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The Emotions: Focus on Inter-Male
Agression and Dominance Systems
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SOCIAL REGULATION FOR INDIVIDUAL
COEXISTENCE IN PYGMY CHIMPANZEES
(PAN PANISCUS SCHWARZ 1929).

by

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Discussion Paper

on

Junichiro Itani's
INEQUALITY VERSUS EQUALITY FOR COEXISTENCE
IN PRIMATE SOCIETIES

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The Social Organization of Pan paniscus and Pan troglodytes
Similarities and Differences

In the outline of the paper to this Meeting submitted by Dr. J. Itani, it was said that the coexistence of groups in non-human primate societies was established on the two principles of equality and inequality. He said, further, that the dominance of either one or the other was generally determined by the primate's phyletic status. He went on to illustrate that among Cercopithecids inequality is dominant, while in the genus Pan for the first time we can see the establishment of equality. He confirmed a difference, too, between the two species Pan troglodytes (common chimpanzee) and Pan paniscus (bonobo or pygmy chimpanzee). He hypothesized that in the latter, especially, one can discern the first step towards an egalitarian society of hunting and gathering people.

P. paniscus and P. troglodytes have the same "basic social unit" (BSU), a fact reflecting their phylogenetical closeness. First, in both species the basal social unit is a unit group (or community) comprised of a plural number of males and females. Second-social fluidity-the members of the unit group undergo fission and fusion in response to social and ecological demands, and form diverse sizes of temporary associations (parties). Third, the rule is that as the female matures, she emigrates to another group while the male does not.

The first characteristic is not unusual in non-human primate societies. But the second and third points are special

characteristics seen only in the genus Pan. However, in their sub-basic social organization these two species, evidence a number of important differences. The members of the basic unit among P. troglodytes have a strong tendency to fission off into many small size parties. The temporary lone individual is common.

For example, in the Kasakela group in Gombe National Park, parties of six or less comprised 82%; those of ten or more members only 9% (Goodall, 1968). Many females with dependent offspring, in particular, separated into their own ranges where they foraged independently. Males and estrus females overlapped these mother-offspring ranges and foraged more widely. Accordingly, the opinion has even been advanced that the unit group and its range must apply only to the males (Wrangham, 1979). In contrast, there is the tendency among P. paniscus for larger-sized parties. For example, in the Wamba E group comprising about 70 members the size of which corresponds to that of the Kasakela group, parties with five or fewer animals were seen in only three instances among a total of 172 (Kano, 1982). The distinguishing characteristic of the P. paniscus party--with rare exceptions--is that, regardless of the party's size, they include all kinds of age and sex classes (adults of both sexes, adolescents, juveniles and infants). Further, the relative ratio of males to females is about 1:1 (Kano, 1982). The equalization of the sex ratio can be applied not only to the party but to the unit group (Kano, 1982). From 1979 to 1982, in two censuses conducted of adults and juveniles in E

group, there was a sex ratio of 1:1, but among the adolescents the number of females greatly exceeded that of males (Table). However that could be attributed to the fact that the adolescent females wandered between unit groups.

Among nonhuman primates, the large incidence of an equal sex ratio in the BSU is found only in P. paniscus (Itani, in a paper submitted to this meeting). In P. paniscus, too, there is evidence that more environmental pressure is working against the males than the females. In a 1982 census of E group, the proportion of individuals with permanent physical impairment (partial or total lack, dislocation, etc. of digits, hands or feet) among the adult females was 56% (n=25) and among adult males 86% (n=28). The sexual difference was significant ($p=0.0146$, also see Kano, in press). But this environmental pressure does not seem to result in effective selection pressure because since 1977, of the identified males, no member has been recorded as having disappeared or died.

The above differences between P. paniscus and P. troglodytes show that, as regards the former, there is more development of social regulations for member coexistence.

The purpose of this paper is to consider the differences in inter-group and inter-individual interactions in these two species and to discuss how these are reflected in the species-specific characteristics of social organization. Such a discussion, however, is somewhat hypothetical and preliminary, the reason being that much of the recorded data has not been analyzed yet and, concerning several important points, a longer,

more detailed study is considered necessary.

Individual Coexistence

Coexistence of Kins

Regarding the coexistence of offspring and mother in P. paniscus, a clear sex difference can be seen. In both sexes, from infancy (0-2 years) through juvenility (3-6 years) dependence on the mother slowly decreases, but late juveniles still move completely with the mother. Upon the advent of adolescence with the first signs of genital swelling, however, the female offspring abruptly sever their connection with the mother and leave the natal group.

All the male offspring, on the other hand, pass through adolescence, and even after entering young adulthood continue to travel with the mother (Some small parties comprise only a young adult male and an aged female. They are the mother and her oldest male offspring). Between them there is frequent co-feeding and mutual grooming; it is also not unusual for the mother to exhibit protective and food-sharing behavior. It is conjectured that their close affiliation probably lasts until one or other dies.

The writer has never observed any dominant behavior on the part of the offspring towards the mother, or fear or deference on the part of the mother towards her male offspring. Among P. troglodytes there are not a few instances of a female remaining in or returning to her natal group once she had separated from her mother (Goodall, 1977). In P. troglodytes a male having entered the adult period is incorporated into

the male bond and its connection with its mother becomes weak. Sometimes the mother comes to fear such a male offspring (Goodall, 1971). Sexual difference in affiliation between an offspring and mother is not as great in P. troglodytes as in P. paniscus.

Immature males, from their infancy on, frequently copulate with adult females. However in P. paniscus sexual inhibition between male offspring and its mother seems established in early infancy. Apart from some exceptional examples of two pairs, there is no recorded instance of copulation between a mother and her offspring. In contrast, it is not unusual to find copulation occurring between mother and immature male offspring among P. troglodytes (Nishida, pers. comm.). The occurrence of sexual interaction between mother and male offspring may have some connection with the term of male offspring dependence on the mother and the dominance relationship between them.

By emigration of the female, coexistence of siblings of different sexes comes to an end at a time when either is of an immature age. In contrast to P. troglodytes, there had been no clear observation of alliance between male siblings in P. paniscus (without exception, the older brother is dominant). One pair of male siblings, however, during the same period fell in rank within a group. Male siblings frequently engage in mutual grooming and never show severe aggression to each other. However, as concerns agonistic interaction with non-kin males, there has been no definite observation of mutual support among male siblings. It seems that they are bound together only

through the mother. As for their ties after the death of the mother, we must wait for further research or clarify that problem.

Coexistence within the Group of Non-Kin

As for the relation between mature, non-kin members within the unit group, excepting male and estrus females, competition has been thought to be the dominant state of affairs. The expression of competition and its regulation, that is, social interaction, is different from class to class.

Coexistence between Males

Compared to that between males and females, or between females only, there is an overwhelmingly high frequency of agonistic episodes between males (Kano, 1980). Aggressive behavior towards the target often takes the form of threat, pseudocharge, charge, and chase. Instances of attack (including such forms of physical contact as kicking, slapping, grappling, and so on) are far fewer. Even if attack should occur, when the victim responds, not by running away but by crouching, the attacker immediately moves to the substitute activity of mounting or of rump contact (two animals joined firmly together at their rumps; Kano, 1980), or alternatively, the attacker leaps over the victim while avoiding direct physical contact. The attacker does not usually attack violently (such as by biting).

While feeding, agonistic interactions take place much more frequently between males than between females, or between females and males. Compared to feeding, there seems to be far less sexual competition though the highest ranking males engage in

sexual interaction with females regardless of place, while lower ranking males lure females away from the others for copulation (Kano, in press c).

Submissive behavior also occurred with the highest frequency among males. The ranking was not necessarily in linear order. In the E group males, at least two alliances were noted. One was when five members formed a high ranking group, but when the fourth and fifth ranked males were separated from their comrades, they sometimes showed submissive behavior (expression of grimace, screeching, avoidance, etc.) to the males whom they usually threatened. One other alliance consisted of three low-ranking males who always traveled together and showed no agonistic behavior to one another. Among the males in these two alliances none was suspected of still having a mother.

There were 12 adult males not in the alliance. Of these, 8 young males often traveled together with a female thought to be the mother. Two males were aged; the other two were physically handicapped and socially inactive. Among the young males, three plus one late adolescent male were for a time extremely assertive among the other males. They were similar in having an aged mother who received respect from the other members. For a while, one of them was even alpha-male (Kitamura, pers. comm.) but when the mother became timid after giving birth, he dropped in rank, returning to the group of males of the lowest rank. A late adolescent male whose mother rose to the rank occupied by the previous female, became dominant to all the other males which associated frequently with him. Also,

in the case of another young male, he received the actual support of his mother. One day he suddenly began direct and persistent charging displays towards the second ranking male. At first the latter ignored him, but then began to punish the attacker by slapping or chasing him. At this time the attacker's mother restrained the second ranked male by barking at or attacking him, sometimes receiving help from other females until she repelled him. A few days later the second ranked male, when faced by a charge from the same young male, instantly ran away. This episode shows that the young male's sudden rise in rank was a sham, depending as it did on the mother's assistance.

This kind of sudden assertiveness is thought to be prompted by a young male's need to enter the ranks of adults, stemming from his physical and social development. But the mother's presence and intervention delays his settling into his proper rank.

Among P. troglodytes, within the unit group, males form a firm bond and among them their ranks are strictly linear. Through frequent social grooming etc., they strengthen their "we-feeling" and cooperate in confronting males of other groups (Nishida, 1979). Among P. paniscus, however, the rank order is not as strict nor is the grooming between males nearly as common as that between males and females and between only females (Kano, 1980; Kuroda, 1980). From this we can deduce that the male's "we-feeling" is correspondingly weaker in P. paniscus.

Coexistence between Adult Males and Adult Females

P. paniscus and P. troglodytes are similar in that the

external genital organs of the females have a swelling cycle.

But there are two points of difference between them.

1. The maximum swelling phase of P. troglodytes averages 7-10 days (Goodall, 1969; Nishida, 1977; Tutin, 1979) whereas it is not unusual for that of P. paniscus to continue more than 20 days (Kano, in press b). One past-prime female even maintained maximum tumescence for about ninety consecutive days.
2. P. troglodytes females neither resume their sexual cycle nor engage in copulation for an average of three years following parturition. P. paniscus females, by contrast, recommence the swelling cycle anywhere from two to three months to a year after parturition and then engage actively in sexual interaction (Kano, in press b).

Females of both species copulate during the period of maximum tumescence. The paniscus female, as noted above, is sexually receptive more continually and involved in sexual intercourse with males far more frequently than her troglodytes counterpart (Kano, in press b).

P. troglodytes become pregnant within two or three cycles after resuming sexual swelling and almost their entire lives are spent either in a nursing or gravid state (Goodall, 1968; Coe et al., 1979). By contrast, P. paniscus females, can be said to spend most of their reproductive life in nursing and copulation. The birth interval of both species, however, is similar (4-5 years). That is, the greater part of copulations of P. paniscus does not lead to pregnancy. It would seem

then that the fact that the paniscus female has prolonged sexual receptivity is more for making coexistence possible with the male than it is for reproduction. Several young females frequently solicited high ranking males in order to get food (Kano, in press b). This is one proof of the socialization of sexual behavior.

Social grooming was most frequent between males and females (Kano, 1980; Kuroda, 1980), yet grooming with the mating partner was rare. Mounting or rump contact between male and female was often seen, although its frequency was less than copulation. It took place more often between males and females who were not yet fully in estrus. It may be that such behavior serves as a form of appeasement between males and females who cannot engage in sexual interaction.

Among P. troglodytes the male generally dominates the female (Reynolds and Reynolds, 1965; Riss and Goodall, 1977). In P. paniscus, however, no clearly dominant/subordinate relationship could be found between an adult female and male. Generally, the paniscus adult female does not hesitate in approaching a male in order to obtain food. Even the highest ranking male is disconcerted at such an approach and often leaves, taking some food with him. As a result, the female supplants that male and has free use of the food left behind. Sometimes a high ranking male, occasionally even an alpha-male, is threatened or chased by a female or group of females. Almost all males of middle lower rank are patently more subordinate than the full adult female in all kinds of social

situations.

The male paniscus even seems to be somewhat psychologically inhibited from demonstrating aggressive or dominant behavior toward an old female. That may very well have some connection to the male's prolonged dependence on its mother.

Coexistence among Females

The adult female troglydytes is characterized by unsociability. During the non-estrus period she lives alone with her offspring; only during estrus does she go with the male. Troglydytes females seldom associate. There is a minimum of social grooming between females (Nishida, 1970; Sugiyama, 1969).

In contrast, P. paniscus females often engage in a variety of social interactions. At times of group excitement, for example when arriving at a feeding site, or when the parties come together, "genital rubbing" (ventro-ventral embracing and rubbing of their sexual organs together) frequently occurs among females (Kuroda, 1980; Kano, 1980). This activity appears to reduce tension among the females and is an activity that permits mutual proximity. This genito-genital contact takes place during the non-swelling phase, too, but is most frequent at the time of maximum swelling. Therefore, the prolongation of the female's maximum tumescence is useful for peaceful coexistence among the females themselves.

Social grooming is more frequent among females than males. Also, there are special females who often associate together. On many occasions females will band together to

counterattack when they are confronted with threats from males. There is obviously some kind of "we-feeling" among these females.

It appears that younger females show respect towards older ones but there is no evident dominant/subordinate relationship among females. Aggression between females is at a minimum. When it does occur, they grapple with one another and roll on the ground. Such fights often bring in many other females and cause a general uproar. Whereas aggression among males is uni-directed, that is, one always shows aggressive behavior to the other who always shows submission that between females is more diffuse, a fact which seems to reflect the lack of a clear rank order among females. The bonds among females may be thus formed on something other than dominant/subordinate relationships.

Immigration of Adolescent Females and Its Process

Among both P. troglodytes (Goodall, 1968) and P. paniscus (Kano, in press b), the genital swelling of adolescent females is smaller than that of adults; adolescent females have no regular cycle and are sterile for 4-5 years. The greatest difference is that among P. troglodytes, in which the adolescent swelling is not attractive to the adult male, mating between an adolescent female and an adult male is very infrequent (Goodall, 1968). Among P. paniscus, however, the mature males are attracted to the adolescent swelling which exhibits maximum tumescence almost continuously.

In short, it is always possible for the adolescent female

to mate with the males and to engage in genital rubbing with other females. This is quite effective in getting them admitted into other unfamiliar groups. The adolescent female is the class that is most active in copulation and genital rubbing. They not only always respond to solicitation for copulation or genital rubbing by presenting or mounting but actively initiate it. They wander to groups other than their natal one and, upon entering late adolescence, become especially close to a certain group. At the time of first parturition (that is, on entry into adulthood) they become a stable member of that group.

It has been the writer's observation that females with offspring have a solid sense of being in the in-group. Only once was a female with young observed associating with an outside group (a P group primiparous female entered the E group for only one day).

Group Coexistence

Among P. troglodytes interaction is represented by antagonism between males. Fights between males of different groups sometimes results in the death of some of the combatants (Goodall et al., 1979).

In P. paniscus the group range largely overlaps (between 40% and 66%, Kano, 1982; in press c) and the important food resource is included in that overlapping portion. Through avoidance, however, group encounters are minimized. Between groups of P. troglodytes, dominant/subordinate relationships do exist, but, in the case of P. paniscus, which group is

dominant or subordinate depends on the circumstances of the moment. The size of the party is especially an important factor. When there is an actual encounter between groups, a variety of behavior ensues, from fighting (Kitamura, pers. comm.) to peaceful mixing in the bordering area. Until now, no observation has been made of participants killed during severe intergroup fights.

Discussion

P. paniscus is more gregarious than P. troglodytes. For intergroup competition it is an advantage to form a large party, but that may also escalate intra-group competition. Many kinds of primates, through strengthening the dominance hierarchy, lower the outbreak of aggression that may arise from intra-group competition. Dominance hierarchy itself does not promote peaceful coexistence between group members. It only acts to suppress excessive outbursts of aggression. Thus, generally, a species which has a more rigid hierarchy shows aggressive and/or dominant/subordinate behavior more frequently.

Dominance hierarchy establishes an order of priority in competition. Accordingly, those lower ranking members have fewer opportunities to get food or approach mating partners than higher ranking ones. Within the same species the male usually makes a stronger dominance hierarchy than the female. This has the effect of making the number of males fewer than females. In the unit group of P. paniscus, however, the

number of males and females is about equal. This means there is no powerful dominance hierarchy within and between all age-sex classes. To put it another way, this suggests that intra-group competition is neatly avoided.

Let us look first at the mechanism for avoidance of competition from the social and then from the ecological side. In the social group of P. paniscus, the dependence of the male on its mother and the long duration of that closeness, the equality of the female vis-à-vis the male, and the coalitions among females, all seem to depress the formation among males of a powerful dominance hierarchy. Among many other primates grooming is the single important friendly behavior among group members. But with P. paniscus, in addition to grooming, a variety of other kinds of behavior have developed to deepen affiliative relations and to dissolve tensions among them. All of those forms include genital contact. That is to say, all originate in copulatory behavior (Kano, in press c).

Copulatory behavior itself exceeds the original purpose of reproduction and is employed to develop affiliation between the male and female. Through the socialization of sexual activity in P. paniscus, peaceful coexistence of the group members of all age-sex class is made possible. In order to reduce sexual competition between males, to strengthen the bond between male and female, and further to facilitate affiliative relations among the females, it is important that the female has attained a condition of semi-continual

estrus.

Much of the major food of P. paniscus is produced in giant trees or huge vines covering the tops of those trees in the rain forest. Those foods change seasonally and are not evenly distributed in the forests. Because their food grows in abundance in one place and changes with the season, P. paniscus, by organizing themselves into large parties, can maximize their feeding efficiency.

In physical ability, the male is superior to the female, and thus has greater access to food. Further, males have almost no direct role in raising offspring. P. troglodytes females with their dependent offspring, by foraging independently avoid direct competition with males and effectively utilize the more widely dispersed food. The disadvantage of paniscus females with young is alleviated by other social means. On reaching a food tree, the low-medium ranking males (which are in most cases in front of the others) first help themselves, but as higher ranking males arrive, they take what food they can carry from the tree and retreat. Females, however, who arrive late, assure themselves of co-feeding through genital rubbing. Some time later, the tree is occupied by two or three high-ranking males and many more females. The result is that these females and their young can enjoy relaxed feeding over a longer time. Thus the higher antagonism between males in a group than between females has a very important bearing on the survival of the females and their young. Because of that, this has a selective advantage.

The fact that the unit group has a large overlapping range in which major food sources are included, increases the efficiency of gathering food occurring in large quantities at one spot.

That males are not lost in P. paniscus society suggests in part that inter-group antagonism is not as strong as in P. troglodytes. The large degree of overlapping area blurs the value of territorial defense. By enlarging their territory, P. troglodytes make available to themselves a larger number of females (Goodall, 1983). But among P. paniscus, the "in-group feeling" among females is strong and expansion of territory is not connected with an increase in available females.

With regard to exploitation of food resources, it appears that P. troglodytes are better at it than P. paniscus. The former has a greater diversity of food and makes use of a larger variety of daily-monthly food (Kano, in press c). They are less conservative in trying new kinds of food (such as crops) and have succeeded in developing a greater variety of animal foods than P. paniscus. For hunting and acquiring food, as well as for processing it, reports have come in from many localities of P. troglodytes' use of tools (e.g., Goodall, 1965, 1968; Nishida, 1973; Nishida and Uehara, 1980; Nishida and Hiraiwa, 1982; McGrew, 1974, 1979; Sugiyama and Koman, 1979; Boesch and Boesch, 1981). As for P. paniscus, however, no such behavior has been reported except a single instance based on indirect evidence from Lomako (Badrian et al., 1981).

Because of their great ability to exploit food resources, P. troglodytes have come to occupy a geographical range (including a diversity and a greater severity of food environments) far wider than that of P. paniscus (Kano, in prep.). By contrast, it appears that P. paniscus live in a more stable food environment (Kano, in prep.). They spend less time on subsistence activities (Kano, in press c). The remaining time they turn to the development of social behavior for coexistence of members, and have succeeded in raising the survival rate of males to be nearly equal to that of females. Perhaps it has retarded the selection rate against some genes in the male. More than P. troglodytes females, P. paniscus females completely break their relation with the natal group. This suggests that the inbreeding coefficient in a P. paniscus unit group may be lower than that of P. troglodytes. This means that the selection rate against certain recessive genes in P. paniscus is slower. This, and the fact that genetically the selection rate is slower, suggests that P. paniscus may preserve a greater primitivity than P. troglodytes.

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Table Composition of the E group in 1979 and 1982

	1979	1982
Adult Males	15	21
Adult Females	16	18
Adolescent Males	5	5
Adolescent Females	8	14
Juvenile & Infant Males	10	9
Juvenile & Infant Females	9	9
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Total	63	76