学位申請論文

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主論文

Male-male relationships of wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire.

Running title: Male relationships of wild bonobos.

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Abstract

Male-male relationships of wild bonobos (Pan paniscus) of two adjacent unit-groups (E1 and E2 groups), which were divided from E group, were studied at Wamba in the Central Zaire Basin, by analyzing the proximity and social interactions among males. Dominant-subordinate relationships between a male-male dyad were easily recognized from the directions of each agonistic interaction. Male bonobos rarely joined forces in aggression. Clear difference of social status existed between adult and adolescent male bonobos in both groups, as reported on that of chimpanzees (Pan troglodytes). The presence of mothers in the unit-group greatly influenced the dominant-subordinate relationships among males through strong mother-son bonds in both groups. However, the degree of the mother-son bonds was different between the groups. Males of E2 group participated more frequently in agonistic or affinitive interactions than males of E1 group did. Males of E1 group were divided into several clusters spatially, while there were cohesive relationships among adult males in E2 group. The difference of the mother-son bonds between the groups may be explained from the way of separation of males at the time of the division of E group. Difference of male-male relationships between bonobos and chimpanzees seems to be related with difference of intra- and inter-unit-group competitions among males between the species.

Key words: Pan paniscus; Male-male relationships; Mother-son bonds; Male cohesiveness; Between group difference.

Introduction

The social unit of bonobos (Pan paniscus) is a patrilineal group; males remain within their natal groups and females transfer between groups (Kano, 1982, 1986; Furuichi, 1989), as that of chimpanzees (Pan troglodytes) (Nishida, 1968; Goodall, 1986). This social unit of bonobos is called a unit-group (Kano, 1982; Kitamura, 1983) corresponding to the unit-group (Nishida, 1968) or communities (Goodall, 1983) of chimpanzees. A unit-group usually splits into several temporary parties in both species (Kuroda, 1979; Kano, 1982; Nishida, 1968; Goodall, 1986).

Male chimpanzees, who are closely related, form a male-cluster which plays an important role in integrating the unit-group (Nishida, 1979; Kawanaka, 1984; Goodall, 1986), and female chimpanzees tend to move alone or in small parties except for the estrous periods (Nishida, 1979; Wrangham, 1979; Halperin, 1979). On the other hand, bonobo females, who are not closely related, aggregate in the center of the party (Kuroda, 1979; Kano, 1982; White, 1988; Furuichi, 1989), and strong male bonds have not been detected in bonobos. Old female bonobos maintain strong bonds with their grown sons (Kano, 1986; Furuichi, 1988; Kuroda, 1989), and the presence of mothers in the unit-group seems to affect their sons' dominance rank (Kano, 1986; Furuichi, 1988, 1991). However, it is males that maintain the boundary of an unit-group of bonobos (Ihobe & Idani, 1988; Ihobe, 1990) as chimpanzees. When two unit-groups of bonobos encountered with each other, males of different unit-groups kept a certain distance between themselves and they rarely participated in affinitive interactions (Ihobe & Idani, 1988: Idani, 1991).

To understand the societies of bonobos, which is patrilineal and has the cohesive nature of females, it is necessary to clarify the social relationships among male bonobos, on which aspect previous studies of bonobos have not been focused. This paper describes the proximity and social interactions among male bonobos of two adjacent unit-groups at Wamba to clarify their social relationships and discuss the difference of their social relationships between the unit-groups in relation to mother-son bonds and the history of the unit-groups.

Methods

Two unit-groups of wild bonobos (Pan paniscus), named E1 and E2 groups, were studied from November 1986 to February 1987 at Wamba (0°01'N, 22°34'E) in the Central Zaire Basin. The bonobos of Wamba have been studied intermittently since 1973 and the main study group (E group) has been habituated and provisioned with sugarcane since 1976 (Kuroda, 1979; Kano, 1982). The E group divided into E1 and E2 groups between 1981 and 1983 (Furuichi, 1987).

Observations were carried out mainly at three permanent provisioning sites named FS1, FS2, and FS3 (Fig. 1). Each permanent provisioning site has an area of about 1000 square meters. Sugarcane, which was cut into 30-40 cm pieces, was placed against fallen trees at regular intervals to accommodate as many individuals as possible. When natural fruits were abundant, they seldom visited these permanent provisioning sites. During such fruit-abundant periods, a small quantity of sugarcane was given near their sleeping sites early in the morning to

observe social interactions in detail. Only the social interactions observed at the permanent provisioning sites and at temporary provisioning sites were analyzed since observation time of each individual were easily detected there.

In the study period, the members of E1 and P groups encountered with each other for about 20 times at FS1 and FS2 (Ihobe & Idani, 1988; Idani & Ihobe, 1988; Idani, 1991). Data obtained on these days were not included since social interactions among males of E1 group seemed to be affected by the presence of P group. E1 group, except for the encounters with P group, was observed on 37 days (108 hr 37 min), and E2 group on 34 days (131hr 26 min). Of the total observation hours of E1 group, 102 hr 50 min was spent at the permanent provisioning sites, 3 hr 35 min at temporary provisioning sites, and 2 hr 12 min was spent following a party in the forest; and that of E2 group, 47 hr 3 min, 26 hr 19 min and 58 hr 4 min, respectively.

Table 1 shows the age-sex compositions of E1 and E2 groups in February, 1987. The classification of age followed Furuichi (1987); adult ($\geq$ 15 years old), adolescent (9-14 years old), juvenile (5-8 years old) and infant (0-4 years old). The adult class was further divided into three categories; old ($\geq$ 31 years old), prime age (20-30 years old) and young (15-19 years old). The subjects of this study were adult and adolescent males of both groups. Social interactions in which these 20 males participated were recorded by the ad libitum sampling method on field notes or in a micro-cassette recorder. Agonistic, grooming and reassurance interactions were analyzed in this paper. Agonistic interactions consisted of dominant behaviors (attack, threat, charge, and chase) and submissive behaviors (scream,

grimace, flee, and crouch) (Mori, 1984). A grooming bout was defined as continuous grooming in the same pair on the same direction. The grooming with a cessation of more than 1 min by the same pair in the same direction was regarded as different grooming bouts. Reassurance interactions consisted of rump contact or mounting behaviors. Table 2 shows the age, presence or absence of mothers in the unit-group, and observation time at the provisioning sites of each male. IB, MN and TW are maternal brothers in E1 group, and TO, JS and TJ are maternal brothers in E2 group.

At the permanent provisioning sites, spatial distribution of each individual was recorded by the scan sampling method with a 15-min interval. The attendance rate at the permanent provisioning sites (ATR), the percentage of scanning spend in the proximity with other males (PRP) and the attendance index at the permanent provisioning sites (ATI) were calculated as

$$ATR = \frac{F(A)}{\text{Total number of scanning}} * 100$$

$$PRP = \frac{FP(A)}{F(A)} * 100$$

$$ATI = \frac{F(A, B)}{F(A)+F(B)-F(A, B)} * 100$$

where F(A) is the total number of scanning for individual A, FP(A) is the total number of scanning in which one or more males were within 3 m of individual A, and F(A, B) is the total number of scanning in which both individuals A and B were present in the

permanent provisioning sites. Also, the proximity index (PRI) was calculated by the same formula as ATI, where F(A) is the same as for ATI but F(A, B) is the total number of scanning in which individuals A and B were found within 3 m.

Results

Dominance relations among males

The dominant-subordinate relationships between a male-male dyad were easily recognized from the direction of each agonistic interaction. Forty-five agonistic interactions among males were observed in E1 group and 70 in E2 group. Only once both males displayed alternately as dominants. In other 114 interactions, the direction of agonistic interactions was clear. Such interactions took the pattern as follows: One male approaches, threats or chases the other male and the latter moves several meters or runs away. After almost half of these interactions, reassurance behaviors were observed between the pairs who participated in the agonistic interactions.

Male bonobos rarely joined forces in aggression. Agonistic interactions in which two or more males attacked single male were observed once in E1 group and in three times in E2 group. Agonistic interactions in which single male attacked two or more males were observed twice in E1 group and once in E2 group. When cooperative attacks of two males occurred, the interactions took the pattern as follows: One male approaches and chases another male and the third male, who is near the males, joins chasing. Such interactions lasted for several ten seconds.

Table 3 shows the number of agonistic interactions and the dominant-subordinate relationships among males for both groups. Since there were few agonistic interactions among adult males in E1 group, the dominant-subordinate relationships in E1 group was determined by the same kind of data obtained in 1985 (Furuichi, 1991). Difference in the frequency of agonistic interactions among all males observed per 10 hours between the groups was not significant (Mann-Whitney's $U=42.5$, $n_1=10$, $n_2=10$, $p>0.05$). However, frequencies of agonistic interactions among adult males observed per 10 hours were significantly higher in E2 group than those in E1 group (Mann-Whitney's $U=7$, $n_1=7$, $n_2=8$, $p<0.05$).

Adult males were clearly dominant over adolescent males. Adolescent males directed no dominant behavior to adult males, while the latter directed no subordinate behavior to the former in either group (Table 3).

In E1 group, adult males, especially TN, frequently attacked HO (Table 3), so the frequency of agonistic interactions between an adult male and an adolescent male was higher than that between adult males in E1 group (Table 4a). On the other hand, this tendency was not found in E2 group (Table 4b).

The presence of mothers in the unit-group seems to affect their sons' rank in both groups. In E2 group, TO, KG, and JS, whose mothers were present in the unit-group, were in relatively higher positions in the rank order than FC, who was almost the same age as them and whose mother is thought to have died in 1985. The alpha male of E1 group (TN) seemed to get this position with the support of his mother (Furuichi, 1988).

Party compositions

The members of E1 group formed a large bisexual party during the first half of the study period, but they split into two bisexual parties on 4th January, and these two parties did not encounter after that day. Since one of these parties (including KK, IB, MN, TW and MO) scarcely visited FS1 or FS2, attendance rates at permanent provisioning sites (ATR's) of these five males were relatively low (Table 5). The members of E2 group usually foraged in a large bisexual party during the study period.

Proximity relations among males

Variances of attendance rates at permanent provisioning sites (ATR's) of males were large in both groups (Table 5). The rank order of ATR's was not correlated with dominance rank among males in either group (E1 group, Spearman's rank correlation coefficient r_s=-0.07, $p>0.05$; E2 group, r_s=0.31, $p>0.05$). The rank order of ATR's was not positively correlated with males' age in E1 group (r_s=-0.21, $p>0.05$), but that was positively correlated with males' age in E2 group (r_s=0.76, $p<0.05$).

The rank order of the percentages of scanning spend in the proximity with other males (PRP's) was not positively correlated with dominance rank among males in E1 and E2 groups (E1 group, r_s=0.24, $p>0.05$; E2 group r_s=0.60, $p>0.05$). The rank order of PRP's was not positively correlated with males' age in E1 group (r_s=0.21, $p>0.05$), but that was positively correlated with males' age in E2 group (r_s=0.66, $p<0.05$).

Frequencies that one or more males were within 3 m of an

adult male were larger than those of an adolescent male. If PRP's of both groups were combined, difference of PRP's between adults and adolescents was significant (Mann-Whitney's U=13, n_1=15, n_2=5, $p<0.05$).

Difference of PRP's between E1 and E2 groups was significant (Mann-Whitney's U=13, n_1=10, n_2=10, $p<0.01$), but ATR's between the groups was not significant (Mann-Whitney's U=27, n_1=10, n_2=10, $p>0.05$). This may reflect the different spatial distribution of males in the party; males of E2 group were in the center of the party, while males of E1 group were divided into mother-son clusters in the party.

Brothers tended to stay at the permanent provisioning sites with each other in both groups (Fig. 2). One of three prominent clusters comprised brothers (IB, MN and TW) in E1 group and one of two clusters was comprised two (JS and TJ) of the three brothers in E2 group.

There was a cohesive male relationship formed by KM, KG, HC, KD, and HJ in E2 group (Fig. 2). By contrast, in E1 group, there was not such a relationship and males were divided spatially into several segments at the permanent provisioning sites.

Figure 3 shows a dendrogram drawn from proximity indices (PRI's) by the group average method. In E1 group, since a linking level was very low, no particular tendency was found. In E2 group, a relatively higher proximity was detected in an unrelated pair (KM and KG).

Proximity relations among sons and mothers

In E1 group, attendance indices at permanent provisioning

sites (ATI's) between all males but MO and their mothers were higher than ATI's between them and other males (Fig. 4). In E2 group, ATI's between all males but YT and their mothers were almost the same as ATI's between them and other males (Fig 4). Since difference between ATI's with mothers and ATI's with other males was significant in E1 group (Mann-Whitney's U-test, $n_1=6$, $n_2=39$, $z=3.24$, $p<0.01$) and the difference was not significant in E2 group (Mann-Whitney's U-test, $n_1=5$, $n_2=35$, $z=0.59$, $p>0.05$), males of E1 group stayed more frequently at the permanent provisioning sites with their mothers than males of E2 group did.

In E1 group, proximity indices (PRI's) between sons and their mothers were extremely higher than PRI's with other males for all the males (Fig. 5). In E2 group, PRI's between sons and their mothers were higher than PRI's with other males for TO and YT, but corresponding values were almost the same as between males for other three males (Fig. 5). Difference between PRI's with mothers and PRI's with other males was significant in both groups (Mann-Whitney's U-test, E1 group, $n_1=6$, $n_2=39$, $z=3.74$, $p<0.01$; E2 group, $n_1=5$, $n_2=35$, $z=2.54$, $p<0.05$). However, if the records of YT, for whom the total number of scanning was only six (see Table 5), were excluded, the difference was not significant in E2 group (Mann-Whitney's U-test, $n_1=4$, $n_2=26$, $z=1.62$, $p>0.05$).

The mother-son bonds seemed to be stronger in E1 group than in E2 group. On the other hand, the male cohesiveness seemed to be stronger in E2 group than in E1 group.

Proximity relations among brothers

Attendance indices at permanent provisioning sites (ATI's)

between brothers were higher than ATI's with other males in E1 group, but ATI's between brothers were almost the same as ATI's with other males in E2 group (Fig 4). Proximity indices (PRI's) between brothers were higher than PRI's with other males in E1 group, but PRI's between brothers were not higher than PRI's with other males in E2 group (Fig 5).

The proximities among brothers may have not been directly caused by the affinitive relationships among them but have been caused by their simultaneous associations with their mothers. For all the combinations of brothers but JS and TJ, they rarely stayed at the permanent provisioning sites without their mothers (Table 6). The frequencies of grooming bouts between their mothers and them were higher than those between brothers as described below (see Table 7).

Grooming interactions

The frequencies of grooming bouts among males were higher in E2 group than those in E1 group (Table 7). The difference, however, in frequency observed per 10 hours between E1 and E2 groups was not significant (Mann-Whitney's $U=37.5$, $n_1=10$, $n_2=10$, $p>0.05$).

Particular pairs of males (e.g., KM and KG of E2 group) frequently groomed each other, and for all pairs in which grooming interactions were observed, the frequencies of grooming bouts were not correlated with attendance indices at permanent provisioning sites (ATI's) in E2 group ($r_s=0.62$, $n=10$, $p>0.05$). The frequency of grooming bouts between the brother pairs was not so high in either group. No grooming interactions were observed

between adult males and adolescent males in E2 group. Mutual grooming was not observed in either group.

In E2 group, there was no tendency that dominants more groomed subordinates or that subordinates more groomed dominants (binomial test, $p=0.38$). However, dominance rank among males was positively correlated with frequencies of grooming observed per 10 hours ($r_s=0.72$, $n=10$, $p<0.05$).

The mother-son bonds were stronger in E1 group than those in E2 group and the male cohesiveness was stronger in E2 group than that in E1 group as similarly indicated from the analyses of proximity relations. The frequency of grooming bouts between mothers and sons was extremely high in E1 group, while the frequency of grooming bouts between males was higher than those between mothers and sons or between males and females in E2 group (Table 8). This difference was significant between the groups ($\chi^2=70.0$, $df=2$, $p<0.01$).

Reassurance interactions

The frequency of this interaction observed per 10 hours was significantly higher in E2 group than that in E1 group (Table 9; Mann-Whitney's $U=2$, $n_1=10$, $n_2=10$, $p<0.01$). The alpha males of both groups participated more often in the interactions. Dominance rank among males was positively correlated with frequencies of reassurance behavior observed per 10 hours in E2 group ($r_s=0.75$, $n=10$, $p<0.05$), but this tendency was not found in E1 group since the interactions were very few.

Discussion

Dominant-subordinate relationships and the presence of mothers

The present study strongly suggests that the presence of mothers in the unit-group is an important factor which influences their sons' social position among males. Both in E1 and E2 groups, young adult males with thier mothers in the unit-groups were dominant over some old or prime adult males. However, a young adult male of E2 group (FC), whose mother is thought to have died, was not so. There were some anecdotal observations that young adult or adolescent males rised suddenly in the rank order by the influence of their mothers (Kano, 1986; Furuichi, 1988).

When males become adolescent or young adult, their mothers may support in agonistic interactions between sons and other group members. When TN became the alpha male of E1 group, his mother frequently supported TN (Furuichi, 1988). Since adult male bonobos are not dominant over females (Kuroda, 1979; Kano, 1986; Furuichi, 1988), adult males may not aggress against the mothers. Moreover, female bonobos tend to move in large bisexual parties (Kuroda, 1979; Kano, 1982; Badrian & Badrian, 1984; Furuichi, 1987), and old females maintain strong bonds with their grown sons (Kano, 1982; Kuroda, 1989; Furuichi, 1989). These tendencies of their association facilitate the support by mothers and result in the influences on the dominant-subordinate relationships among males.

Difference of social relationships between E1 and E2 groups

The degree of the influence of the mothers' presence seems to correspond to the degree of the mother-son bonds. From the analyses of grooming interactions and proximity relationships between mothers and sons, it was found that the mother-son bonds were stronger in E1 group than those in E2 group. After the division of E group, sudden rises of young adult or adolescent males in the rank order were only observed in E1 group (Furuichi, 1988).

The difference of the degree of mother-son bonds between the two groups seems to be related with other differences of social relationships among males. Proximity relationships among males were different between E1 and E2 groups. Males of E1 group were divided into several clusters spatially, while there were cohesive relationships among adult males in E2 group. Also, the frequency of social interactions among males was different between the groups. Males of E2 group participated more frequently in agonistic or affinitive interactions than males of E1 group did (Table 3 and 7).

In E1 group, strong mother-son bonds were detected. Such strong mother-son bonds in E1 group made males separate from each other into mother-son clusters in the unit-group and the frequency of social interactions among males decreased. On the other hand, in E2 group in which strong mother-son bonds were not detected, several adult males became a core in the proximity relationships and they frequently participated in social interactions among themselves.

The difference of the degree of the mother-son bonds between

the groups was also related with difference of frequencies of agonistic interactions among adult and adolescent males. The frequencies of these interactions among adult and adolescent males were higher than these among adult males in E1 group, but this tendency was not found in E2 group (Table 4). When the mother-son bonds are stronger like in E1 group, mothers more frequently support their adolescent sons and agonistic interactions more frequently occur among adult and adolescent males.

Small differences were observed between the habitats of E1 and E2 groups (Kano & Mulavwa, 1984). The group sizes and the sex-ratio of adults were almost same between the groups. Social relationships among males and females seem to be little different between the groups. The difference in the degree of mother-son bonds between the groups may be explained from the way of separation of males at the time of the division of E group. Before the division of E group, KM, whose mother was thought to have not been in the unit-group, was the alpha male of E group. KM and other four prime adult males (including HC) without their mothers in the unit-group formed cohesive relationships in E group and they were clearly dominant over the other males (Kuroda, 1982). Except for these five adult males, IB was the most dominant, and KR and KK were dominant next to IB. KK was gradually declining in the rank order (Kuroda, 1982). The five dominant males became members of E2 group and IB became the alpha male of E1 group. In E2 group, the dominant males of prime age could maintain their status probably through the strong cohesive relationship among them, and the presence of mothers in the unit-group did not affect their social relationships. By contrast,

dominant prime adult males were few and the strong cohesiveness among prime adult males was not formed in E1 group. The presence of mothers in the unit-group may easily exert influence on the social relationships among males in such a situation.

Comparison with chimpanzees

Clear difference in social status exists between adult and adolescent male bonobos like in chimpanzees (Bygott, 1979; Kawanaka, 1989; Hayaki, Nishida & Huffman, 1989). As Mori (1984) pointed out, adult male bonobos are clearly dominant over adolescent males. Adolescent males directed no dominant behavior to adult males and the latter directed no submissive behavior to the former in E1 and E2 groups. No grooming interactions were observed between adult and adolescent males in E2 group.

Adult male bonobos seem to be more cohesive than adolescent males like chimpanzees. From the analyses of percentages of scanning spend in the proximity with other males (PRP's), it was found that there were more males near adult males than near adolescent males. The prime or old adult males of chimpanzees tended to gather together, while young adult or late adolescent males were separated from those senior to themselves (Kawanaka, 1989).

Male chimpanzees compete for priority of mating with estrous females within a unit-group (Nishida, 1983), but they form a male-cluster within a unit-group against the males of different unit-groups because of agonistic relationships between the unit-groups (Wrangham, 1979). Male chimpanzees must intentionally form ambivalent or complicated relationships in which they

simultaneously associate and compete with one another (Nishida & Hiraiwa-Hasegawa, 1987; Takahata, 1990). Symmetrical interactions as mutual grooming, which avoid the overt expression of rank difference, frequently occur among males, and these interactions may facilitate complicated relationships among them (Takahata, 1990; Kawanaka, 1990). Males try to manipulate social relationships for getting a high mating success through coalitions (de Waal, 1982; Nishida, 1983).

On the other hand, competitions for reproductive success among male bonobos within a unit-group seem to be less than these among male chimpanzees because of prolonged female receptivity (Furuichi, 1989). Frequencies of mating were not correlated with dominance rank among males in E2 group (Ihobe, unpubl.). Relationships between the unit-groups of bonobos are never as fierce as those reported for chimpanzees (Ihobe & Idani, 1988; Idani & Ihobe, 1988; Idani, 1991). Male bonobos rarely joined in aggression, and mutual grooming among them was not observed in this study. In such a situation, complicated relationships among males detected in chimpanzees may not be formed and males become less cohesive.

Although bonobos and chimpanzees have patrilineal unit-groups and the boundary of a unit-group is maintained by males in both species, the coexistence of males in a unit-group may be achieved differently in the species. Male chimpanzees may achieve coexisting by manipulating ambivalent relationships caused by intra- and inter-unit-group competitions among them, while male bonobos may achieve coexisting by decreasing intra- and inter-unit-group competitions among them.

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Table 1. Age-sex compositions of E1 and E2 groups in February 1987.

E1 group	Adult	Adolescent	Juvenile	Infant	Total
Male	7	3	1	4	15
Female	9[1)]	1	3	4	17
Total	16	4	4	8	32
E2 group					
Male	8	2	2	4	16
Female	11	3+[2)]	3	3	20+
Total	19	5+	5	7	36+

1) Including a primiparous female of 11 years old; 2) there were several unidentified adolescent females other than three identified adolescent females.

Table 2. Adult and adolescent males in E1 and E2 groups and observation time of them.

Name (abbr.)		Age in years (* estimate)	Mother's presence	Observation[1)] time (min.)
a. E1 group				
Ten	(TN)	15	+	5948
Kake	(KK)	40*	-	2220
Ibo	(IB)	24	+	1504
Mon	(MN)	19	+	2572
Ika	(IK)	25*	-	4514
Hata	(HT)	30*	-	3426
Kuro	(KR)	35*	-	2768
Tawashi	(TW)	12	+	1037
Mitsuo	(MO)	11	+	1516
Haruo	(HO)	9	+	6427

(continued)

(continued)

b. E2 group

Kuma	(KM)	40*	-	2957
Tareo	(TO)	15	+	1879
Koguma	(KG)	18	+	3254
Jes	(JS)	22	+	2661
Kurodashi	(KD)	30*	-	2642
Hachi	(HC)	35*	-	3372
Hanajiro	(HJ)	30*	-	3703
Fuchi	(FC)	15	-	2954
Taji	(TJ)	9	+	1738
Yunota	(YT)	9	+	1405

1) Observation time at the permanent provisioning sites and at temporary provisioning sites.

Table 3. Numbers of dominant or subordinate behaviors among males.

a. E1 group

	Subordinate										
Dominant	TN	KK	IB	MN	IK	HT	KR	TW	MO	HO	Total[1)]
TN	--				3	2	1		2	13	21 (2.12)
KK		--								6	6 (1.62)
IB			--							2	2 (0.80)
MN				--				1		1	2 (0.47)
IK					--	4	2	1		4	11 (1.46)
HT					1	--		1	1	1	4 (0.70)
KR							--			1	1 (0.22)
TW								--			0
MO									--	1	1 (0.40)
HO									1	--	1 (0.09)
Total	0	0	0	0	4	6	3	3	4	29	49

(continued)

(continued)

b. E2 group

	Subordinate										
Dominant	KM	TO	KG	JS	KD	HC	HJ	FC	TJ	YT	Total[1)]
KM	--	1	1			2	1	1		1	7 (1.42)
TO		--	7	3	3		7	4	1	3	28 (8.94)
KG			--	1	1		5		6	1	14 (2.58)
JS				--	2		2				4 (0.90)
KD					--	1	1			1	3 (0.68)
HC	1		1			--	2		1	2	7 (1.25)
HJ	1				1	1	--	6		1	10 (1.62)
FC								--		1	1 (0.20)
TJ									--		0
YT										--	0
Total	2	1	9	4	7	4	18	11	8	10	74

1) In parenthesis, frequencies of dominant or subordinate behaviors observed per 10 hours were indicated.

Table 4. Frequency of agonistic interactions of males.

a. E1 group

	Adult male-adult male	Adult male-adolescent male	Total
Observed	13	34	47
Expected*	31.3	15.7	47

b. E2 group

Observed	56	18	74
Expected*	57.6	16.4	74

* Probability of the age combination of two males if sampled randomly from the study groups; calculated according to the proportion of the age composition in the study period.

Table 5. Attendance rate at the permanent provisioning sites (ATR) and percentage of scanning spend in the proximity with other males (PRP) of each males (For caluculation, see Methods).

	Attendance rate at permanent provisioning sites (ATR)[1)]	Percebtage of scanning spend in the proximity with other males (PRP)
a. E1 group	N=276	
TN*	55.1 % (152)	15.1 %
KK	14.1 (39)	5.1
IB*	18.8 (52)	34.6
MN*	27.2 (75)	21.3
IK	58.7 (162)	14.8
HT	39.9 (110)	20.0
KR	24.6 (68)	17.6
TW*	12.0 (33)	12.1
MO*	22.5 (62)	6.5
HO*	65.6 (181)	9.9

(continued)

(continued)

b. E2 group N=87

KM	71.3 %	(62)	62.9 %
TO*	20.7	(18)	22.2
KG*	90.8	(79)	57.0
JS*	44.8	(39)	35.9
KD	64.4	(56)	37.5
HC	94.3	(82)	25.6
HJ	86.2	(75)	40.0
FC	47.1	(41)	22.0
TJ*	42.5	(37)	35.1
YT*	6.9	(6)	0.0

* Males whose mothers are in the unit-group. 1) In parenthesis, total number of scanning of each male were indicated. IB, MN and TW are maternal brothers in E1 group, and TO, JS and TJ are maternal brothers in E2 group. Males are arranged in dominance rank.

Table 6. Numbers of scanning whether mothers of brothers were present or absent in the permanent provisioning sites.

Name of brothers who were in the permanent provisionig sites	Numbers of scanning		Total
	Mothers present	Mothers absent	
IB only	3	0	3
MN only	1	32	33
TW only	2	0	2
IB-MN	19	0	19
IB-TW	5	3	8
MN-TW	0	1	1
IB-MN-TW	19	3	22
TO only	1	5	6
JS only	5	7	12
TJ only	4	4	8
TO-JS	0	0	0
TO-TJ	2	0	2
JS-TJ	6	12	18
TO-JS-TJ	6	2	8

Table 7. Numbers of grooming bouts among males.

a. E1 group

	Groomee										
Groomer	TN	KK	IB	MN	IK	HT	KR	TW	MO	HO	Total[1)]
TN	--		1		1						2 (0.20)
KK		--									0
IB	1		--		1						2 (0.80)
MN				--			3				3 (0.70)
IK	2		1		--						3 (0.40)
HT			1			--					1 (0.18)
KR				2			--				2 (0.43)
TW			1					--			1 (0.58)
MO									--		0
HO					2					--	2 (0.19)
Total	3	0	4	2	2	2	3	0	0	0	16

(continued)

(continued)

b. E2 group

	Groomee										
Groomer	KM	TO	KG	JS	KD	HC	HJ	FC	TJ	YT	Total[1)]
KM	--		10			5					15 (3.04)
TO	1	--				1					2 (0.64)
KG	20		--			1	16				37 (6.82)
JS				--	2						2 (0.45)
KD					--		5				5 (1.14)
HC						--					0
HJ		1	10		4		--				15 (2.43)
FC				1				--			1 (0.20)
TJ									--		0
YT										--	0
Total	21	1	20	1	6	7	21	0	0	0	77

1) Total number of grooming bouts in which each male groomed other males. In parenthesis, frequencies of grooming bouts observed per 10 hours were indicated.

Table 8. Frequency of grooming bouts among males in each of three combinations.

	Male-male	Male-female	Son-mother	Total
a. E1 group				
Observed	16 (15.0%)	52 (48.6%)	39 (36.4%)	107
Expected*	33.2	69.4	4.4	107
b. E2 group				
Observed	77 (64.7%)	38 (31.9%)	4 (3.4%)	119
Expected*	28.9	86.8	3.2	119

* Probability of the age-sex combination of two individuals if sampled randomly from the two groups; calculated according to the proportion of the age-sex composition in the study period.

Table 9. Frequency of reassurance behaviors observed between males.[1)]

a. E1 group

	TN	KK	IB	MN	IK	HT	KR	TW	MO	HO	Total[2)]
TN	--				7	3				2	12 (1.21)
KK		--									0
IB			--		1						1 (0.40)
MN				--							0
IK					--						8 (1.06)
HT						--	1		1		5 (0.88)
KR							--				1 (0.22)
TW								--		1	1 (0.58)
MO									--		1 (0.40)
HO										--	3 (0.48)

(continued)

(continued)

b. E2 group

	KM	TO	KG	JS	KD	HC	HJ	FC	TJ	YT	Total
KM	--		20	1	3	10	6	6			46 (9.33)
TO		--	2		1	1	4			2	10 (3.19)
KG			--	1			8		2		33 (6.08)
JS				--	3		1				6 (1.35)
KD					--	3					9 (2.04)
HC						--		1			15 (2.67)
HJ							--		1		21 (3.40)
FC								--		1	8 (1.62)
TJ									--		3 (1.04)
YT										--	3 (1.28)

1) This table does not indicate the directions of mounting behavior; 2) total number of reassurance interactions in which each male participated. In parenthesis, frequencies of reassurance behaviors observed per 10 hours were indicated.

Figure legends

Fig. 1. Home ranges of six unit-groups (E1, E2, P, B, K and S groups) of bonobos at Wamba in the study period. Asterisks indicate the permanent provisioning sites. E1 group visited FS1 and FS2, and E2 group visited FS3 in this period.

Fig. 2. Dendrogram among males drawn from attendance indices at the permanent provisioning sites (ATI's) by the group average method. Names combined with lines indicate brothers.

Fig. 3 Dendrogram among males drawn from proximity indices (PRI's) by the group average method. Names combined with lines indicate brothers.

Fig. 4. Attendance indices at permanent provisioning sites (ATI's) between males and other males and between sons and mothers for all males whose mothers are in the unit-group. Males are arranged in dominance rank from left to right. Under lined names indicate brothers. "M" indicates mother.

Fig. 5. Proximity indices (PRI's) between males and other males and between sons and mothers for those whose mothers are in the unit-group. Males are arranged in dominance rank from left to right. Under lined names indicate brothers. "M" indicates mother

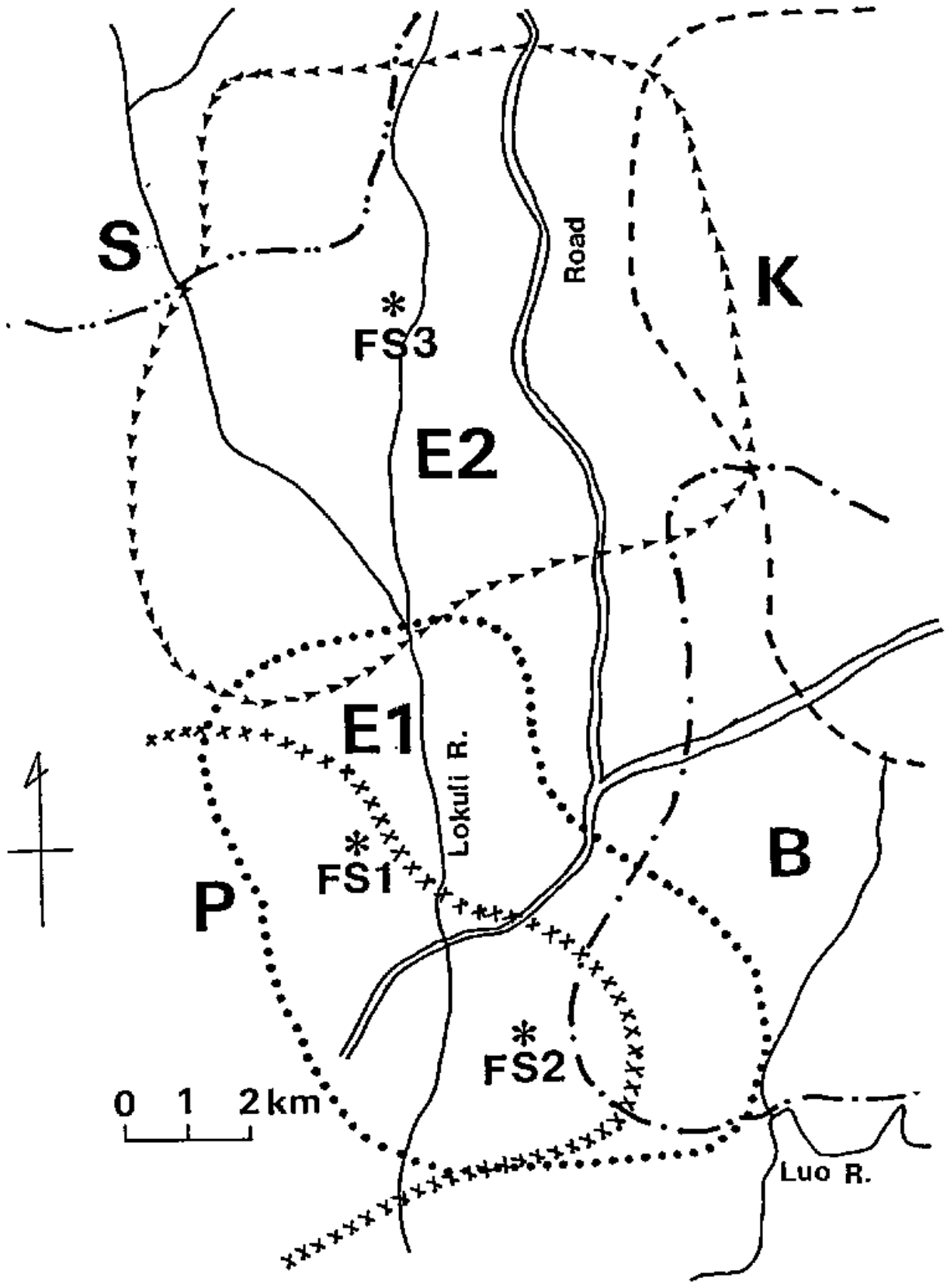

Fig. 1

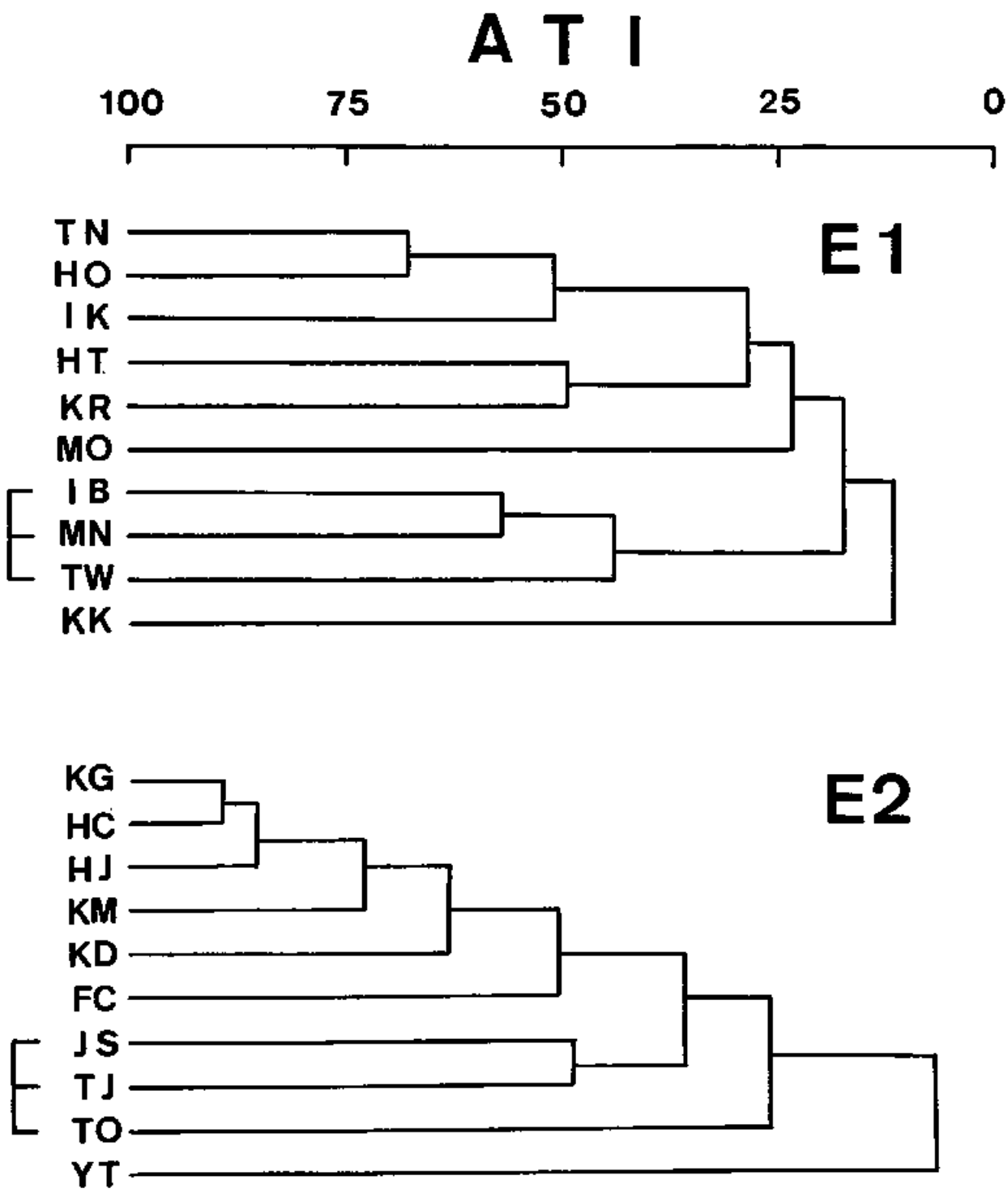
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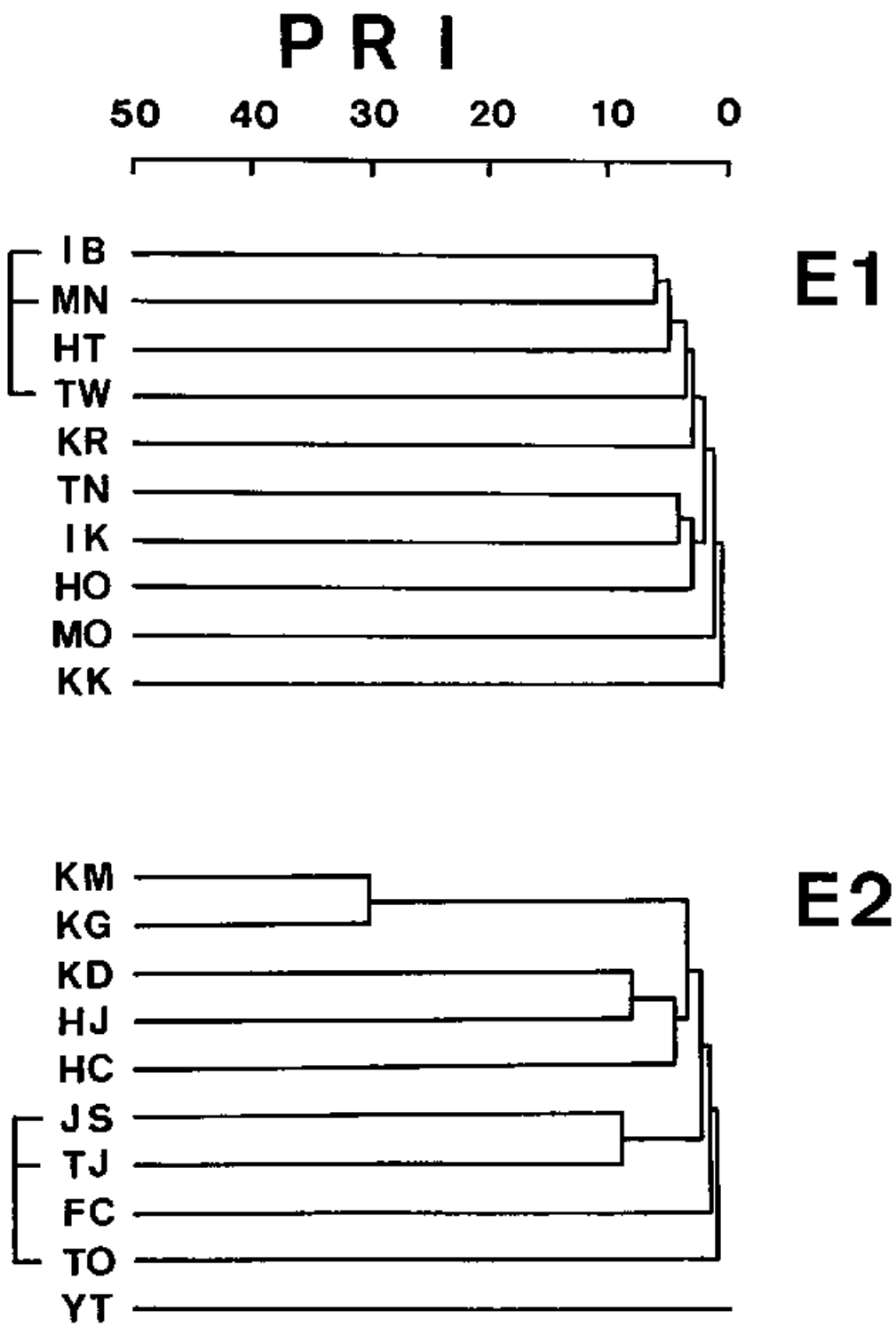
Fig 2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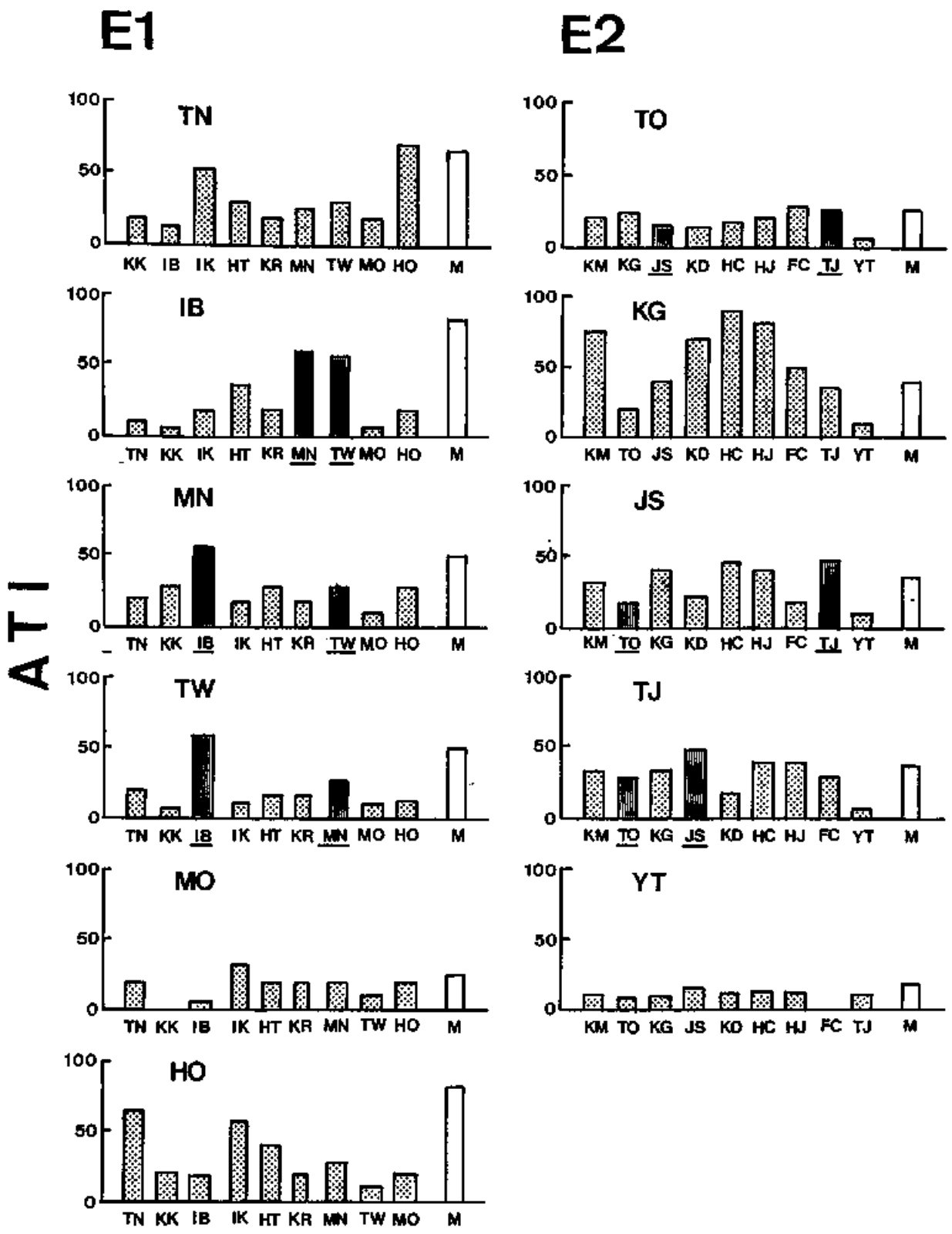
TO
YT
E2

Fig 3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E2
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IB
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TW
TN KK IB IK HT KR MN MO HO M
MO
TN KK IB IK HT KR MN TW HO M
HO
TN KK IB IK HT KR MN TW MO M
TO
KM KG JS KD HC HJ FC TJ YT M
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50
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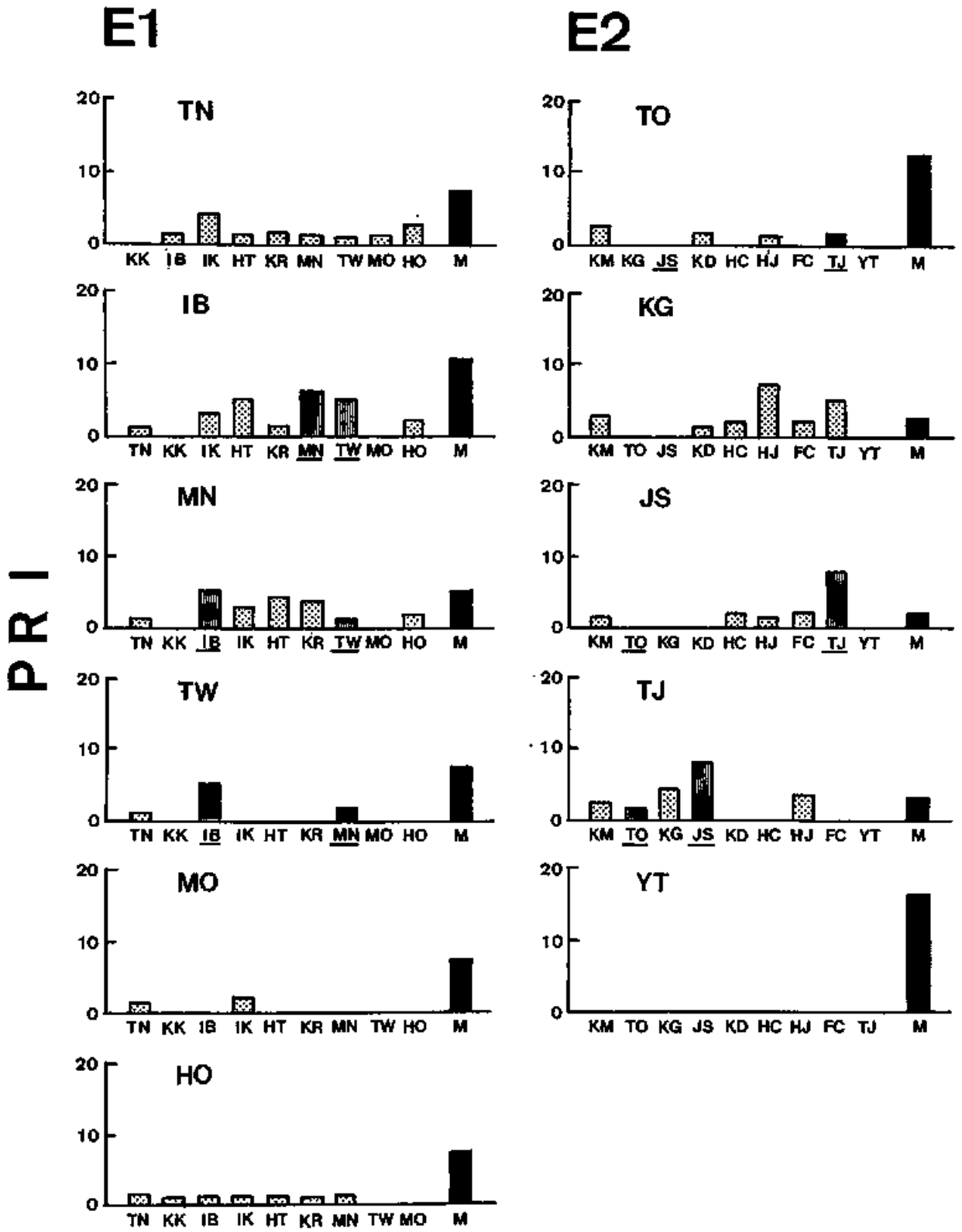
Fig. 4


E1
E2
PRI
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KK IB IK HT KR MN TW MO HO M
IB
TN KK IK HT KR MN TW MO HO M
MN
TN KK IB IK HT KR TW MO HO M
TW
TN KK IB IK HT KR MN MO HO M
MO
TN KK IB IK HT KR MN TW HO M
HO
TN KK IB IK HT KR MN TW MO M
TO
KM KG JS KD HC HJ FC TJ YT M
KG
KM TO JS KD HC HJ FC TJ YT M
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KM TO KG KD HC HJ FC TJ YT M
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KM TO KG JS KD HC HJ FC TJ M
20
10
0

Fig. 5