

SHORT COMMUNICATION

Association and Social Interactions Between Strangers and Residents in Bonobos (*Pan paniscus*)

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ABSTRACT. This study reports on close spatial association and repeated behavioural interactions between two strange adult male bonobos with residents of another community. Over a period of 12 months one of the two males developed friendly social relations to some of the females and other residents, which were indistinguishable from those existing between co-residents. Aggression by resident males against the strangers decreased but the former remained intolerant. The strange males appeared at a time when the number of adult resident males was lower as in the years before and when the adult sex ratio (number of adult females per male) was higher as in the years before. Using definitions from studies on dispersal patterns of male gorillas (HARCOURT, 1978) and female bonobos (FURUICHI, 1989) the spatial association between the two strange males and residents could be described as male transfer.

Kew Words: Bonobo; *Pan paniscus*; Inter-community relations; Transfer.

INTRODUCTION

In group-living animals, variation in group composition is affected by demographic factors such as birth, death, and natal dispersal. While birth rates of males and females are normally close to equilibrium (FISHER, 1930), rates of dispersal are usually biased. Out of 64 primate species where information on dispersal is available, 34 (53.1%) are male biased, 10 (15.6%) are female biased while in 20 species (31.2%) both sexes disperse (ROWE, 1996). The tendency of female primates to remain in their natal group is causally linked to the quality of major foods such as fruit, seeds etc., which are more likely to be contested than a folivorous diet (WRANGHAM, 1980; VAN SCHAIK, 1989). In species with male philopatry such as *Colobus badius* (STARIN, 1994), *Papio hamadryas* (SIGG et al., 1982), *Ateles chamek* (SYMINGTON, 1987), *Brachyteles arachnoides* (STRIER, 1993), *Pan troglodytes* (GOODALL, 1983; NISHIDA et al., 1990), and *P. paniscus* (IDANI, 1991; FURUICHI, 1989), adult males usually tolerate the presence of only natal males. Dominant males may derive payoffs when subordinates keep in resource defence (WATTS, 1989). ROBBINS (1995) suggested that tolerance by older, dominant males of the mating activities of younger males may be a strategy to reduce the risk of later infanticide by them. Young males of low rank may gain benefits from mating within their natal group when the costs of transfer are high (ALBERTS & ALTMANN, 1994) or when information about potential cost and benefits are ambiguous (NUNN, 1999). Reviewing published data from various taxa of birds and mammals, GREENWOOD (1980) found that males of many avian species were philopatric, whereas males of most mammalian species were exogamous. He suggested a causal relationship between dispersal pattern and mating system, with resource defence promoting

male philopatry and mate defence favouring female philopatry. The aims of males joining another group are variable and may change with age, social circumstances, and demographic conditions (for a review see PUSEY & PACKER, 1987). Intrasexual competition and inbreeding avoidance are thought to be major forces for natal dispersal of males (HARCOURT, 1978; PACKER, 1979; POPE, 2000). The potential to increase in dominance status may also promote natal dispersal (CHENEY & SEYFARTH, 1983). Secondary dispersal of older males is thought to be related to suboptimal breeding conditions (PAUL & KUESTER, 1985) or the result of forceful eviction (SOMMER, 1988).

In bonobos dispersal is characterized by female exogamy. Evidence comes from two long-term studies. From Wamba, FURUICHI (1989) and FURUICHI et al. (1999) reported on a number of cases of immigration by females. Analyzing mitochondrial DNA from the same community, HASHIMOTO et al. (1996) found that residents belong to different matriline, a result which also supports the idea of female exogamy. Information from early research at Lomako also suggests migration by females (THOMPSON-HANDLER & MALENKY, 1993). During observations on one community, conducted between 1990 and 1998 at the same site, several females visited the community for short periods and one immigrated (own unpubl. data). Analyzing genetic relations between members of this community, GERLOFF et al. (1999) found that resident females were unrelated but most adolescent and adult males lived with close relatives. However, average relatedness among males and among females did not differ (GERLOFF et al., 1999). The lack of disparity in relatedness coefficients between males and females may be due to small sample size, but two alternative explanations are possible: (1) resident females mate with males from other communities; or (2) male transfer. In the following we report on the development of behavioural interactions between members of a habituated community of bonobos and two outside males.

MATERIAL AND METHODS

Observations of the Eyengo community by the author and other researchers started in 1990 and continued in annual field seasons lasting 4 – 12 months (50 months in total). The community occupies the eastern part of the Lomako study site and their home range overlaps with that of at least two other communities (BADRIAN & BADRIAN, 1984). Earlier studies sometimes referred to this community as the “Rangers” (WHITE, 1988). The community and its neighbours belong to a larger population inhabiting the forest between the Lomako and Yekokora Rivers (ERIKSSON, 1999).

After 16 months of field work (1990/1991/1992) the identity of adult and subadult community members was known. Stable markers such as missing digits or limbs, patterns of pigmentation, and other disfigurements facilitated identification of individuals. During the following six field seasons (1993 – 1998) members of the Eyengo community were observed for 34 months by researchers who were familiar with the identity of residents. Until 1996, the number of adult and subadult residents remained relatively stable, thereafter, it decreased.

Figures for community size refer to the total number of adolescent and adult residents and offspring. Most newcomers joining the community were infants, born to resident females. One adult female joined the community in 1995 and stayed until August 1998. At different times, four adolescent/adult females without infant visited the community for up to one week but disappeared thereafter. Without precise information on age, we distinguished between adolescents and adults on body size, testes size, cyclic changes in female swellings, and behavioural traits. Socioeconomic sex ratio was calculated by dividing the number of adult and adolescent females by the number of adult and adolescent community members.

Table 1. Total number of days/hours of observation of members of the Eyengo community and number of days/hours, residents from this community were seen together with the two strange males.

Year	Month	Total observation time days/hours	Strange males and residents (days/hours)
1997	September	27/151	5/32
1998	April	30/166	6/40
1998	July	10/59	3/20
1998	August	15/67	4/17

Observations were recorded *ad lib* from September 1997 to August 1998. The term "strangers" is used to distinguish the two males from residents. It does not imply that these males were unknown to residents since they may have been members of a neighbouring community. Data on behavioural interactions between residents and the two strange males are available from three periods (Table 1). From November 1997 till March 1998 and from May till June 1998, the author was absent from the site and bonobos were observed by students. During this period the two males were seen together with members of the Eyengo community every month at least once.

Faeces were used as a source for DNA. Samples were collected a few minutes after defecation from known individuals and were only sampled when we found no signs suggesting contamination with material from other individuals. Five unlinked CA-microsatellite loci tested to be polymorphic in bonobos (GERLOFF *et al.*, 1995) were used for comparison, following a procedure described by GERLOFF *et al.* (1999).

RESULTS

BEHAVIOURAL OBSERVATIONS

After seven months of absence from the study site, field work was resumed on September 23, 1997. On October 1, two strange males were seen within the central part of the home range of the Eyengo community. Both individuals showed signs of fear although no other bonobos were seen. Body size, size of testes, and other visible traits suggested that both males were fully adult. One individual showed signs of old age (wrinkled face, sparse hair), the other had no signs of aging.

October 4, 1997: The same males were seen again, this time in sight of members of the Eyengo community. Resident males and females charged the two strangers who responded with submissive vocalizations and retreated. Following a joint attack by three adult females, the older male bled from wounds on one leg and both hands. After 70 min the residents left and the two males were not seen again that day.

October 13, 1997: In the late afternoon, residents encountered the same two males when they travelled in the western part of their home range. Again, resident males made agonistic displays and adults of both sexes charged the strangers. Some of the joint attacks by residents involved severe physical aggression. That night the two males built their nests about 200 m from the residents.

October 14, 1997: After leaving their nests, the residents of both sexes harassed and charged the two males. The two males followed a mixed party of residents for about 2 hr before the males disappeared.

October 28, 1997: The two males were seen early in the morning in close vicinity to a mixed party of residents feeding in a fig tree. Two resident males charged one of them. Thereafter, they were not seen again that day.

For the next five months (November 1997 till March 1998), the two males were seen on and off by student assistants who were familiar with the residents. Figures of the frequency of sightings are not available for this period but all occurred within the range of the Eyengo community. When the author returned to field by the end of March 1998, the following changes in the relation between the two males and residents were noted.

March 30, 1998: The younger one of the two males who had travelled together with a mixed sex party of residents nested in close vicinity (20 – 30 m) to one resident female. Next morning the male was feeding undisturbed at a distance of about 20 m from residents for 30 min. He left the food patch when residents moved on and travelled together with them for the next 3 hr before he disappeared.

April 2, 1998: The two males joined an all-female party of residents and followed it over the day without being harassed. An oestrous female approached the younger one of the two males who had mated dorso-ventrally. None of the resident males were present at that time.

April 3, 1998: The older male had genital contact (GGR *sensu* KURODA, 1980) with a juvenile female.

April 10, 1998: Both males followed a mixed-sex party of residents. Resident males directed agonistic displays against the two strangers but did not charge or attack them.

July 16, 1998: The younger one of the two males had rested for about half an hour together with two females in a food tree. When the male departed both females followed immediately.

July 30, 1998: An oestrous female presented to the younger male who mounted and mated with her ventro-dorsally two times. When the same female presented a third time, he ignored her. No other males were present.

August 19, 1998: The younger male ate with three adult females in the same tree. Later that day, an adult female groomed the younger male.

August 20, 1998: The younger male played with an adolescent resident male.

From March till August 1998, one or both males were seen on 37 days. On 18 days, they were seen together with members of the Eyengo community, on 19 days, the two males appeared to travel solitary. All sightings were made in the northern region of the Eyengo home range used by residents during that time (Fig. 1). There is evidence that the range of the Eyengo community overlaps with that of neighbouring communities but the size and extend of these areas is unknown. On days when both strangers and resident males were travelling together ($N = 20$), all matings with adolescent and adult resident females ($N = 18$) involved resident males. When the younger one of the two strange males was seen to mate with a resident female ($N = 3$) none of the resident males was present.

GENETIC RELATIONS

During this project, four adult males of the Eyengo community disappeared (Table 2). All four showed signs of aging before they disappeared. Two of them had missing digits and other irreversible disfigurements. The remaining two males had no such signs. The younger male clearly did not correspond in age with the former residents but the older one did belong to the same age class. Therefore, we could not exclude the possibility that one of the two strange males was a former resident of the Eyengo community. To test this possibility, we extracted DNA from fresh faeces from the old male and compared alleles of five micro-satellite loci available from the old strange male and former resident males. Alleles of three loci of the old male were different from those of adult males who had disappeared from the Eyengo community since 1991 (Table 2).

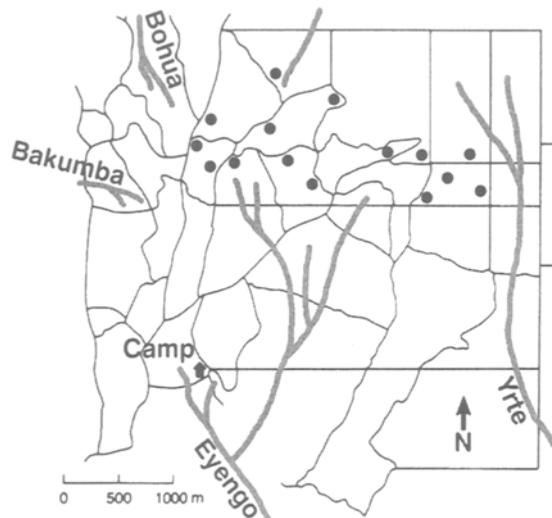


Fig. 1. Map of the central part of the home range of the Eyengo community. It shows trails (thin lines), rivers (thick lines), and places where the two strange males were observed (dots). Each dot represents the site where the two males were encountered first on a given day and some dots represent several days.

Table 2. Alleles from five loci from resident males who had disappeared from the community (Samuel, Max, Karl, Renki) and from one strange male (new male) belonging to the same age category. In three loci (D1, D6, D16) the new male differs from former residents.

	New male	Samuel	Max	Karl	Renki
D1 S207	175/153	167/153	171/147	157/151	157/151
D2 S141	145/143	145/143	144/144	143/139	143/139
D6 S271	190/190	190/182	186/182	190/182	190/182
D16 S402	176/172	168/162	168/164	170/166	166/162
D17 S791	166/158	166/156	166/158	158/158	158/156

DEMOGRAPHIC DEVELOPMENT

Table 3 shows data on demographic developments in the Eyengo community from 1991 to 1998. During this period, community size and number of adult females remained relatively stable. However, the number of adult males dropped from 7 (1993) to 3 (1998) and the number of adult females per adult male increased from 1.7 (1994) to 4.0 (1998).

Table 3. Demographic changes of the Eyengo community between 1991 and 1998.

	1991	1992	1993	1994	1995	1996	1997	1998
CS	33	35	34	36	34	33	30	30
NAF	14	14	14	12	15	15	12	12
NAM	6	6	7	7	6	5	4	3
SSR	0.68	0.68	0.70	0.68	0.71	0.75	0.75	0.80
ASR	2.3	2.3	2.0	1.7	2.5	3.0	3.0	4.0

Figures given for community size (CS) refer to all identified adult and adolescent individuals and their offspring seen during the course of the respective field season. NAF: Number of adult females; NAM: number of adult males; SSR: socionomic sex ratio (number of adolescent and adult females/number of adolescent and adult individuals); ASR: adult sex ratio (number of adult females/number of adult males).

DISCUSSION

In spite of the large number of publications reporting on inter-group transfer, operational definitions separating this event from other types of contacts between members of different groups are scarce. Studying inter-unit-group transfer of female bonobos at Wamba, FURUICHI (1989) distinguished between temporary visits and permanent transfers. The former category referred to non-resident females who disappeared again shortly after visiting another unit-group. The second category refers to females who became stable members, that is, individuals who did not emigrate shortly after immigration. HARCOURT (1978) distinguished "visits" (less than one day) from "transfers" (longer than one day). Using these terminologies, the association of the two males with residents of another community can be termed transfer. What remains to be seen is whether or not the two males will become stable long-term members of the community.

In primates male intruders may have different aims: (1) They may invade home ranges of neighbouring communities to recruit females (GOODALL, 1983); (2) Males may visit neighbours in order to seek additional mating opportunities outside their own group or community (PALOMBIT, 1994; REICHARD, 1995); (3) Males may enhance mating opportunities by transferring in another group with a more favourable socioeconomic sex ratio (PACKER, 1979); or (4) in groups providing them with better opportunities to raise in rank (CHENEY & SEYFARTH, 1983).

There was no evidence that the two males tried to lead resident females away from their home range and their inferior behaviour towards residents makes any speculations in this direction very unlikely. Did the two males gain mating opportunities? As described above, one male was seen to mate with a resident female three times. Considering the opportunistic way of data collection, it is very likely that mating of strangers with resident females occurred both, at an earlier time and more frequently. During encounters of mixed parties of different communities, resident females may mate with strange males within few minutes after an encounter had taken place (THOMPSON-HANDLER, 1990; IDANI, 1990; KANO, 1992). Compared with encounters between mixed-sex parties of different communities, resident females remained aversive for a very long time. Considering the long time of female resistance together with the frequency and intensity of attacks by residents, it seems that the strange male gained mating opportunities at relatively high costs.

Could the efforts by the two males to associate with members of the Eyengo community have been made in attempt to transfer into that community? If so, they took place when conditions were most favourable: First, because of the drop of the number of adult males the potential of resident males to prevent access to females was reduced. Second, the two males appeared in the home range of the Eyengo community at a time when the number of adult females per male had doubled compared to previous years.

Because of the lack of any information on the previous history of the two males, their social status and possible changes remain unknown. It was found that the rank of male bonobos decreases with age (KANO, 1992; FURUICHI & IHOBE, 1994). In this case, older males may be attracted by communities with fewer male residents.

Reports of male chimpanzees joining established communities come from three sites. At Mahale, one juvenile male came into contact with members of another community when his mother temporarily joined this community. Both individuals were attacked by resident males and females (NISHIDA & HIRAIWA-HASEGAWA, 1985). At Bossou, two adult males joined another group for several days, another one stayed for several months (SUGIYAMA, 1999). Although tension was high, visitors and resident males were seen to interact in a friendly manner with each other. At Gombe, two immature males immigrated together with their mothers and became

members of this community (GOODALL, 1986). Evidence for occasional male transfer into mixed-sex groups is also available from mountain gorillas at Karisoke (STEWART & HARCOURT, 1987).

In African Great Apes, inter-community transfer by adult males is apparently rare and may occur only under certain social or ecological conditions. It could be argued that male transfer is a relic of an ancestral trait and no longer adaptive. However, if female exogamy causes large inter-community variation concerning the number of females per male, male transfer may indeed become a beneficial strategy.

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