were individually identified, and inter-individual interactions were recorded.

Fifty-nine members of E group were identified: 16 adult males, four subadult males, 19 adult females, eight juveniles, and 19 infants (Kitamura, 1983). Age classifications follows Kuroda (1979). For convenience, in this report, the adults and subadults will be referred to as "mature," while juveniles and infants as "immature."

Various kinds of GG contacts occur in pygmy chimpanzees with various combinations of two individuals. Most of the contacts have a typical pattern for each of the combinations based on age-sex classes. For example, copulation occurs in the mature male-mature female combination, and genito-genital rubbing occurs in the mature female-mature female combination.

However, there are some difficulties in classifying pygmy chimpanzee GG contacts by combinations of age-sex classes. First, age-sex classifications that accurately reflect the individual behavioral variations can not be easily defined. Some GG contacts can occur across the age categories. Second, even in combinations that exhibit the typical interaction pattern, an interaction with different patterns can occur.

RESULTS

Figure 1 is a matrix prepared from the four elements based on the two age-sex categories, mature-immature, and male-female. Ten forms of combinations are considered. According to the alphabetical order in Figure 1, the GG contacts typical to each combination will be presented. The GG contacts which are unavoidably overlooked, or do not fit to the presumed categories will be considered in part V.

I. Copulation Between Mature Males and Mature Females (A in Figure 1)

1. Courtship

Copulation conceivably can be initiated by either male or female, but it may not

Mature Male	Mature Female	Immature Male	Immature Female	
C	A		D-b	Mature Male
	B	D-a		Mature Female
				Immature Male
				Immature Female

Fig. 1. A matrix of age-sex class combinations in which various patterns of GG contacts occur. Alphabets indicate the order that the GG contacts typical to each combination are described in the text.

be very meaningful to classify which sex initiated each and every copulation by simple, uniform standards. The interactions that precede copulation will be examined here from several angles.

One noteworthy behavior pattern that precedes copulation is the male "courtship display" (van Lawick-Goodall, 1968). The courtship displays observed among pygmy chimpanzees during the present study can be classified into two types. In the first type, common among adult males, the male squats facing the female, body held vertically, and display the erect penis. Sometimes he may lightly raise his arms while rocking the torso back and forth, and/or side to side. If the male is in a tree, he may hold on to a nearby branch and shake it. In the second type, seen among young males, the male stands bipedally near a female and gestures to her with movements of hands and/or arms (Savage-Rumbaugh et al., 1977). He may often slightly touch the female's body.

On studies of small captive groups, Patterson (1979) has reported only the first behavior, while Savage & Bakeman (1978) have reported only the second. These results may reflect the ages of the subjects they studied (14 years old in the former, 6.5-7.5 years old in the latter). But during the present study, adult males were also seen inviting females by standing bipedally, and the contrasts were only relative.

The courtship display exhibited by male pygmy chimpanzees differ from the common chimpanzee in that the behavior does not contain any element of aggression. Van Lawick-Goodall (1968) has given six types of male courtship displays for common chimpanzees, of which four types occurred frequently during aggressive behavior. She has also stated that 40 per cent of the copulations were initiated by the approach of a male with hair erect.

The common pattern in pygmy chimpanzees is that copulation results from the approach of a female to a male with penis erect. In these cases, since the male's penis is erect, the initiator can be interpreted to be the male. But many cases were observed in which the female's active effort led to copulation.

Savage & Bakeman (1978) have stated that copulation is sometimes accompanied by food sharing, and the present study confirms this. Copulation can result after a female repeatedly presents to a male with food. In between copulations, the female may actively beg for food. These episodes observed during the present study all involved sugar cane provided by the researchers, but Kano (1980) has observed similar episodes involving *Treculia africana*.

The females clearly seem to be initiating copulation in these cases. The males are annoyed by the female's persistent begging and try to escape. The following example illustrates this point.

29 January 1979, 6:50 a.m.

Bihi (young adult female) approaches and presents to Ibo (young adult male), who is eating sugar cane: ventro-dorsal copulation. Then Bihi sits down in front of Ibo and begs by placing a palm over his mouth. After several attempts she finally receives a piece. She begs and receives repeatedly. Ibo rises to move away but Bihi quickly presents. Ibo changes the direction he was facing and starts to mount, but then dismounts and sits down. Bihi presents again while looking back. This time Ibo relents: ventro-dorsal copulation. Ibo moves immediately after he finishes. Bihi follows right away. When Ibo stops, Bihi sits down next to him.

There was an episode in which a female conspicuously presented to a male who was on his way to another female, and attracted the male to herself.

29 January 1979, 7:53 a.m.

Ibo (young adult male) and Halu (adult female) copulate ventro-dorsally. Five minutes later Mon (subadult male, believed to be Ibo's younger sib), approaches Halu, but Ibo chases him away with exaggerated gestures, and then goes to sit behind Halu. Then Chiyo (adult female), who was four meters away, lay down and moved her buttocks back and forth in Ibo's direction. Seeing this, Ibo approaches her on the run while emitting small cries, and mounts ventro-dorsally. But after only a few thrusts Ibo dismounts, and Ibo's penis is not erect.

In these ways, copulation can be initiated by either male courtship displays or active solicitation by the female. But, obviously, the females may ignore the persistent courtship displays of the males. On the other hand, the impression was gained that males rarely ignored a female's solicitation, but, as in the cases described above, mounting may not lead to complete penile insertion. While copulation may not result even with active solicitation, the opposite, in which copulation occurs without active solicitation, can be imagined. Savage & Bakeman (1978) have stated that prolonged mutual eye contact is an important component in the initiation of copulation in pygmy chimpanzees.

Van Lawick-Goodall (1968) has reported that copulations occur most frequently when a group arrives at a favored food site or when males are socially excited after an encounter with another group. This is consistent with the results of the present study. In these situations, the males often exhibit the charging display accompanied by penile erection. Copulation becomes frequent in the midst of such social excitement. Among pygmy chimpanzees, not only male-female copulations, but also genito-genital rubbing between females occur frequently. When both males and females are socially excited, copulations need not be initiated by obvious invitations, but may proceed immediately upon mutual eye contact and approach. In such situations,

a male with a penile erection is often approached by a female and begins copulation, but penile erection does not seem to be a display directed towards any particular female.

2. Copulation

Pygmy chimpanzees exhibit a variety of copulatory postures. In particular, ventro-ventral copulation, not seen in the common chimpanzees, has been the focus of great interest (Savage-Rumbaugh et al., 1977; Savage & Bakeman, 1978; Patterson, 1979). During recent field studies, ventro-ventral copulations were commonly observed, but not at frequencies equaling, or even approaching, ventro-dorsal copulations (Kano, 1980).

During the present study, mature male-mature female copulations were observed 267 times. The copulatory postures were identified in 258 cases: 233 ventro-dorsal, 22 ventro-ventral, one ventro-lateral, and two cases in which ventro-dorsal was switched to ventro-ventral. If at least one of the participants, male or female, was young, the probability of ventro-ventral copulation was high. In the ventro-ventral copulations among mature individuals, both participants were identified in 13 cases, and of these, in 11 cases, the male was a subadult or younger, or else the female was young and had never given birth. In the immature male-mature female copulations, 51 cases were ventro-dorsal, 34 cases ventro-ventral, and in one case ventro-dorsal was switched to ventro-ventral. There was a statistically significant correlation between whether the male was mature or immature, and whether the posture was ventro-dorsal or ventro-ventral ($\chi^2 = 44.1$, $df = 1$, $p < 0.001$).

(1) Ventro-dorsal copulation

No clear differences can be discerned between the ventro-dorsal copulatory postures of the two species of chimpanzees, although the slightly ventral position of the pygmy chimpanzee female's vagina may be reflected in the posture. In one episode, a female presented with all four limbs bent, and the male, standing in behind, could not insert his penis. He had to sit down, extend his arms behind for support his body, and only then achieved penile insertion.

Savage & Bakeman (1978) have reported that during copulation either party may manipulate the other's genitals with a foot. During this study, males were not seen using either hands or feet to manipulate the female's genitals. Males did touch their own penis at penile insertion. Females often touched the male's scrotum with either a foot or hand during ventro-dorsal copulation. There was one episode in which a female manipulated her own genitals. On October 15, the first day the chimpanzees appeared at the feeding site during the present study and were very tense, a female with sagging sexual skin held it up while inviting a male to ventro-dorsal copulation. She continued to hold her sexual skin with one foot during copulation. During one ventro-dorsal copulation between a juvenile male and mature female, the female squatted and placed both feet on the male's scrotum.

(2) Ventro-ventral copulation

Immediately prior to ventro-ventral copulation the female lies face up on the

ground or a branch while raising the buttocks and presenting the genitals, and the male leans over from in front. During some cases of ventro-ventral copulation in trees, the female did not completely lay down. Once while copulating in a sitting posture, the male extended an arm behind the female, and in another case, the participants were standing almost vertically. In both cases the male was young. In the examples in the following sections, when ventro-dorsal postures are switched to ventro-ventral, the female's body was raised, and not completely on the ground when the posture switch was made.

(3) Other copulatory postures

One example of a ventro-lateral posture, in which the body planes of the partners were 90° apart, was observed during copulation within a tree. During copulation in trees, the partners often must hold on to branches for support, and the postures become modified. The lateral posture can be considered an extreme case of this. Savage & Bakeman (1978) have reported a single case of the ventro-lateral posture.

The postures can change in the midst of copulation. This can be clearly distinguished from the changing of postures during the short interval between two successive copulations. It occurs when the female shifts her position: body contact and penile insertion are maintained. All posture changes were from ventro-dorsal to ventro-ventral. Three cases were observed during the present study, and Kano (1980) has observed three cases in a separate study. In every case, the males were of juvenile, subadult or young adult ages, and the females were also fairly young.

(4) The variability of copulatory interactions

As stated above, the pygmy chimpanzees have a variable repertoire of copulatory postures. Savage & Bakeman (1978) have emphasized that a rather complex communicative decision making process is necessary to achieve a compatible posture. Savage-Rumbaugh et al. (1977) have shown that certain gestures are followed by particular postures at statistically significant frequencies. In the field, however, the frequency of ventro-ventral copulation is low, and in most cases ventro-dorsal copulation follows penile display by the male and approach-presentation by the female. A complex process to determine the copulatory posture may not occur frequently. But the interactions involving young males are consistent with the observations on captive animals.

3 February 1979, 6:58 a.m.

Ten (juvenile male) approaches Kame (adult female) and lightly touches her shoulder. Kame responds by lying down face up, but Ten does not mount. Kame remains as she is, until after a while, Ten approaches again and touches her shoulder in a subtle way. Kame gets up and raises her buttocks and they copulate ventro-dorsally.

Copulatory postures may be determined without clear communicative gestures. Episodes were observed in which a male responded to female's ventro-dorsal presentation by approaching from in front, resulting in ventro-ventral copulation. At other times the partners achieved the ventro-dorsal posture, but the male did not insert the

penis until the female had shifted her posture for ventro-ventral copulation, or the reverse occurred, in which the partners did not begin until the female had shifted her position for ventro-dorsal copulation.

In reality, the only individuals exhibiting the full postural repertoire are the males of juvenile, subadult, or young adult ages. The ontogeny of sexual behavior in pygmy chimpanzee males is a continuous process which begins immediately upon gaining the ability to leave the mother. Even during the stage when a male is being carried about by its mother, it begins to effectively use a highly variable contact repertoire. During the juvenile stage, not only can a male perform all adult sexual behaviors, but in fact shows greater variability.

II. Genito-Genital Rubbing Between Mature Females (B in Figure 1)

Pygmy chimpanzee females embrace each other ventro-ventrally and rub their genitals together. This type of contact bout is unique to pygmy chimpanzees, and Kuroda (1980) has termed it genito-genital (GG) rubbing. During the present study, GG rubbing between mature females was observed 179 times.

GG rubbing is carried out either on trees or the ground. In trees, both partners support their own weight by holding on to branches with their arms, while one partner wraps her legs around her partner. On the ground, or a large branch, one partner stands quadrupedally while the partner hangs underneath.

There are interactions that precede GG rubbing as well. It may result simply from approach and presentation, but mutual eye contact occurs in every case. Even after the initiation of rubbing, the partners maintain eye contact. One side may also exhibit a gesture in which she stands bipedally and raises the arms while maintaining eye contact.

A female presents by lying down on her back on the ground or branch and presenting the genitals. This posture is the same as the presentation for ventro-ventral copulation. The partner bends over from in front, but the subsequent actions are not the same as in male-female copulation. Male pelvic thrusts are back and forth, but female GG rubbing is done side to side. In order for the genitals of the partners to rub effectively each genitals must move in opposite directions, and the frequency of movement must be adjusted appropriately.

Unless hip movement is synchronized, GG rubbing may end immediately. A female in B group was observed that had abnormally large sexual swellings which interfered with GG rubbing. This individual could not properly synchronize her movements and attempts at GG rubbing were immediately abandoned.

In this way the partners simultaneously perform identical actions. But this does not mean that the forms of embrace are completely symmetrical. Only one partner wraps her legs around her partner. In this posture, the individual hanging below may have greater freedom of movement of the hips, and the amplitude is, in fact, greater. The chimpanzees themselves seem to be aware of a difference. Preceding GG rubbing on the ground, prospective partners repeatedly present to one another to determine which will have the lower position.

14 February 1979, 2:55 p.m.

Nami (adult female) approaches Kame (adult female), lies down on her back, and presents. Kame passes by Nami and lies down on a nearby log. Seeing this, Nami gets up, passes under the log to the other side, and lies down again. Kame gets off the log and lies down next to Nami. Nami finally seems to give in and GG rubbing ensues with Kame below and Nami above.

Interactions through which the females determine who shall take the lower position indicates that they clearly discriminate the two positions. But it also means that who takes what position is not predetermined. The individuals in the example above were observed performing GG rubbing with the positions reversed in another episode on February 2. Kame first presented, then Nami presented in return, to which Kame obliged herself by taking the upper position. However, there is a tendency for younger individuals to take the upper position, and some old individuals tended to be in the lower position. Kame, an old female appearing in the above examples, was observed GG rubbing in 89 cases, of which the positions of the partners were identified in 66 cases. Kame was in the lower position in 59 cases, and above in seven cases.

GG rubbing can be clearly differentiated from male-female copulation, or other types of GG contact, by the fact that hip movement is from side to side. This type of contact occurs only among females, and can occur not only among mature individuals, but also between mature and immature individuals ($N = 11$), or among immature individuals ($N = 5$). This is also the only form of GG contact among females.

III. GG Contact Between Mature Males (C in Figure 1)

Mounting between males with postures indistinguishable from ventro-dorsal copulation have been observed in many primate species, including the pygmy chimpanzees. Another peculiar type of contact of the anal region, rump-rump contact, has also been observed (Kuroda, 1980; Kano, 1980).

Four types of GG contact can be observed among mature males. Consider two males X and Y . First, X may mount Y . Second, Y may mount X . Third, rump-rump contact may take place between X and Y . Fourth, X and Y may embrace ventro-ventrally with pelvic thrusts. In rump-rump contact both X and Y can be considered to be acting as mountee, while both may be acting as mounter in the ventro-ventral embrace. Every permutation of mounter and mountee roles for X and Y is possible. Thus GG contact between mature males can be thought of as combinations of the two contrasting roles involved in ventro-dorsal mounting, regardless of role overlap.

During the present study, mounting bouts between mature males was observed 39 times, rump-rump contact 10 times, and the ventro-ventral embrace once.

Although the ventro-dorsal mounting posture can not be distinguished from copulation, mounting between males does not involve penile insertion, and sometimes does not involve pelvic thrusts. Mounting postures between males showed some modifications, probably because of the lack of penile insertion. Episodes were observed in which two males stood bipedally and one embraced the other from behind.

In copulations, obviously, males are always the mounter, and females are the

mountee. In inter-male mounting the identity of the participants probably has an effect on which becomes the mounter and which the mountee, but the same pair of individuals may switch roles. In other words, there is no strict rule that dominant individuals mount subordinate individuals. Of the 38 cases in which both participants were identified, the exchange of roles was observed 13 times (three pairs). Subordinate individuals were believed to have unilaterally mounted dominant individuals six times (two pairs). However, in the five cases involving the alpha male, he was always the mounter. Dominant individuals will also present, but sometimes in a threatening way that may involve pelvic thrusts. A mounting bout in which the mountee exhibited pelvic thrusts has been observed. On the other hand, the mounters have been observed screaming and grinning while thrusting.

Rump-rump contact results when one male presents to another, but instead of mounting, the other male places his own anal region in contact with the presenting individual's. Each participant may either make rapid pelvic thrusts, or stand perfectly still. The directions in which the partners stand may not coincide, and rump contact may be achieved at an angle. In the following example, rump-rump contact takes place in between exchanges of mounting. It seems to occur because both partners simultaneously behave as the mountee.

10 February 1979, 9:43 a.m.

Yasu (adult male) picks up a stick and runs with it toward Ibo (young adult male). Yasu assaults Ibo, Ibo presents and Yasu mounts. Then the pair fall apart, and move toward an area with scattered sugar cane, but come close to each other again. Both present to each other, resulting in an incomplete rump-rump contact at right angles. Then Yasu mounts Ibo. Immediately afterwards, Yasu presents and Ibo mounts.

Besides the GG contacts described above, one case was observed in which a mature male pair embraced ventro-ventrally and performed pelvic thrusts together. One example each of this contact were also observed between infant males, and between a subadult and juvenile male. The peculiarity of this contact is that both partners perform pelvic thrusts, and the genitals are presumably in contact.

GG contact between mature males is often preceded by aggressive chases (Kano, 1980). But episodes were observed in which a male invited another male, as in female GG rubbing, by standing bipedally and raising the arms, which led to rump-rump contact. In the example below, GG contact does not actually occur, but it clearly shows that GG contact does not take place solely in aggressive contexts.

7 February 1979, 6:25 a.m.

Kuma (E group alpha male) turns toward Hachi (4th ranking male), spreads his legs, displays an erect penis, and rocks his torso back and forth. Seeing this, Hachi approaches Kuma, stands bipedally, and slowly raises his arms. Hachi watches Kuma's reaction, but Kuma does not respond. Hachi moves away.

IV. GG Contact Involving Immature Participants

1. Copulation Between Immature Males and Mature Females (D-a in Figure 1)

Immature males mount mature females with either ventro-dorsal or ventro-ventral

postures, insert the penis, and perform pelvic thrusts ($N = 93$). If copulation is considered a mounting bout with penile insertion, but not necessarily ejaculation, this type of GG contact is copulation, and does not differ in other ways from copulation between mature participants.

There are no clear discontinuities between the behavior patterns of the mature and immature males. All postures seen in adult copulations are also exhibited. But the interactions preceding copulation change gradually in relation to the age of the immature males. These changes are progressive and can not be divided into definitive stages.

Male infants often copulated with the mature female immediately after the female had completed copulation or GG rubbing ($N = 20$). The infant male either waited for the mature individuals to complete what they were doing, or climbed on to the mature individuals. Infants often climbed on the back or held on to the abdomen of mature individuals in the midst of copulation or GG rubbing. The infants hold still, and may scream or grit their teeth. If the infant was male, the penis was always erect. Immediately upon the completion of GG rubbing ($N = 7$) or copulation ($N = 1$), the male infant slid down to the female's hips, inserted the penis, and thrust.

In the single episode involving copulation, the male infant climbed atop the head of a mature female that was copulating with the infant's brother. Immediately upon the ending of copulation, the infant slid down to the female's abdomen, inserted his penis, and began to thrust. In this case the posture was ventro-ventral, but the female was standing quadrupedally and the infant was clinging on as well as he could. Ventro-ventral copulation with the male in the lower position has not been observed among adults.

An infant male may wait beside the copulating or GG rubbing adults, and approach the female when they are done ($N = 12$). In the example below, the infants could not join the adults during copulation, but managed to copulate with the female immediately afterwards.

14 February 1979, 9:10 a.m.

Hachi (adult male) displays his erect penis at Lan (young adult female), and invites her to copulation. Lan turns around; they copulate ventro-dorsally. Seeing this Bafubafu (infant II male; age classification follows Kuroda, 1979) and Tawashi (infant II male) rush to the copulating pair. Hachi shoves them away. They try to climb on to Lan, but fail. When copulation ends, the infants copulate ventro-dorsally with Lan.

In these examples, the infants made no attempt to gain the female's consent. Clear displays by the infant males rarely preceded copulation between mature females and infant males. The female may shift her position slightly to facilitate penile insertion, but more often shows no obvious reaction.

11 December 1978, 8:55 a.m.

A mature male is grooming a mature female. An infant II male approaches the female, inserts the penis, and begins to slowly thrust. The female takes no notice and continues to groom.

A female may change her posture after an infant male unilaterally begins copulation.

12 December 1978, 6:18 a.m.

An infant II male comes out of its bed, and approaches Kame (adult female), who is sitting nearby. The infant moves around Kame and attempts penile insertion. Kame shifts her position, and with her hand, supports the infant in a ventro-ventral position. The infant inserts his penis and slowly thrusts. When finished, the infant returns to its bed.

By the time males reach juvenile age, they no longer unilaterally begin copulations, and their behavior preceding copulation is indistinguishable from mature individuals. Males of juvenile age or above, including subadults and young adults, tend to first approach a female, then exhibit gestures, such as standing bipedally and waving the arms or hands. As stated earlier, these young males fully utilize the variable repertoire of copulatory interactions exhibited by pygmy chimpanzees.

2. GG Contact Between Mature Males and Infants (D-b in Figure 1)

Mature males embrace and perform pelvic thrusts with infants of both sexes, and with both ventro-dorsal and ventro-ventral postures. The mature male's penis is erect at these times. Penile insertion has not been observed, and in fact, is believed impossible even with female infants.

During the present study, GG contacts between mature males and infants was observed 49 times. The infant's sex was: male 30 cases, female 17 cases, unknown two cases. The postures were: ventro-dorsal 24 cases, ventro-ventral 24 cases, unknown one case. The ventro-dorsal mounting bouts were nearly identical to copulation, and the males were mounter and the infants were the mountee.

There are special behavior patterns exhibited during the ventro-ventral mounting bouts. The mature male extends a leg around the back of the infant and rhythmically moves it up and down. This was most often observed in the ventro-ventral posture ($N = 9$). This has never been observed during copulations between males and females. Besides this, there have been examples of males that thrust while squatting ($N = 5$), or while standing bipedally, holding the infant ($N = 4$).

GG contact may be initiated in several ways. An infant may respond to a male's display. Or else an infant may actively solicit a mounting bout.

12 November 1978, 6:30 a.m.

A subadult male turns toward an infant II female sitting on the same tree, stands bipedally with penis erect, grasps a few small branches over head, and shakes them slowly. The male continues this for a while, and then the infant female approaches and presents. The male mounts ventro-dorsally, and thrusts vigorously. They change postures several times, and the male continues to thrust vigorously. During ventro-dorsal mounting bouts the female's hand was touching the male's scrotum.

One episode was observed in which a mature male displayed his erect penis towards a mature female, but an infant II male nearby responded, resulting in ventro-dorsal mounting.

26 January 1979, 7:45 a.m.

Yasu (adult male) raises his torso and displays an erect penis at Kame (adult female). Kan (infant II male), seeing this, runs over and presents to Yasu. Yasu holds the infant ventro-dorsally and thrusts. The infant screams and grins. Following this, Yasu displays to Kame again resulting in ventro-dorsal copulation.

In these examples, a mounting bout occurs after a male displays and an infant responds. On the other hand, mounting bouts may occur after an infant's active solicitation. Food sharing is also accompanied by mounting bouts between infants and mature males.

21 January 1979, 8:37 a.m.

Kan (infant II male) sits down next to Ibo (young adult male), who is eating sugar cane. The infant extends a palm to beg and receives a piece. Ibo stands and the infant hurriedly presents. Ibo mounts ventro-dorsally and thrusts. When he finishes, the infant starts to beg, and receives again. Both Ibo's and the infant's penis are erect at this time. Later, Ibo holds the infant ventro-ventrally and thrusts vigorously. Upon finishing, the infant begs again and receives a large piece. When finished with that piece the infant grabs Ibo and begs by holding its palm over Ibo's mouth, then presents. Ibo mounts ventro-dorsally and thrusts. When finished, Ibo moves rapidly away.

It has already been mentioned that infants may participate in copulations between mature individuals. When the infant was female, it presented to the mature male that had just completed copulation, resulting in ventro-dorsal mounting.

V. Other Types of GG Contact

1. GG Contacts Between Males

GG contacts between mature males have been described in part III, but the same interaction patterns have been observed in GG contacts between mature and immature males, and among immature males. In other words, the two contrasting roles that form ventro-dorsal mounting bouts are combined in various ways across age categories as well. However, rump-rump contacts between immature individuals were not observed during the present study. The ventro-ventral embrace in which only one partner performed pelvic thrusts occurred in dyads including an immature male, but was not seen between mature males.

As it has already been pointed out, when male behavior in copulations with mature females was considered, no absolute discontinuity between mature and immature could be found. This fact is clear for GG contact between males as well. In two consecutive mounting bouts between a subadult and a juvenile male, mounter and mountee roles were switched. The combinations in which the interaction patterns described in part III appear, can not be strictly defined according to age-sex criteria, such as "mature male." The range of combinations must be expanded.

What becomes a problem here are the GG contacts occurring in the mature male-infant male combination. Up to this point, the GG contacts of various combinations have been considered and a typical interaction for each has been presented. As described in part IV-2, in the interaction pattern between mature males and infant males, the mature male is always the mounter, and is the only one that performs pelvic thrusts. But an infant male close to juvenile age has mounted and thrust on a subadult male ($N = 2$).

28 January 1979, 6:37 a.m.

Bafubafu (infant II male) approaches Mon (subadult male), embraces ventro-ventrally, and thrusts slightly. Later, Bafubafu moves behind Mon, mounts ventro-dorsally and thrusts.

Furthermore, juvenile males have been observed ventro-ventrally embracing infant males, extending a leg around the back of the infant, and rhythmically moving the leg up and down ($N = 3$). This is an interaction pattern typical to contact bouts between mature males and infants, as described in part IV-2. Therefore, the range of combinations exhibiting these interaction patterns must also be expanded.

The examples above show that in GG contacts between males, even the contrast between mature and infant is not absolute. This means that in GG contacts between males in general, two types of interaction patterns, those typical between mature and infant, and those typical between the mature, can not be differentiated, and it can be thought that the relative age differences bias the behavior patterns which can occur between males. However, during the present study, infant males never mounted and thrust on adult males, and the behavior unique to the mature male-infant combination was not seen among males of juvenile age or above. In other words, within these combinations, the differences between mature and infant are not simply relative ones.

How clearly these two interaction patterns can be differentiated will be dealt with from the point of view of how to classify all GG contacts in general in the discussion section. What must be pointed out here is the obvious fact that entirely different interaction patterns may occur even in the same combinations. Not only do copulations occur in the biologically determined combinations, such as male-female, but there are GG contact interaction patterns that are clearly different from those.

2. GG Contacts Involving Mature Females

Ventro-dorsal copulation between a mature male and mature female occurs when the female presents and the male mounts. One case of the reverse was observed in which a male pushed his buttocks in front of a female, and she stood bipedally behind the male in a posture suggesting mounting. In this case the female grinned and screamed. The only other examples in which a male presented to a female resulted in rump-rump contacts ($N = 2$). One case was observed in which a mature female mounted another mature female ventro-dorsally and pressed the mountee's genitals. The mounter screamed in this case.

In the situations where a mature female presented and a mature male mounted, penile insertion often did not occur. The mounting male sometimes did not show any pelvic thrusts. By examining all these examples, it can be seen that virtually all forms of GG contact occurring between mature males, also occurred between mature males and mature females, excluding copulation. By expanding the perspective, it can be said that exactly the same types of GG contact occur in a social set consisting of mature males and mature females, as in the social set consisting of mature males. This matter will be considered in the discussion.

3. GG Contacts Left Unclassified

The GG contacts left unclassified were observed only very few times during the present study. Classification was impossible because the number of observed cases were so few.

Of those that were rarely observed during the present study were GG contacts

involving juvenile females, and between infant females and immature males. The latter is probably due to chance. Most of the observations on GG contact were made on the individuals that appeared frequently at the artificial feeding site after January. They comprised only 28 of the 59 individuals identified in E group (Kitamura, 1983), and included only one infant female. Furthermore, this infant was newborn, and had no contacts with any individuals except its mother. But considering that GG contacts between infant females and mature males were observed during other study periods ($N = 17$), GG contacts with immature males may actually be rare.

Two juvenile females were under observation frequently during the present study, but GG contacts of these individuals were rare. There was one case each in which the females were the mountee in a ventro-dorsal mounting bout with a young adult and juvenile male, one case in which a female ventro-dorsally mounted an infant male and moved her hips sideways, and three cases of GG rubbing with adult females. Of these, GG rubbing can be considered normal behavior for females, but there is no point in attempting to classify the other interactions. The point of interest is simply that GG contacts of juvenile females is so infrequent. By this fact, mature females can be clearly differentiated from immature females in the female's role as a participant in GG contacts with males.

DISCUSSION

Various patterns of GG contact occur in pygmy chimpanzees. This report has attempted to classify them based on five types of age-sex class combinations. These five types are: mature male-mature female, mature female-mature female, mature male-mature male, immature male-mature female, and mature male-infant. The interaction patterns typical to each combination have been presented. Most GG contacts of the other possible combinations can be included in one of the five types given. No discontinuity could be discerned between the behaviors of mature males and immature males concerning copulations with mature females. GG contacts between females were the same interaction, GG rubbing, regardless of whether the participants were mature or immature. From these results, GG contacts can be classified into four categories according to the interaction patterns.

- (1) male-mature female
- (2) mature male-infant
- (3) female-female
- (4) mature male-mature male

These age-sex categories represent the GG contacts typical to each combination. But they do not include all forms of GG contact seen in a combination, and some interaction patterns were seen in different combinations.

The four categories are related in such a way as to represent two general types of interaction patterns.

A) interactions occurring between two mutually exclusive social sets.

B) interactions occurring within a social set.

Type A interactions include categories (1) and (2), and Type B interactions include categories (3) and (4). The meaning of this will be discussed below.

The characteristic common to (1) and (2) (type A) is that the two individuals involved are elements of two mutually exclusive sets. In their contact the two participants simultaneously perform clearly contrasting but complementary behavior patterns. Which behavior pattern each participant adopts is determined by which set it is an element of, and their roles are never reversed. That is to say, in (1) the mounter is a male and the mountee a female; in (2) the mounter is a mature male and the mountee an infant.

The contacts in categories (3) and (4) (type B), in contrast, occur between elements of the same set. The contacts of type B have characteristics clearly different from contacts of type A.

First, consider the interaction consisting of two contrasting but complementary behavior patterns. Contact can occur between any two elements within a set, but unlike in type A interactions, which behavior each individual exhibits is not predetermined. Almost all of the individuals will exhibit both behavior patterns at one time or another. As the two participants cannot perform the same behavior pattern at a time, only one individual in a set has the possibility of continuing one of the behavior patterns, if this type of contact occurs in every pair. Even by taking into account that it may not occur with certain pairs of elements within a set, the interaction pattern seen in (1) and (2) can not emerge unless the set is subdivided into two exclusive subsets.

This point is well exhibited in the ventro-dorsal mounting bouts seen between mature males, category (4). The roles of mounter and mountee are exchanged even between the same two individuals. Other forms of GG contact between mature males are rump-rump contact, and the ventro-ventral embrace with both partners performing pelvic thrusts. These can be considered derivative interaction patterns resulting from the exchange of mounter and mountee roles.

GG rubbing between females, category (3), is similar to category (4) in that it occurs between any two elements of the same set, but the way the behavior patterns are paired is different. Females exhibit nearly identical behavior patterns during GG rubbing. Their behavior pattern does not change no matter who the partner is, and, on this point, is similar to categories (1) and (2). However, GG rubbing among females maintains the characteristic of interactions within a set by focusing on the differences in position for GG rubbing, and examining how the two participants deal with the differences. Even if dominant-subordinate relationships or age differences are reflected on which individual takes the upper or lower position, each female may sometimes be above and sometimes below.

These two general types of interaction patterns, type A and type B, can be distinguished from each other by examining how the participants deal with the differences in the roles for interaction. However, interactions in which the participants perform identical acts are typical forms for those between any two elements of the same set. For example, greetings interaction among humans includes bowing among the Japanese, hand-shaking, embracing, or kissing among Westerners. The characteristic common to all of these is that both participants simultaneously perform identical acts. In these interactions, there are no differences in the roles between participants, and these forms of interaction are not the sort of interactions expected between two

mutually exclusive sets. Also on this point, GG rubbing between females must be distinguished from the interactions of type A.

For female pygmy chimpanzees, their behavior patterns do not change no matter who the partners are, in copulations with males and in GG rubbing with other females. Then can it be said that females exhibit one of the two different behavior patterns depending on whether the partner is male or female? If it were yes, GG rubbing between females might not necessarily be distinguished from the interactions of type A.

Mature male pygmy chimpanzees exhibit the same behavior pattern of mounter role in copulations with females, but they do not have the identical behavior pattern exhibited no matter who the partner is in GG contact with other mature males. Even though they have the interaction patterns in which the participants perform identical acts, rump-rump contact and ventro-ventral embrace, they also perform ventro-dorsal mounting bout at another time. GG contact between mature male as a whole can be thought of as combinations of two and two alternatives of choice between two contrasting behavior patterns involved in ventro-dorsal mounting. That is to say, each mature male may sometimes act as mounter and sometimes as mountee, independent of which role the partner may take. This is a unique but definite interaction pattern expected within a set.

Males of many other primate species perform ventro-dorsal mounting bouts which are similar to those of male pygmy chimpanzees, but they do not have any forms of interactions in which the participants exhibit identical acts. Hence each male shows one of the two roles, the mounter and the mountee, avoiding role overlap.

Female individuals of other primate species do not have any form of interaction performed only among themselves. Accordingly these females do not have identical behavior pattern exhibited to other females, although they always act as mountee in copulations. Female pygmy chimpanzees are unique on the point that they have the particular form of interaction performed only among themselves, rather than that they have the identical behavior pattern exhibited no matter who the partner is in interaction with other females.

This distribution, among the primate species, of various interactions which occur in arbitrary dyads among females, among males, and between males and females can not be explained by the regularity of behavior partners depending on the sex of the partners. Classification of them on the level of interaction patterns is needed for clear understanding. First of all, copulations between males and females must be separated from the others. These are universal among all primate species, in which males are always the mounter and females the mountee.

The others are interactions of type B which occur in arbitrary dyads among females or among males. These interactions maintain definite patterns or no patterns. At least three interaction patterns can be detected: (1) two contrasting roles distributed to two elements of a social set regardless of role overlap, (2) two contrasting roles distributed without role overlap, and (3) the same role shared by two elements. These patterns correspond to, respectively, GG contact among male pygmy chimpanzees, ventro-dorsal mounting event among males of many primate species, GG rubbing among female pygmy chimpanzees. In the first two, which behavior each participant

exhibits may possibly change according to who the partner is. The role distribution in these interactions is not determined on absolute attributes of the participants, but on their relationship within a certain social set. Then, by performing the interaction, the participants virtually manifest that they regard themselves as members in the same set, in other words, as individuals on an equal footing. This point is the fundamental characteristic common to all interactions of type B, and this characteristic can be clearly seen also in the third category in which both participants perform identical acts.

What has been attempted by this classification system is: (1) to clarify the inter-relationships of each GG contact category within the pygmy chimpanzee's flexible repertoire, and (2) to be able to compare the GG contact of separate species by the criteria presented here.

On the GG contacts in Japanese macaques (*Macaca fuscata*), an extremely detailed study was made by Hanby (1974). Hanby attempted to show that there are considerable differences between male-male mount events and male-adult female mount events. She emphasized that male-male mount events had a multiplicity of causal factors and must not be simply labeled as homosexual or dominance interactions. She showed how male-male and male-adult female mount events differed in form, frequency, and contexts, and correlated them with differences in causation.

Hanby has given, as the differences between male-male and male-adult female mount events, frequency of mounts per encounter, seasonal patterning, and context. However, as Hanby herself points, the same criteria cannot be used for comparison with non-seasonal breeding species with a single mount-to-ejaculation pattern, such as the chimpanzee. The seasonal patterning depends on the fact that Japanese macaques are a seasonally breeding species, and differences in the frequency of mounts per encounter, and some contexts depend on the fact that Japanese macaque male-adult female breeding season mounting usually occurs in a series.

In this report, attempts to explain the interactions in terms of presumed function or motivational states have been avoided. Causal analysis has also been avoided. As a result, obviously my classification does not simply correspond with any functional or causal classification. The present classification is an attempt to show that an analysis is possible from a perspective entirely different from functional or causal analysis with the purpose of, using Hanby's words, "seeking to understand what the mount can reveal about the individuals, social situation, group or species (Hanby, 1974: 837)." This may be termed a "syntax" analysis of interactions in a certain social system.

According to this analysis, for both pygmy chimpanzees and Japanese macaques, by exactly the same standards, male-adult female copulations are entirely different types of interactions from male-male mounting bouts. The male-adult female copulation falls within type A interactions, while the male-male mounting bout falls within type B interactions.

With this classification system it can not be easily determined in what category an observed interaction should be placed. It focuses on the regularities of interaction patterns occurring between various combinations of individuals within a social

system. These regularities of interactions can not emerge from the pairing of two independently determined behaviors. An individual does not always exhibit identical behaviors, according to its biological attributes. The behavior an individual exhibits to its partner is affected by situational conditions. In a general sense, two interaction patterns classified separately can and do occur between the same pair of individuals.

These situations occur in extreme form in human society. For example, the interaction between a waitress and customer in a restaurant can be classified as an interaction occurring between elements of two mutually exclusive sets. The waitress behaves as a waitress no matter who is the customer. The customer behaves the same no matter which one of the numerous waitresses may serve him. Furthermore, a woman, who is a waitress, behaves as a customer when she sits down in a restaurant, and the other customers will not treat her as a waitress even if they know her profession.

Even in pygmy chimpanzee social interactions, males do not always behave sexually toward a mature female. They sometimes show behavior patterns treating her as a member of the same set. This is true, even if the behavior pattern concerned is almost indistinguishable from sexual behavior. Some GG contacts between males and females have the interaction patterns of intra-set interactions.

What I wished to point out with this analysis is that the regularities seen in how the GG contacts occur are not determined on the level of behavior patterns exhibited by each participant. The regularities appear on the level of interaction patterns determined by whether the interactions are intra-set or inter-set. In other words, social sets are the units of interaction with which dyads are arbitrarily formed, either within a set or between sets.

One more important interaction type remains to be classified by this perspective. This is not the sort of interactions expected in arbitrary, intra-set or inter-set, dyads, but only within specific dyads. The most obvious example of this type of interaction among primates occurs between a mother and her infant. This interaction is not thought to occur between elements of the mother set, and elements of the infant set. Consider mother-infant pairs, X - x and Y - y . X and Y are elements of the mother set, and x and y are elements of the infant set. However, X is the mother of x , and Y can never be mother for x , and vice versa.

Quite often the analysis of social structure is attempted by accumulating data on the frequency of various interactions occurring in particular dyads, and postulating several kinds of social relationships for each dyad. But with only this type of analysis, all that is accomplished is the creation of a list of social relationships, which does not clarify the inter-relationships of social relationships. Furthermore, it is entirely useless for comparisons with different species which have different interaction repertoires.

The classification attempted in this report has identified at least three types of interactions and clarified their inter-relationships. These interactions occur in arbitrary dyads within a set, arbitrary dyads between sets, and specific dyads. These types of interactions may occur in, respectively, dominant-subordinate relationships, sexual relationships, and mother-infant relationships.

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