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SOCIOLOGICAL COMPARISON BETWEEN TWO WILD GROUPS OF ANUBIS-HAMADRYAS HYBRID BABOONS

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ABSTRACT

In the Awash Valley, Ethiopia, observed were 2 groups of anubis-hamadryas hybrid baboons to make a comparative study of their social organizations. Morphologically and genetically, one group (the Gorge group) was closer to anubis, while the other (the Kerrayu group) was closer to hamadryas. The entire Kerrayu group was very cohesive, whereas the Gorge group often splitted into several parties without stable membership. In the Gorge group, 8 subgroups were distinguished: 3 multi-male groups and 5 one-male groups. The Kerrayu group had 2 large one-male units, several small one-male units, and 8-9 pair units. The infra-units within the Kerrayu group were spatially more cohesive than the Gorge subgroups. In both Kerrayu and Gorge groups, the distinctive affinitive bonds, which seemed to be based on kinship, existed among females. The males of the Kerrayu group had a stronger social disposition towards each other's proximity than those of the Gorge group. The linearity of dominance order among males in the Gorge group was more distinctly established than in the Kerrayu group. In the Awash Valley anubis and hamadryas populations have had mutual gene flow. The inflow of anubis genes into the hamadryas band has strongly affected the possesseive behavior of hamadryas males towards females, but has exerted little effect on the mutual bonds among the males. The inflow of hamadryas genes into the anubis troop has severely affected its integration. It was concluded that the band to be the basic social utit of hamadryas baboons, and it was speculated that some sociological and ecological factors promoted the formation of multi-level system of hamadryas baboons.

INTRODUCTION

Nagel (1973) made ecological comparisons between anubis baboons (Papio anubis), hamadryas baboons (Papio hamadryas), and their hybrids in the Awash Valley, Ethiopia. He paid special attention to the fact that at the species border, phylogenetic characteristics of the behavior and those resulting from recent ecological adaptations could be distinguished from each other. He also proposed hypotheses for the process of hybridization between the two species in this region, based on a broad survey along the Awash Valley. Although he compared the social organization of the hybrid groups with that of the original species (Nagel, 1971), the details of the internal structure of the hybrid groups were not clearly resolved.

Based on a sociological study in this region, Kawai and Sugawara (1976) suggested that immigration of solitary males of each species into bands or troops of other species might be more important as the main process leading to hybridization than abduction of anubis females by

hamadryas males, which was proposed by Nagel to be the only possible cause. They also discussed the significance of the hybridization in relation to the evolution of primates. Furthermore, Sugawara (1979) selected one hybrid group inhabiting this region, and elucidated its internal social structure. Nagel (1973) stated that all hybrid groups in the Awash Valley were closer to hamadryas than to anubis, and that there were only slight genetic differences among the hybrid groups. However, Sugawara demonstrated that the group which he studied intensively was morphologically closer to anubis than to hamadryas, and the same group was also shown to be genetically closer to anubis based on a population genetical study of blood protein variations (Shotake et al., 1977).

In the present article, the author attempts to make sociological comparisons between the group closer to anubis, of which the social structure had already been analyzed, and a group closer to hamadryas, which was newly studied during the second research period, based on quantitative data collected during the latter period from the 2 hybrid groups by the same sampling methods. The first purpose of making these sociological comparisons was to elucidate what kinds of social structure the groups composed of anubis-hamadryas hybrids have, and what degree of stability the social structures of these hybrid groups assume. At the same time, confirmation was sought of the social processes by which hybridization can progress between 2 species which differ drastically in their social organizations, as well as how to predict the social dynamics in the hybrid zone in the future.

Secondly, it was hoped to elucidate both the essential differences and common elements in the social structures of anubis baboons and hamadryas baboons, after 2 or more hybrid groups with different genetic compositions were compared and the features of the social organizations of these hybrid groups were related to those of the original species. Needless to say, the most fundamental difference between the anubis and hamadryas societies is that anubis baboons form a one-level society whereas hamadryas baboons have a multi-level social organization based on the one-male unit (harem). In other words, the most distinctive feature of the basic social structure of hamadryas baboons resides in the persistent "possession of females" by males (Kummer, 1973). However, in aspects other than the "possession of females", the differences and common elements of the anubis and hamadryas societies have not yet been fully discussed. The most important aspect is in what points the male-male or female-female relationship of hamadryas baboons differs from that of anubis baboons, and how the features of the relationships among individuals of the same sex are correlated with the existence of the persistent male-female bond.

Thirdly, based on the wide variations among individuals, especially among males, composing the hybrid groups as regards their morphology, social behavior, and patterns of inter-individual relationships, it was hoped to elucidate the correlation between the patterns of social behavior performed by one animal and the patterns of social relationships which it has with other animals, or between the variations in social behavior and the morphological variation. In this way, it should be possible to determine which pattern of individual behavior is effective or indispensable for the formation of any particular pattern of inter-individual relationships. Furthermore, by examining the correlation between morphology and behavior, some insights should be gained for making a valid distinction between 'innate' and 'learned' patterns of social behavior in the hybrid baboons.

In order to resolve this third and last problem, ethological analysis of the social behavior of hybrid baboons is required. Since the present paper is focussed primarily on making sociological comparisons between

hybrid groups, the detailed ethological analysis and full discussion of the social behavior of the hybrid baboons will be given elsewhere (Sugawara, in prep.).

MATERIALS AND METHODS

Field studies were carried out for about 135 days from October 30, 1978 to March 11, 1979 in the Awash National Park, Ethiopia. A general description of the natural environment and landscape has been given previously by Nagel (1973). During an earlier study from October, 1975 to March, 1976, the author habituated one hybrid group, the Gorge group, which was the first group living in the canyon below the Awash Fall. Its social organization and inter-individual relationships have been described elsewhere (Sugawara, 1979). This time the author habituated another hybrid group, the Kerrayu group, which neighbors the Gorge group downstream, and made intensive observations of this group. In addition to these 2 hybrid groups, a third group neighboring the Kerrayu group downstream (the Shelko group) was also occasionally observed. Since the animals of the Gorge group were so familiar with the observer that they spent a relatively long time at the feeding site, most observations of this group were carried out only in and around the 2 feeding sites, G and B (Fig.1). As a rule, the Kerrayu group was fed on the plains above its main sleeping cliffs (O, Dj, A, K, and L) early every morning, and thereafter its nomadic movements were traced all day long. However, when the baboons of this group retired into the riverine forest in the afternoon,

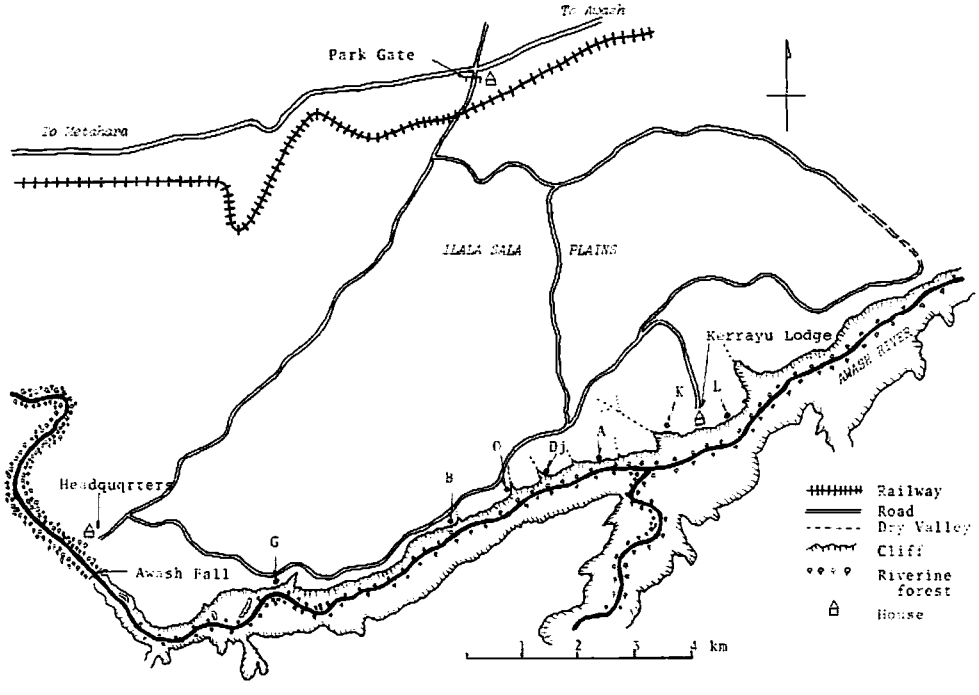


Fig. 1. Map of the study area. Black dots represent the feeding sites of the Gorge group (G and B) and the main sleeping sites of the Kerrayu group.

the author sometimes called them and induced them to climb the cliff, gave them food on the plain, and thereafter traced them until they arrived at the sleeping site in the evening. About 3 kg of maize grain was thrown about as widely as possible at each feeding session.

The author identified all the individuals over the age of puberty in both of the Gorge group and the Kerrayu group. He also identified all the adult males of the Shelko group. Morphological hybrid indices (Nagel, 1973) were calculated for all the adult males of these 3 groups. Moreover,the author calculated the hybrid indices of all the adult females of both the Gorge group and the Kerrayu group. The relevant data were collected by three kinds of sampling methods, as follows.

I. Focal-Male Sampling

All the males which were in clear association with one or more particular females were chosen as focal animals (Altmann, 1974). In the Gorge group 10 focal males were traced during 3940 min, while in the Kerrayu group 13 males were traced during 7810 min (Table 1). During each sample session, the spatial distances between the focal male and each of its partner females were estimated by eye at every 5th minute. At the same time, the shortest distances between the focal male and other males were estimated, and the name of the nearest male was recorded. Social interactions in which at least either the focal male or one of its partner females participated were recorded sequentially using abbreviated symbols of social behavior. In particular, the duration of grooming interactions was measured by scoring in units of 30 sec (e.g. if one grooming bout continued for 3 min and 10 sec, the recorded measurement was 3.5 min).

II. Ad Libitum Sampling

All the social interactions between identified animals in which neither the focal male nor any of its partner females participated were included as ad lib. samples (Altmann, 1974). In the present article, ad lib. samples are used mainly for comparison of the grooming budget between two groups, and for analyzing the social relationships among

Table 1. Duration of focal-male sampling

Kerrayu group		Gorge group	
Focal male	Duration (min)	Focal male	Duration (min)
Geta	690	*Robes*	375
Yabelo	605(+145)*	*Hagos*	390
Nigus	605	*Zare*	400
Stav	530	*Chilotta*	400
Zefen	620	*White*	395
Doro	600	*Baboof*	410
Posta	605	*Necker*	380
Hakeem	615	*Danielle*	400
Uzo	605	*Maler*	390
Kusil	590	*Matiou*	400
Jirat	620	-	
Villa	645	-	
Feres	335**	-	
Total	7665(+145)		3940

* Data collected from *Yabelo* for 145 min after the collapse of his one-male unit were excluded from the quantitative analysis. ** Data collected from *Feres* for 335 min before his deprivation of a female were used only for the analysis of the spatial relationships among males.

bachelor males.

III. Sampling of Agonistic Interactions in the Feeding Situation

The author recorded on a cassette tape recorder the agonistic interactions between males which occurred during the period he scattered maize grain at the feeding site. The time duration of one recording ranged from 10 to 20 min. Fourty-four recordings were made over 36 days in the Kerrayu group, and 30 over 18 days in the Gorge group. These data were used for analyzing the organization of behavior in the agonistic interactions and the dominance hierarchy among the males.

For the statistical examination, following 4 kinds of test were used; chi-square test for 2 independent samples, Mann-Whitney U test, Kolmogorov-Smirnov 2-sample test, and Spearman rank correlation coefficient (Siegel, 1956).

GROUP COMPOSITIONS AND INTERGROUP RELATIONSHIPS

1. Degree of Hybridization

The age-sex compositions of the 3 hybrid groups are shown in Table 2. It should be noted that the socionomic sex ratio of the Kerrayu group is remarkably high. The Kerrayu group had been estimated to be composed of less than 60 animals from occasional observations made during the previous study period (Sugawara, 1979). Such underestimation of the actual size of this group may be ascribed to the poor conditions under which it was observed during the previous study period, a number of animals in the group not being sufficiently habituated to the observer to dare approach the feeding site. A comparison of the degree of hybridization was made among the 3 groups by means of the morphological hybrid index devised by Nagel (1973). In the Kerrayu group about 70% of all adult males had a closer appearance to hamadryas than to anubis, showing hybrid indices of less than 7, whereas in the Gorge group about 80% of the males were closer to anubis in their appearance, showing hybrid indices of over 9. Most of the males in the Shelko group showed intermediate values in their hybrid indices. By averaging the hybrid indices of all males in the respective groups, the group hybrid indices (Nagel, 1973) were calculated as 10.1 for the Gorge group, 5.8 for the Kerrayu group, and 7.9 for the Shelko group (Fig.2a).

Furthermore, the author attempted to represent the morphological features of adult females by the index. Although the morphological differences between the two species are not so conspicuous in females as in males, the author chose 4 characters (i.e. color of the face, shape of the muzzle, color of the fur, and bending of the tail) which were believed to differ most clearly between anubis and hamadryas females. Applying the

Table 2. Age-sex compositions of 3 hybrid groups

	Male			Female						
Group	Adult	Adol.	Pub.	Adult	Adol.	Pub.	Juv.	Inf.	Total	S.S.R.
Gorge	14	1	3	19	4	2	11	15	69	65.2
Kerrayu	18	4	2	23	3	0	18	16	84	84.6
Shelko	8	1	2	10	2	1	9	8	41	75.0

S.S.R. indicates the socionomic sex ratio of each group, where S.S.R., [(Number of adult and adolescent males)/(Number of adult and adolescent females)]x100. Adol.=Adolescent; Pub., Pubescent; Juv., Juvenile; Inf., Infant.

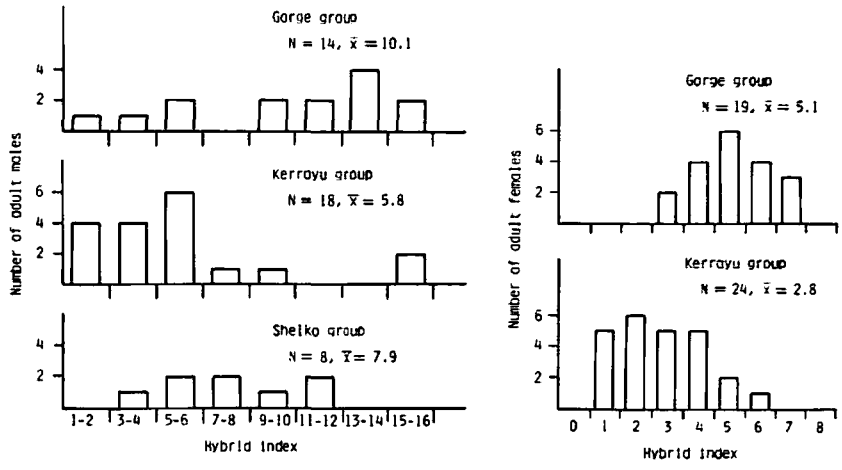


Fig. 2a. Hybrid indices of adult males in 3 groups. Eight morphological characters were given scores of 0, 1, or 2 for hamadryas, intermediate, or anubis appearance, respectively. Thus, a male with pure hamadryas appearance has an index of 0, and an anubis male an index of 16 (left).

2b. Hybrid indices of adult females in 2 groups. Four morphological characters were chosen, and each was given 3 grades of score so that a female with pure hamadryas appearance has an index of 0, and an anubis female an index of 8 (right).

same procedures as for the calculation of male hybrid indices, each character was given a score 0 for hamadryas appearance, score 1 for intermediate appearance, and score 2 for anubis appearance. The sum of the four scores was designated as 'the female hybrid index.' The female hybrid index was calculated for 19 adult females of the Gorge group, and for 24 adult females of the Kerrayu group (Fig.2b). In the Gorge group there was no females with an index of less than 3, while none of the females in the Kerrayu group showed an index of over 7. The average was 5.1 in the former case, and 2.8 in the latter. Thus, the external appearance of the females was also closer to anubis in the Gorge group, and closer to hamadryas in the Kerrayu group.

The hybrid groups, i.e. the Gorge group, the Kerrayu group, and the Shelko group, can be assumed to correspond to Nagel's groups C1 (N=81±2, G.H.I.=ca.14.0), C2 (N=83±5, G.H.I.=ca.6.0), and C3 (N=51, G.H.I.=ca.5.8)*1 respectively, judging from their locations along the Awash River. In particular, both the size and the group hybrid index of the Kerrayu group correspond well with those of group C2. However, there are discrepancies between the Gorge group and group C1, as well as between the Shelko group and group C3, both in size and group hybrid index. According to Nagel, 3 hybrid groups (C2, C3, and C4) could be arranged on a very smooth morphological gradation from anubis to hamadryas in appearance, corresponding to their order of location along the river. In contrast, it was found in the present study that anubis features were relatively more prevalent in the Shelko group than in the Kerrayu group. Thus, at least insofar as these two groups are concerned, a consistent transition from anubis to hamadryas features along the Awash River cannot be recognized.

2. Encounters between Groups

During the study period, encounters between the Kerrayu group and the Shelko group were observed 8 times, 6 occurring at the feeding site and 2 under natural conditions. Encounters between the Kerrayu group and the Gorge group were observed only twice, once at the feeding site and once under natural conditions (Table 3). Whenever two groups met each other at the feeding site, violent agonistic interactions arose between the members of the different groups. As a result, the Kerrayu group drove away another group from the feeding site in every case. However, under natural conditions, the encounters between two groups turned out to be far calmer than at the feeding site, although the animals of both groups did display signs of tension.

> Case 1. December 13. 10:48 a.m. On the savanna halfway between Site-O and Site-B, an adult male (Doro) and an adolescent male (Bal) of the Kerrayu group which had been walking on the periphery of the traveling party, began to chase one adolescent male (Kire) of the Gorge group which had approached from upstream. The skirmish caused almost all of the members of the Kerrayu group to begin gathering into a body on the downstream side so as to confront the animals of the Gorge group which was lining up on the upstream side at an interval of about 30 m.
> 10:51 a.m. The Kerrayu group began to march forwards upstream, while the Gorge group began to retreat slowly.
> 11:05 a.m. The observer shifted his position from near the Kerrayu group to within the Gorge group. This appeared to encourage the animals of the Gorge group, since they immediately began to march towards the Kerrayu group and the latter in turn retreated.
> 11:08 a.m. The Kerrayu group stopped retreating and the animals sat and stared at those of the Gorge group which had also stopped to sit down. At this point, the distance between the 'fronts' of the 2 groups was near to 10 m.
> 11:12 a.m. A pair comprising a male and a female (Jirat and joniya) from the Kerrayu group approached to within the vicinity of 2 m of a bachelor male (Yosa) of the Gorge group and began to

Table 3. Encounters between the Kerrayu group and other hybrid groups

Date	Opponent group	Site	Contact duration	Antagonism	Driving away
Dec. 12	S	K	14 min	++	K → S
Dec. 13	G	savanna	2 hours	(+)	–
Dec. 17	S	K	35 min	+	K → S
Dec. 30	S	Dj	11 min	(+)	K → S
Jan. 13	S	K	20 min	+	K → S
	S	cliff	12 hours?	–	–
Feb. 11	G	B	33 min	++	K → G
Feb. 14	S	L	18 min	+	K → S
Feb. 20	S	savanna	26 min	–	–
Mar. 4	S	L	22 min	+	K → S

S and G indicate the Shelko group and the Gorge group, respectively. The intensity of agonistic interactions which occurred during each encounter is represented by 4 grades in the column labeled 'Antagonism': ++, Physical conflicts and confrontations with barks; +, Confrontations with barks; (+), Signs of tension; –, Calm. 'K → S' indicates that the Kerrayu group drove away the Shelko group from the feeding site.

groom each other.
11:22 a.m. The animals of the Gorge group began to return upstream, while those of the Kerrayu group moved downstream and climbed the Acacia trees (Acacia tortilis). However, an adult male (Chilotta) and 2 females (genet and chikka) of the Gorge group moved downstream.
11:28 a.m. These 3 animals approached to a proximity of only 0.3 m from a pair comprising a male and a female (Feres and fossy) of the Kerrayu group and remained seated near the latter for 3 min.
11:31 a.m. Chilotta began to return upstream, urging on his partner females. Then, for about 70 min, the 'fronts' of the 2 groups continued feeding on the trees at an interval of about 30 m.

Chilotta who engaged peacefully into close proximity with the members of the Kerrayu group, had not been present in the Gorge group during the previous study period. The fact that he gave no sign of tension or alarm against the Kerrayu group suggests that he might possibly have immigrated from the Kerrayu group into the Gorge group.

An encounter between the Kerrayu group and the Shelko group was observed above the sleeping cliff (Site-L) on one evening. In this case, both groups were very calm. Two leader males of one-male units belonging to the different groups sat within 10 m of each other. Within a 'buffer zone' between the 2 groups, more than 10 juveniles intermingled and played together. During the night the 2 groups were thought to utilize the same sleeping cliff in common. According to Kummer (1968), in the Erer-Gotta hamadryas population, two or more bands gather together to form a large "troop" at the sleeping rocks. In contrast, the above is the only case where the Kerrayu group and the Shelko group were found to utilize the same sleeping cliff in common during the present study period. It can be concluded therefore that these 2 groups only rarely form a "troop". One of the reasons for rare formation of a troop may well be that, as Kummer pointed out, "the walls of the Awash Valley offer almost too many sleeping rocks" (Kummer, 1968: 19)

Estimations of the outlines of the home ranges of the 3 hybrid groups reveal that the Gorge group and the Kerrayu group share a relatively small area with each other, whereas the area of overlap between the Shelko group and the Kerrayu group amounts almost two-thirds of the entire area used by the Kerrayu group (Fig.3). In his previous article, the author suggested that the Gorge group and the Kerrayu group maintained antagonistic relationships between each other. This is confirmed by the above analysis. On the other hand, the Kerrayu group appears to maintain more tolerant relationships with the Shelko group than with the Gorge group. In other words, the antagonistic relationships between the Gorge group and the Kerrayu group are comparable to the intertroop relationships of savanna baboons, whereas the relationships between the Kerrayu group and the Shelko group may be similar to those between different bands of hamadryas baboons in that the degree of exclusiveness for usage of the respective home ranges is very low.

3. Male Transfers between Groups

Three cases of transfer of males between groups were encountered (Fig.4). At the beginning of the study period, 2 adult males (Louis and Danton) which had belonged to the Gorge group during the previous study period, were found within the Kerrayu and Shelko groups, respectively. Danton remained continuously in the Shelko group throughout the present study period. However, Louis appeared at the feeding site (G) occupied by the Gorge group on December 22 and stayed in this group for the succeeding 4 days, occasionally having grooming interactions with a

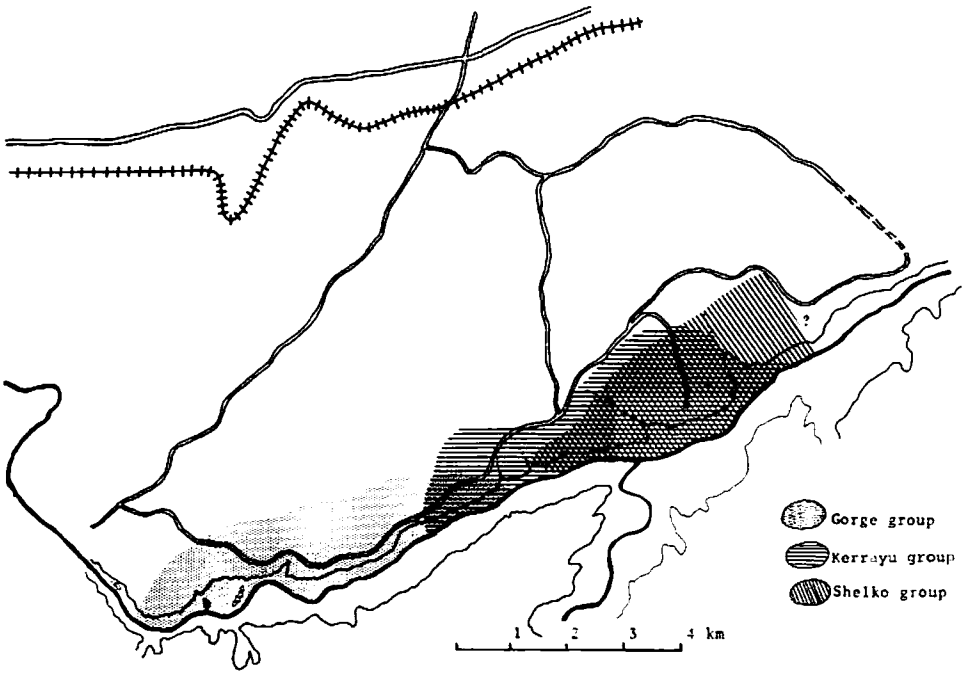


Fig. 3. Estimated outlines of the home ranges of 3 hybrid groups. The outline for the Kerrayu group was based on recorded routes of the nomadic movement of this group, while those for the Gorge group and the Shelko group were estimated by connecting together points where the observer met each group. The downstream area within the range of the Shelko group was rarely surveyed.

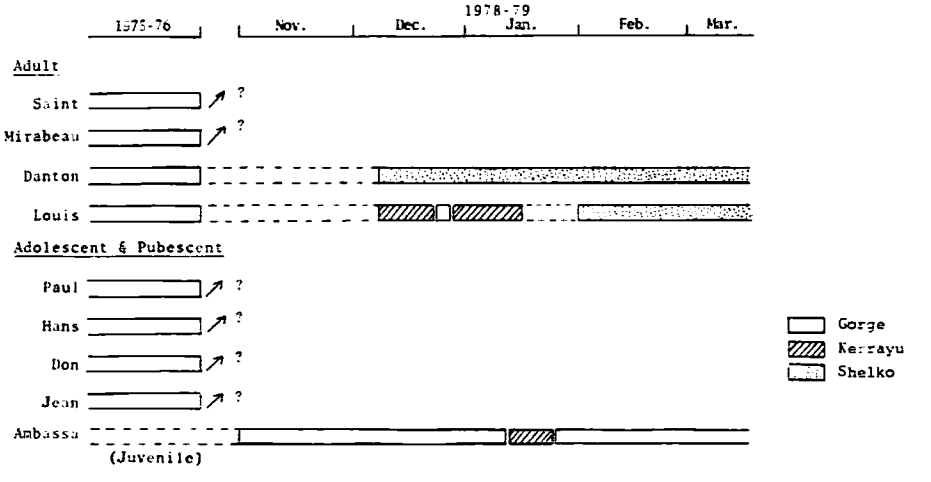


Fig. 4. Disappearance of males which had been present in the Gorge group during the previous study period and their transfers between groups.

pubescent female (Ras), a pubescent male (Ambassa), and an old bachelor male (Green). Subsequently, Louis returned to the Kerrayu group, but again disappeared on January 15. On February 1 he was found to be present within the Shelko group, and stayed in this group until the end of the study period.

Another case was observed where a pubescent male shifted group temporarily. Ambassa, who had belonged to the Gorge group, traveled together with the Kerrayu group for 11 days from January 12 to 23. However, on January 25 he was again found within the Gorge group, and stayed in it throughout the remainder of the study period.

The external appearance of Louis was that of a pure anubis, and Danton, whose hybrid index was 12, was also closer to anubis than to hamadryas in morphology. Special attention should therefore be paid to the possibility that males which are close in appearance to anubis males may tend to shift from group to group in short cycles. On the other hand, it is believed that transfer of males which are close in appearance to hamadryas also occurs between groups. Two of 4 adult males, which had immigrated into the Gorge group from elsewhere after the end of the previous research period, were closer to hamadryas baboons, their hybrid indices being 5 and 6, respectively. They might well have come from downstream hybrid groups. Furthermore, it has been reported that 2 males of hamadryas appearance had stayed in the anubis troop (Ittu troop) living 5 km upstream from the Awash Fall (Kawai & Sugawara, 1976; Sugawara, 1979). At the present time, a male of hamadryas appearance was again found in the same troop, although it could not be judged whether it was identical to one of the animals seen three years ago (Shotake, personal comm.).

It must be emphasized that the members of a group appeared to be receptive to males which had seceded from that group, when they revisited their old place. As stated above, no members of the Gorge group made any attempt to exclude Louis from his participation in friendly interactions, while he was staying in this group. A parallel relationship was recognized to be maintained between Danton and the members of the Kerrayu group. Even when the members of this group, barking and roaring violently, were attempting to drive those of the Shelko group away from the feeding site, Danton alone could not only feed surrounded by the animals of the Kerrayu group but also sometimes threatened some adolescent males of this group. It is thought therefore that this male might have lived with the Kerrayu group before he immigrated into the Shelko group.

It is also inferred from the case of Ambassa that the members of any hybrid group may be generally tolerant to a male newcomer whom they have never seen. While staying in the Kerrayu group, Ambassa frequently played or had grooming interactions with the males of about the same age, such as Ruz or Wib, or with younger juveniles. Such receptiveness of group members to transferring males may well enable males to shift from group to group. In this sense, these hybrid groups have 'open' social systems common with those of the anubis troops among which frequent transfers of males have been ascertained to occur (Packer, 1977).

4. Subgrouping and Infra-units

During the previous study period, the Gorge group comprised 8 subgroups with a stable membership. Three types of subgroups were distinguished: one-male groups, pair groups, and multi-male groups. These subgroups repeatedly joined and parted from each other (Sugawara, 1979). At the present time, the same grouping pattern (i.e. joining and parting of subgroups) was maintained in the group, but the compositions of the subgroups had changed drastically.

Regarding the disappearance of individuals, 4 (30.8%) of 13 adult males which had been present in this group during the previous study period, had disappeared. As stated above, 2 of these 4 males were found out in other hybrid groups. Four (66.7%) of 6 males which had been adolescent or pubescent 3 years previously, had disappeared, and none of them was discovered again. Three (13.6%) of 22 females had also disappeared.

On the other hand, 4 adult males (Zare, Ain, Chilotta, and Ebert) were found to have immigrated into the Gorge group. Furthermore, 4 adolescent females were newly identified, which were presumed to represent unidentified juveniles of the Gorge group from 3 years previously. In the previous study, based on the sudden disappearance of a healthy young adult females from the Gorge group, the author assumed that transfer of females into another hybrid group might occur. However, in the present study period, no data supporting this hypothesis were obtained. Since the rate of disappearance of adult females during 3 years was rather low, it can be considered that the 3 females which disappeared might have died.

In the previous study, the subgroups was defined as a minimum unit of joining and parting. Namely, with few exceptions, every female was always found to be together with the particular male within the same party, which was defined as a group of baboons which appeared simultaneously at the same feeding site (Sugawara, 1979: 26). However, at the present time the formation of the subgroup had become more complicated and ambiguous. From an SLCA-dendrogram (Morgan et al., 1977; Sugawara, 1979) representing the tendencies of any 2 animals to be together in the same party, 3 multi-male groups and 5 one-male groups can be distinguished (Fig.5). Here, the male linked with a female at the greatest similarity is regarded as the partner male of that female. It is immediately seen that 7 females are linked with their partner males at especially low levels of similarity (less than 450). A brief sketch of these 'unstable' members in each subgroup is given below.

A female, marie (mr), who was found to be together with Matiou (Mt) most frequently in the same party, was often observed to copulate, as well as to groom, with Chilotta (Ch). Matiou and Chilotta appeared to compete with each other for marie, the former being at a disadvantage, since it was occasionally observed that as soon as Chilotta appeared at the feeding site Matiou who had been sitting in proximity of marie, would abruptly wake up and go away from her hurriedly. Another adult female, kitsune (kt), who was repeatedly in estrus during the study period had consort relations with Danielle, Maler, and Robes one after another. Three adult females, witch (wc), genet (gt), and sala (sl), all of whom were sexually inactive because of lactation or gestation during the study period were often absent from the parties where their respective partner males were present. The multi-male group, Bf-MMG, including Baboof (Bf) and Necker (Nc), which had been the largest subgroup 3 years previously, barely preserved its integration, and revealed a clear tendency to split into 2 'one-male groups,' i.e. (Baboof, bayech, fox) and (Necker, rose, sala). An adult female, astere, occupied an intermediate position between these 2 'one-male groups.'

The changes which had occurred over a period of 2.5 years in the composition of the subgroups of the Gorge group are summarized in Table 4. It can be reasonably concluded that the membership of the Gorge group, as a whole, had been relatively stable. However, the internal structure itself had undergone drastic transformations. Excluding the females who had disappeared and those who were sexually immature and had no obvious bond with particular males during the previous study period, 11 (64.7%) of 17 adult females had changed their partner males within the 2.5 years. The factor which caused these changes will be

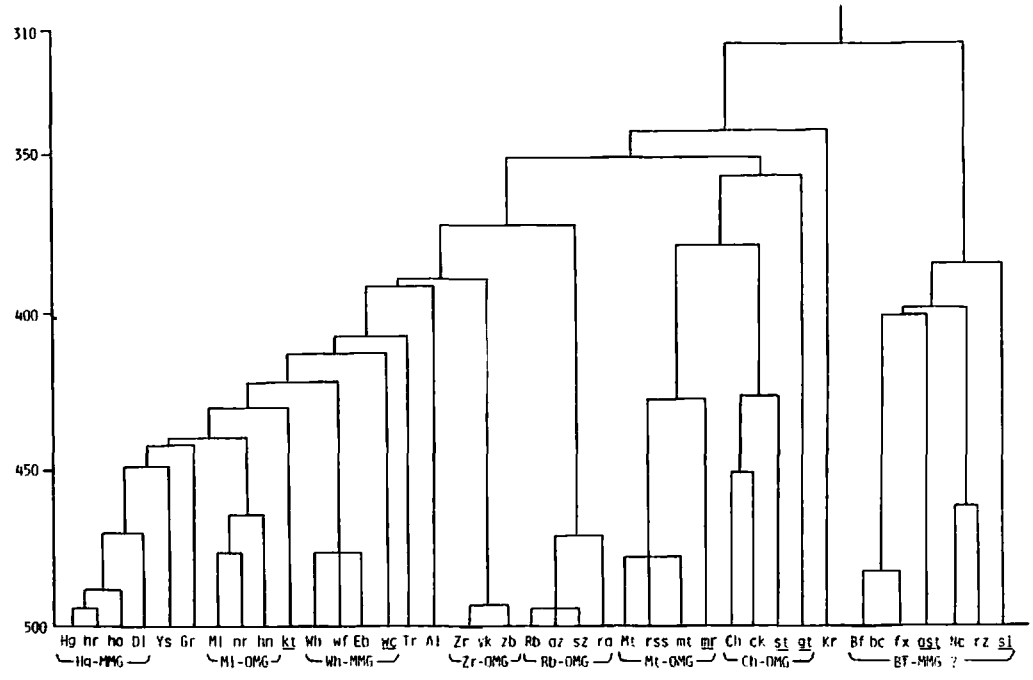


Fig. 5. SLCA-dendrogram representing the likelihood of any 2 animals being together in the same party within the Gorge group. The similarity (S) was calculated from the following formula: S=1000xN(A,B)/N(A)+N(B), where N(A) or N(B) indicates the number of parties in which the individual A or B was present, and N(A,B) indicates the number of parties in which both A and B were found together. The underlined names represent females which are linked with their partner males at only low levels of similarity (less than 450). In all, compositions of 91 parties were recorded.

examined in the Discussion section. In the previous study, it was concluded that the basic mechanism of joining and parting of subgroups within the Gorge group consisted of an alternation of fusion and separation between two major clusters, the G-cluster and the B-cluster. At the present time, such a distinction between two major clusters was not discernible (see Fig.5). However, 6 males which had belonged to the G-cluster [Hagos (Hg), Danielle (Dl), Maler (Ml), White (Wh), Yosa (Ys), and Green (Gr)] were also included in a single cluster at a level of similarity of more than 420. Thus, if only co-existing relationships among males are considered, the process of change in the basic social structure within the Gorge group can be summarized as a breakdown of the B-cluster. In particular, Bf-MMG showed a strong tendency to separate from the rest of the group, as well as to split into 2 parts within it.

The degree of group cohesion was compared between the Gorge group and the Kerrayu group in terms of the numbers of animals which were present during every feeding session (Fig.6). The sizes of the parties of the Gorge group were strikingly variable, reflecting the fluid grouping of this group. On the other hand, in the Kerrayu group, 86% of the total times of recording the number of animals were concentrated in the range of

Table 4. Transformations of the compositions of subgroups within the Gorge group from 1975 to 1978

1975			Transformation		1978			
Subgroup	Male	Female	I	II	Subgroup	Male	Female	
							Stable	Unstable
Rb-OMG	*Robes(Rb)*	*romi(rm)*	→?		*Rb*-OMG	*Robes*	*suzanne*	
		roze(rz)		→*Nc*			*armaz*	
		rossa(rss)		→*Mt*			[*ras*]	
		armaz(az)			*Zr*-OMG	*Zare*↓	*yoko*	
		rolita(rl)		→?			[*zinab*]	
St-OMG	*Saint(St)*↑	*suzanne(sz)*		→*Rb*	*Ch*-OMG	*Chilotta*↓	[*chikka*]	*soutella*
		soutella(st)		→*Ch*				*genet*
		sala(sl)		→*Nc*				
Hg-OMG	*Hagos(Hg)*	*hana(hn)*		→*Ml*	*Hg*-MMG	*Hagos*	*honey*	
	[*Hans(Hs)*]↑	[*haru(hr)*]	→*Ml*	→*Dl*		*Danielle*	*haru*	*kitsune*
Wh-OMG	*White(Wh)*	*wufarem(wf)*			*Wh*-MMG	*White*	*wufarem*	
	[*Danielle(Dl)*]	*witch(wc)*				*Ebert*↓		*witch*
Ml-PG	*Maler(Ml)*	*meskel(mk)*		→?	*Ml*-OMG	*Maler*	*hana*	
Ys-PG	*Yosa(Ys)*	*yoko(yk)*		→*Zr*			*nureme*	
Bf-MMG	*Baboof(Bf)*	*astere(ast)*			*Bf*-MMG?	*Baboof*	*bayech*	
	Necker(Nc)	*bayech(bc)*					*fox*	
	Danton(Dt)↑	*genet(gt)*		→*Ch*				*astere*
	[*Paul(Pl)*]↑	*fox(fx)*				*Necker*	*roze*	
		scarlet(sc)		→?				*sala*
Gr-MMG	*Green(Gr)*	*kitsune(kt)*		→*Dl*→*Ml*→*Rb*	*Mt*-OMG	*Matiou*	*rossa*	*marie*
	Matiou(Mt)	*marie(mr)*	→*Ys*	*Mt*⇄*Ch*			[*meto*]	
		[*nureme(nr)*]		→*Ml*				
Bachelors	*Louis(Ls)*↑				Bachelors	*Green*, *Yosa*		
	Mirabeau(Mb)↑					*Ain*↓, [*Kire*]		
	[*Don(Dn)*]↑					[*Tara*], [*Ambassa*]		
	[*Kire(Kr)*], [*Jean(Jn)*]↑					[*Feked*]		

Transfers of females between subgroups or their disappearance observed during the previous study period are shown in column I. Female transfers between subgroups occurring since the end of the previous period are shown in column II. Up-directed and down-directed arrows indicate disappearance and immigration of males, respectively. Adolescent and pubescent members during each period are shown in brackets. Abbreviated names are given in parentheses. OMG, One-male group; MMG, multi-male group; PG, pair group.

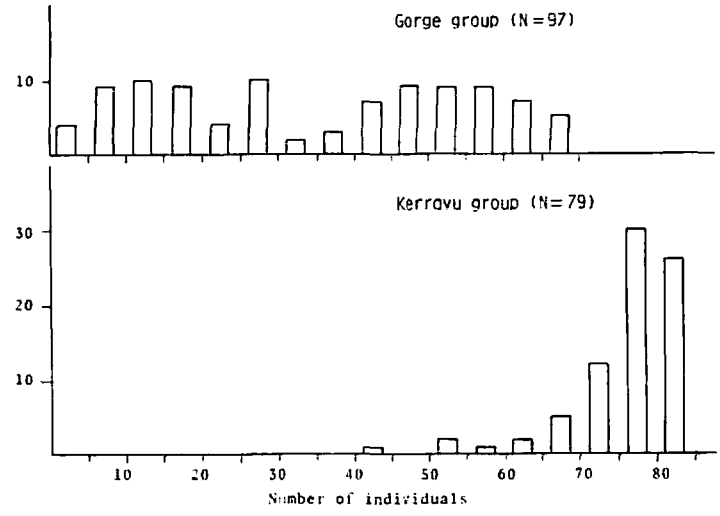


Fig. 6. Distribution of sizes of parties in 2 hybrid groups. The party sizes were ascertained by counting the numbers of animals which were present at the feeding site during each feeding session.

71 to 85 animals. The primary reason for the variation in number of counted animals in the Kerrayu group within this range was that observational conditions were different among the 5 feeding sites: at some, it was often difficult to count all the animals present at a glance. It is considered that all the members of the Kerrayu group are, in contrast to those of the Gorge group, usually united into a single group during its nomadic movements. Only one occasion was confirmed where the Kerrayu group split into 2 parts which traveled independently, separating from each other, for more than a day.

> Case 2. On March 4 at 3:05 p.m., the entire Kerrayu group appeared at Site-L. After eating the artificial food, the animals rested and groomed there. At 3:56 p.m., the group began to travel upstream on the savanna and arrived at Site-Dj at 5:45 p.m. Observations for the day were brought to a close there. On March 5 in the morning, the Kerrayu group could not be found. At 3:08 p.m., the observer found it staying in the riverine forest under the cliff near Site-B. He called and induced the animals to ascend Site-B. However, the group was found to be composed of only 55 animals, with about 30 animals including 5 adult males (Geta, Posta, Jirat, Villa, and Stav) and 2 adolescent males (Bal and Emoly) being absent. This 'party' of 55 animals barely moved, and on the same evening it settled on the cliff only a few hundred meters away from Site-B. On March 6, this party traveled on the savanna until 10:51 a.m. It then descended the cliff into the riverine forest, where the animals foraged and rested for about 3.5 hours. In the afternoon, they moved downstream very slowly under the cliff. At around 3:00 p.m., they ascended to the savanna halfway between Site-O and Site-Dj. At 4:05 p.m., another party of about 30 animals appeared running from the north on the savanna, and joined the major party. The entire Kerrayu group then returned upstream, arriving at Site-O at 5:40 p.m. and staying there on that evening.

The rapid movement on the evening of March 4 is thought to have been one of the factors causing the separation into 2 parties. Furthermore, it is considered that this separation influenced the major party in its choice of sleeping site, because the cliff near Site-B was never used as the sleeping site by the Kerrayu group throughout the study period except on this occasion. It is concluded therefore that the cohesiveness of the Kerrayu group is usually very high.

In describing the social organization of the Kerrayu group, the term 'infra-unit' or 'unit' is applied to any specific association between a male and one or more females. At the beginning of the study period, the Kerrayu group consisted of 2 large one-male units (OMU) containing 5 or 6 females, 3 small one-male units containing only 2 females, 9 pair units (PU) composed of a male and a female, and 9 bachelor males over the age of adolescence (Table 5). In addition to these, 2 pubescent males were identified. During the nomadic movements of the Kerrayu group, juveniles were observed to form several traveling or playing parties which were accompanied by some of the bachelor males.

Throughout the study period, two cases were observed in which a male of a pair unit was deprived of his female by the male of another pair unit, which developed into a small one-male unit as a result. At the same time, two cases of sudden breakdown of one-male units were observed (Fig.7).

On December 30, Doro formed an association with ore, who had been associated with Asama until that time, and copulated with her frequently. The female, ore, had been showing maximum swelling of her perineum from 2 days before. After this alteration of male-female association, the deprived male, Asama, remained a bachelor until the end of the study period. The pregnant female, ino, who had been associated with Doro until this alteration, subsequently followed Gt-OMU for about a month, giving birth on January 14, but again became in company with Doro from January 29.

On February 7, Uzo began to follow fossy who had been possessed by Feres and had shown a partial swelling since the day before. On February 13, her perineum reached the stage of maximum swelling and she began to copulate with Uzo frequently.

Two days before when Doro began to possess ore, Asama was found to be wounded on his cheek. Furthermore, on the same day that Uzo began to possess fossy, 4 other males (Stav, Hakeem, Posta, and Doro) were wounded. It is considered therefore that the sexual attractiveness of a female at the peak of oestrus may spark attempts by other males to take her from her possessor, and that an alteration in the possession of the female may be realized through physical conflicts among 2 or more males. This process closely resembles that observed in the Gorge group during the previous study period. On the other hand, the sudden breakdown of the one-male unit can be started by the weakened condition of the leader male as a result of a disease or wound.

On February 8 an aged male, Stav, was found to be absent from the Kerrayu group, and 2 females, sonja and sasha, which had been possessed by him were absorbed into Yb-OMU and Zf-OMU, respectively. On February 12, Stav appeared in the Kerrayu group looking emaciated, but subsequently disappeared again twice, from February 13 to February 15 and from February 19 to February 21. On February 19, when the Kerrayu group was staying near Site-L, Stav was found out together with only one juvenile at the edge of a cliff near Site-Dj, about 3 km upstream away from the group. He was probably too wasted by disease to follow the rapid movements of the Kerrayu group. On and after March 3*[2], Stav showed recovery and traveled with the group, but he could no longer possess any females. Furthermore, on the early morning of February 19,

Table 5. Individual compositions of infra-units within the Kerrayu group confirmed at the beginning of the study period

Types and names of infra-units		Male		Female	
		Adult	Adolescent	Adult	Adolescent
One-male unit	*Yb*-OMU	*Yabelo(Yb)*		*yome(ym)*	*boke(bk)*
				yase(ys)	
			[*Chatto(Ch)*]	*tare(tr)*	
				magari(mg)	
				yobo(yo)	
	Gt-OMU	*Geta(Gt)*		*tsahaye(ts)*	
				fekelta(fk)	
		[*Tadji(Tj)*]		*tamble(tb)*	
				kogomi(kg)	
				kokeb(kb)	
	Ng-OMU	*Nigus(Ng)*		*nege(ne)*	
				netsa(nt)	
	Sv-OMU	*Stav(Sv)*		*sonja(so)*	
		[*Djoro(Dj)*]		*sasha(sa)*	
	Zf-OMU	*Zefen(Zf)*		*woly(wo)*	*chame(ch)*
Pair unit	*Hk*-PU	*Hakeem(Hk)*		*hela(hl)*	
	Pt-PU	*Posta(Pt)*		*pon(pn)*	
	Uz-PU	*Uzo(Uz)*			*ume(um)*
	Kl-PU	*Kusil(Kl)*		*konjo(kj)*	
	Jr-PU	*Jirat(Jr)*		*joniya(jo)*	
	Vl-PU	*Villa(Vl)*		*vita(vt)*	
	Fs-PU	*Feres(Fs)*		*fossy(fo)*	
	Dr-PU	*Doro(Dr)*		*ino(in)*	
	As-PU		*Asama(As)*	*ore(or)*	
Bachelors		*Igir(Ig)*	*Bal(Bl)*		
		Louis(Ls)	*Emoly(Em)*		
		Quonta(Qt)			
Total		18	4	23	3

During the study period, *Sv*-OMU, *As*-PU, and *Fs*-PU were broken down and the 3 males, *Stav*, *Asama*, and *Feres*, became bachelors (see Fig. 7). Abbreviated names are given in parentheses. Three bachelor males which followed particular one-male units are shown in blackets and arranged within the row corresponding to the respective units.

Yb-OMU, which had been the largest infra-unit of the Kerrayu group, was found to have broken up. Although Yabelo had given no sign of weakness until the previous evening, on that morning he showed difficulty in walking, being barely able to walk with series of several tens of steps repeatedly interrupted by lying on his belly. Of the 7 females which he had possessed, only yome, who had been in the closest proximity to Yabelo, continued to follow him faithfully. Two of the other 6 females were escorted away by the adolescent male, Chatto, who had been the

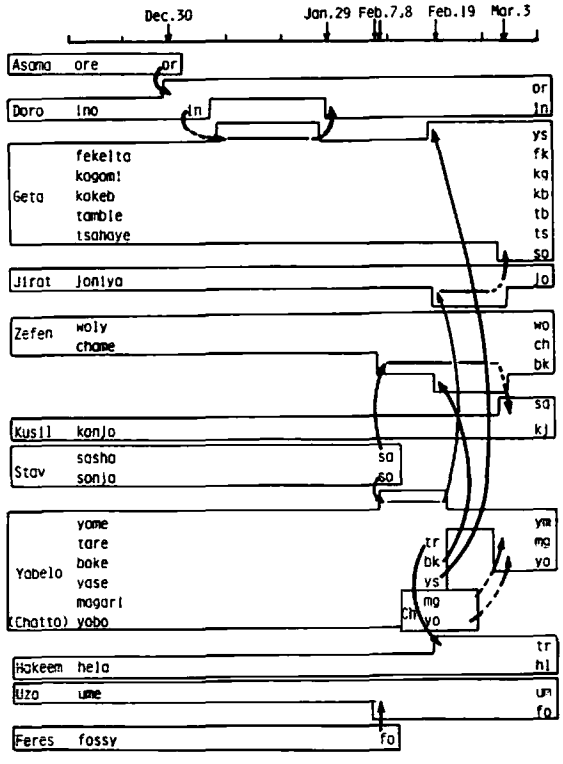


Fig. 7. Changes in composition of infra-units in the Kerrayu group. The Kerrayu group was observed intensively from December 10 to March 10. Fourty-three animals were caught on March 11 for collection of blood samples by another researcher.

"follower" (Kummer, 1968) of Yb-OMU (see Fig.9), and the remaining females were possessed respectively by 4 different males. As Yabelo had no external injury apart from a bend on the base of his tail, he was presumed to have suffered a heavy bruise on his loins, which might possibly have been caused by a fall from the precipice at the sleeping site. By March 3 he had completely recovered, and had retrieved the 2 females from Chatto.

The most distinctive feature of the process of the breakdown of the one-male unit in the Kerrayu group was that females who had been possessed by a male were individually divided among different males. This point will be further examined later, since it provides a valuable clue to the basic mechanism of integration of the one-male unit in the hamadryas society.

Taking into account the alterations in possession of females by males described above, the correlation between the tendency of males to possess females and their hybrid indices was examined. The tendency of the males to possess females was represented by the mean number of females which were possessed by each male per day during the study period. Adolescent males, which did not yet show mature character in their external appearance, were excluded from this study (Table 6). There was a significant correlation between the males' tendency to possess females

Table 6. Correlation between the hybrid index of each male and the mean number of females possessed by him per day

Name of male	Hybrid index	Number of female	
		range	average
Geta	2	5–7	5.64
Yabelo	2	1–7	5.20
Nigus	2	–	2.00
Stav	2	0–2	1.32
Hakeem	3	1–2	1.22
Posta	3	–	1.00
Uzo	4	1–2	1.35
Kusil	4	1–2	1.09
Jirat	5	1–2	1.13
Villa	5	–	1.00
Zefen	6	2–4	2.47
Tadji	6	–	0
Djoro	6	–	0
Igir	6	–	0
Feres	8	0–1	0.65
Doro	9	1–2	1.45
Quonta	16	–	0
Louis	16	–	0

The mean number of females per day was obtained by dividing the accumulated number of females possessed by each male throughout the study period by the total number of observation days (91 days). Adolescent bachelor males were excluded from this analysis.

and their morphological features (Spearman's rank correlation: $r_s = 0.6428$, $p < 0.01$, one-tailed). In other words, the closer a male is to hamadryas in its appearance, the more females it tends to possess.

In the Kerrayu group there are far more males close to hamadryas than in the Gorge group, as many as 14 males showing hybrid indices of less than 7. However, even among these males which are close to hamadryas in their appearance, there is wide variation in the tendency to possess females, which in turn correlates with the morphological variations significantly. This suggests that the tendency to possess many females may depend highly on behavioral traits which are genetically determined. Such behavioral traits will be analyzed elsewhere (Sugawara, in prep.).

INTRAGROUP SPACING MECHANISM

1. Spatial Relationships among Males

Firstly, the spatial relationships among males will be examined for the Kerrayu group, which could be thoroughly traced on its daily nomadic routes. The male which was found at the shortest distance from the focal male in each "scan" (Altmann, 1974) was designated as the "nearest neighbor" (Abramovich, 1976). The distribution of distances between the focal males and the nearest neighbors were compared between the resting situation and the foraging situation. All inter-individual distances which were measured after the baboons had finished eating artificial food until they began to depart from the feeding site, were regarded as data for the resting situation. Even during group movements, the moment when either

the focal male or at least one of his partner females participated in the grooming interaction was included in the resting situation. If the focal male had been sitting continuously without feeding for more than 5 min at the same point, the inter-individual distances measured during these moments were retrospectively included in the resting situation.

In the resting situation, distribution curves of the distances between focal males and the nearest male neighbors show a clear exponential pattern. During about 90% of the total resting time, at least one other male is present within a radius of 5 m from the focal male. On the other hand, in the foraging situation the exponential curve becomes smoother, the mode being in the range of 1-2 m. At least one other male is present within 5 m from the focal male during about 60% of the total foraging time (Fig.8). Thus, in the Kerrayu group the males display a conspicuous tendency to be proximal to each other in the resting situation. In the foraging situation the distances between males become longer than in the resting situation, but the males still show a slight tendency to walk or feed at relatively short distances from each other.

Secondly, the spatial relations among males are compared for the Kerrayu group and the Gorge group. Since observations of the Gorge group were made only when the baboons were resting at and around the feeding site, the data collected for the Kerrayu group in the resting situation only were compared with the entire data from the Gorge group (Fig.8). The spatial relation among males of the Gorge group and of the Kerrayu group differed from each other significantly, not only in the mean value of the distances but also in the patterns of their distribution (Kolmogorov-Smirnov test: $D_r = 0.453$, $p < 0.01$, two-tailed). In other words, at least in the resting situation, the males of the Kerrayu group have by far the stronger tendency to be proximate to each other than those of the Gorge group.

Thirdly, a profile of the relationshiops among the infra-units of the

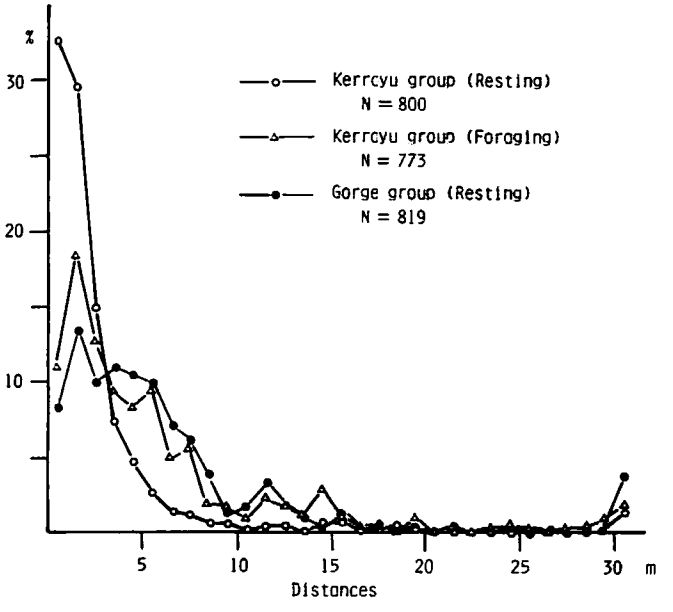


Fig. 8. Distribution of distances between focal males and the nearest male neighbors in 2 hybrid groups.

Kerrayu group could be visualized by making use of the spatial relations among males. A sociogram covering the entire Kerrayu group was constructed by connecting each focal male with the males which were the first and the second frequent nearest neighbors (Fig.9). In this procedure, scans in which the nearest neighbor was found at a longer distance than 15 m from the focal male were excluded. This sociogram is valid for demonstrating the relationships among the focal males or between focal males and bachelor males, although the relationships among bachelor males cannot be determined from it.

There are several kinds of conspicuous partnerships between certain particular males in the Kerrayu group. The first is the close relation between the leader of the one-male unit and the bachelor male following that unit. Examples of such a relation were seen in the dyads of Getà-Tadji, Doro-Igir, Stav-Djoro, and Yabelo-Chatto. Moreover, close associations can be discerned between particular infra-units. The most conspicuous of such associations were found between 2 small one-male units (Zf-OMU and Ng-OMU), and between Yb-OMU and Hk-PU. As described later, no close association existed between the one-male units except that between Zf-OMU and Ng-OMU. There were also close relationships in 3 pairs composed of a one-male unit and a pair unit each, i.e. Ng-OMU and Kl-PU, Gt-OMU and Uz-PU, and Dr-OMU and Uz-PU. Since 4 of the 5 associations between possessor males mentioned above were formed reciprocally, it is believed that the neighborhood relationships between these particular infra-units are not accidental results of random spacing within the group, but represent some aspect of the stable social relationship among males in this group.

In order to express in a more quantitative way the intensity of the

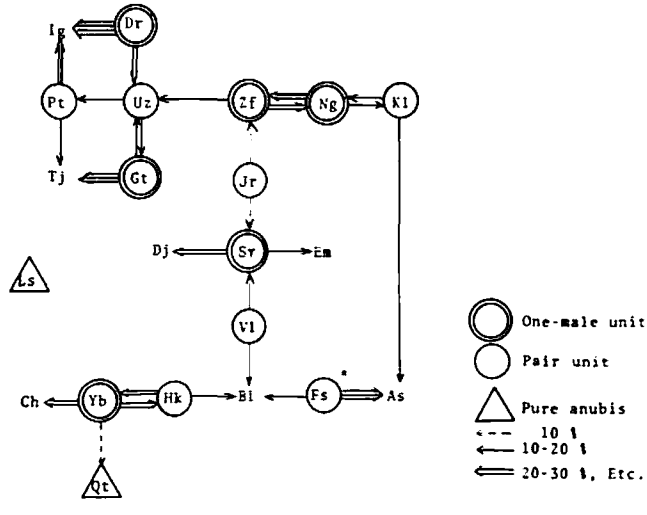


Fig. 9. Sociogram of the Kerrayu group based on the spatial relations among males. Each focal male is connected by arrows with the first and second closest neighbors. *Feres (Fs) was traced for only 335 min, while each of the other possessor males was traced for more than 500 min. "A→B" indicates that B was the nearest neighbor of A in 10-20% of the total scans during focal-male sampling from A. The number of lines represents the value of the percentage.

neighborhood relationship among focal-males, or possessors, the 'neighborhood index' was calculated for every possessor-possessor dyad. The neighborhood index is given by the sum of the frequencies, obtained respectively as a percentage of the total number of 'scans,' with which each male was the nearest neighbor of the other male during Focal-Male Sampling of the latter. The neighborhood indices among possessor-possessor dyads of the Kerrayu group are shown in Fig.10.

According to the number of females possessed by each male, the possessor-possessor dyads could be categorized into the following 3 kinds: dyads among leaders of one-male units (O-O dyads), dyads among males of pair units (P-P dyads), and dyads composed of a leader of a one-male unit and a male of a pair unit (O-P dyads). The mean values of the indices were 7.83 among 15 O-O dyads, 11.54 among 15 P-P dyads, and 11.61 among 36 O-P dyads. Thus, neighborhood relationships appear to be the closest among O-P dyads, whereas O-O dyads in general show only low values for the neighborhood index.

Statistically speaking, the difference in neighborhood indices was not sufficiently significant between the O-P dyads and P-P dyads (Mann-Whiteny U test: $U_{cal}=178$, $z=-1.9019$, $p<0.058$, two-tailed), but the neighborhood indices of the O-O dyads were significantly smaller than those of the O-P dyads ($U_{cal}=159.5$, $z=-2.284$, $p<0.023$, two-tailed) and the P-P dyads ($U_{cal}=22$, $p<0.02$, two-tailed). It is concluded therefore that the one-male units have a tendency for avoiding each other's spatial proximity. The close association between Zf-OMU and Ng-OMU was the only exception.

Kummer (1968: 152), describing the coordination between one-male units probably of the same band on the march, concluded that "the

	ONE-MALE UNIT						PAIR UNIT					
	Gt	Yb	Sv	Ng	Zf	Dr	Hk	Pt	Uz	Kl	Jr	Vl
Gt		0	7.6	8.6	8.1	0	7.7	8.7	27.6	7.8	12.5	9.2
Yb			4.4	6.4	5.0	4.1	56.1	5.7	4.8	12.2	0.8	7.2
Sv				10.0	2.7	1.0	5.2	0.8	12.6	5.1	16.1	21.2
Ng					46.6	6.3	4.7	8.0	9.2	24.6	7.8	3.8
Zf						6.6	6.6	9.1	20.3	11.4	17.6	8.9
Dr							7.9	4.8	34.3	9.7	7.1	0.8
Hk								15.0	8.4	10.8	8.6	11.4
Pt									20.8	12.2	12.9	9.4
Uz										11.0	13.1	10.7
Kl											10.3	8.5
Jr												10.0
Vl												

Fig. 10. Neighborhood indices of possessor-possessor dyads in the Kerrayu group. If A was the nearest neighbor of B in p% of the total scans during focal-male sampling from B, and if B was the nearest neighbor of A in q% of the total scans during focal-male sampling from A, the neighborhood index for the A-B dyad is given by the sum of these two percentages (p+q).

immediate cause of the existence of bands...is the attraction among their males." In the Kerrayu group, it was found that not only was the entire group very cohesive but there were also distinctive social bonds among the adult males which each possessed one or more females. This suggests that the social structure of the Kerrayu group has a fundamental affinity with that of the hamadryas band. At the same time, as was demonstrated by the above analysis, it must be emphasized that the spatial relationship, or the formation of "the coordination of travel" (Kummer, 1968), is strongly affected by the number of females possessed by each male.

2. Spatial Relations between Males and Females

The spatial relations between males and females belonging to the same infra-unit or subgroup were compared between the Kerrayu group and the Gorge group. It was expected that much of the spacing mechanism between the males and females would depend on how many females simultaneously had associations with a certain male. In the previous study, it was elucidated that in the Gorge group the spacing pattern between male and female within the one-male group containing more than 2 females differed greatly from that of the pair group or pair-link composed of a specific association between a male and a female (Sugawara, 1979).

In order to make a comparison between 2 groups which were under as equivalent conditions as possible to each other, the objects of comparison were confined to males which had stable associations with more than 2 females throughout the whole period during which Focal-Male Samples were collected from each of them. The data of the resting situation only from the Kerrayu group were compared with the entire data for the Gorge group. In accordance with the above conditions, 6 males were chosen from the Kerrayu goup, i.e., Geta (N*) =66), Stav (N=64), Nigus (N=61), Zefen (N=36), Doro (N=62), and Yabelo (N=68), whereas 7 males were chosen from the Gorge group, i.e., Baboof (N=84), White (N=82), Chilotta (N=85), Maler (N=85), Zare (N=83), Matiou (N=84), and Robes (N=79).

Of the 2 or more females which were possessed by a focal male, the female which showed the least mean value of individual distances from the focal male was designated as 'the nearest female' and that which showed the greatest mean value was designated as 'the farthest female. In the Kerrayu group, the mean value of the individual distances was calculated from the entire samples, including those collected in the foraging situation.

The distribution of distances between the focal males and either the nearest females or farthest females is illustrated in Fig.11. Both in the Gorge group and in the Kerrayu group, the distribution curves of the distances between the possessor and both of the nearest and the farthest females are of exponential form, as has also been found in the distribution of individual distances between males and females within the one-male units of gelada baboons (Kummer, 1974; Kawai et al., 1979). However, both the nearest and the farthest females tend to be present at significantly shorter distances from the possessor male in the Kerrayu group than in the Gorge group (Kolmogorov-Smirnov test: D_r =0.184 for the nearest females, D_r =0.174 for the farthest females, $p<0.001$, two-tailed). In other words, the one-male units in the Kerrayu group can be said to be spatially more cohesive than the one-male groups in the Gorge group.

Examinations were made of how the spacing mechanism between male and female varies according to the number of females possessed by the male, based on a comparison of the distribution patterns of male-female distances among the infra-units of the Kerrayu group. This comparison was based on the entire sapmles including those collected in the foraging situation (Fig.12). The 3 males, Villa, Hakeem, and Kusil, possessed only

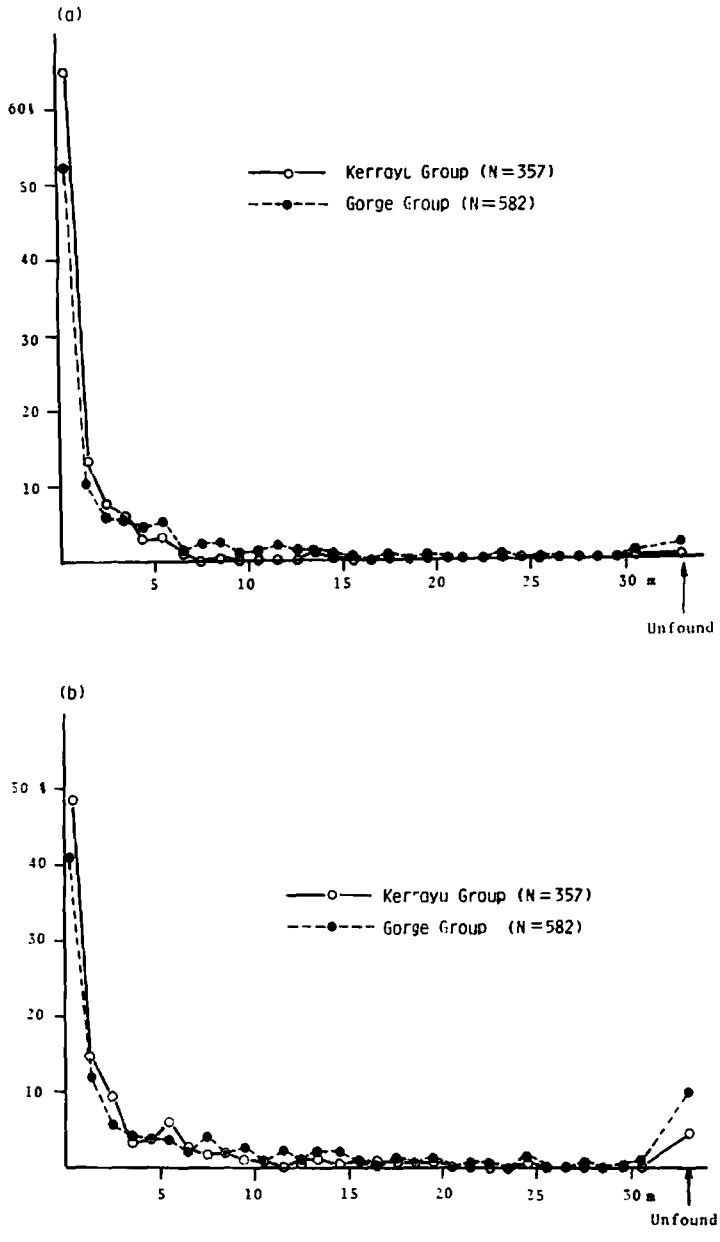


Fig. 11. Distribution of individual distances between males and the nearest and farthest partner females in 2 hybrid groups. (a) Nearest females; (b) farthest females. For the Kerrayu group, only data for the resting situation were used. The data from 6 males were collected together in the Kerrayu group, while the data from 7 males were collected together in the Gorge group.

one female each throughout the period during which they were traced as focal animals. In these male-female dyads, it was very frequent for the male and the female to be in the proximity of within 1 m from each other (55.3%-66.9%). The distances between them rarely exceeded 10 m, and never exceeded 20 m (Fig.12a).

Another 3 males, Nigus, Stav, and Doro, possessed 2 females each throughout the sessions of focal-male sampling. The data from them therefore represent the spacing pattern between males and females within relatively small one-male units (Fig.12b). Comparing these spacing patterns with those observed within the pair units, it can be seen that the frequency with which the male and the female were proximate to each

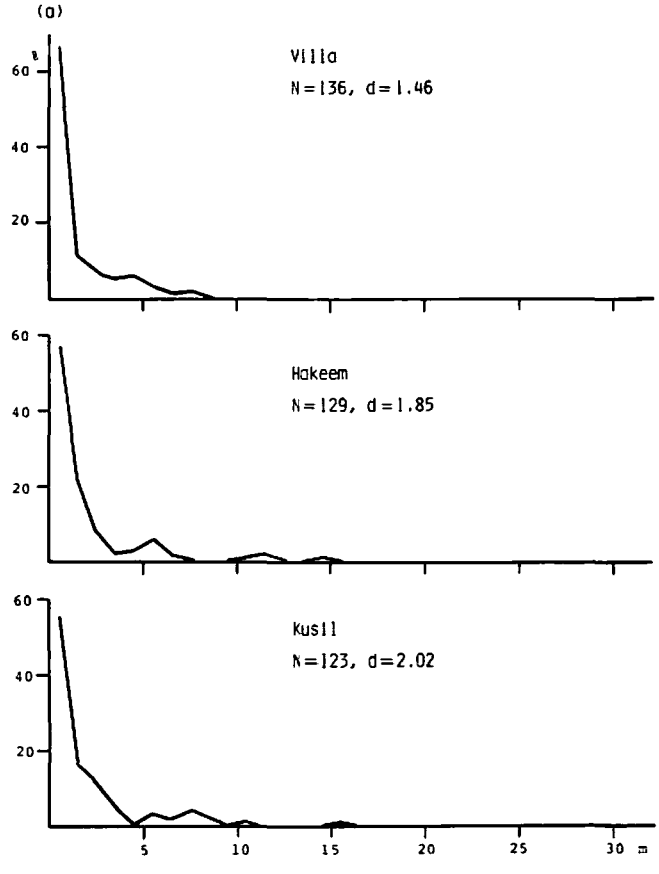
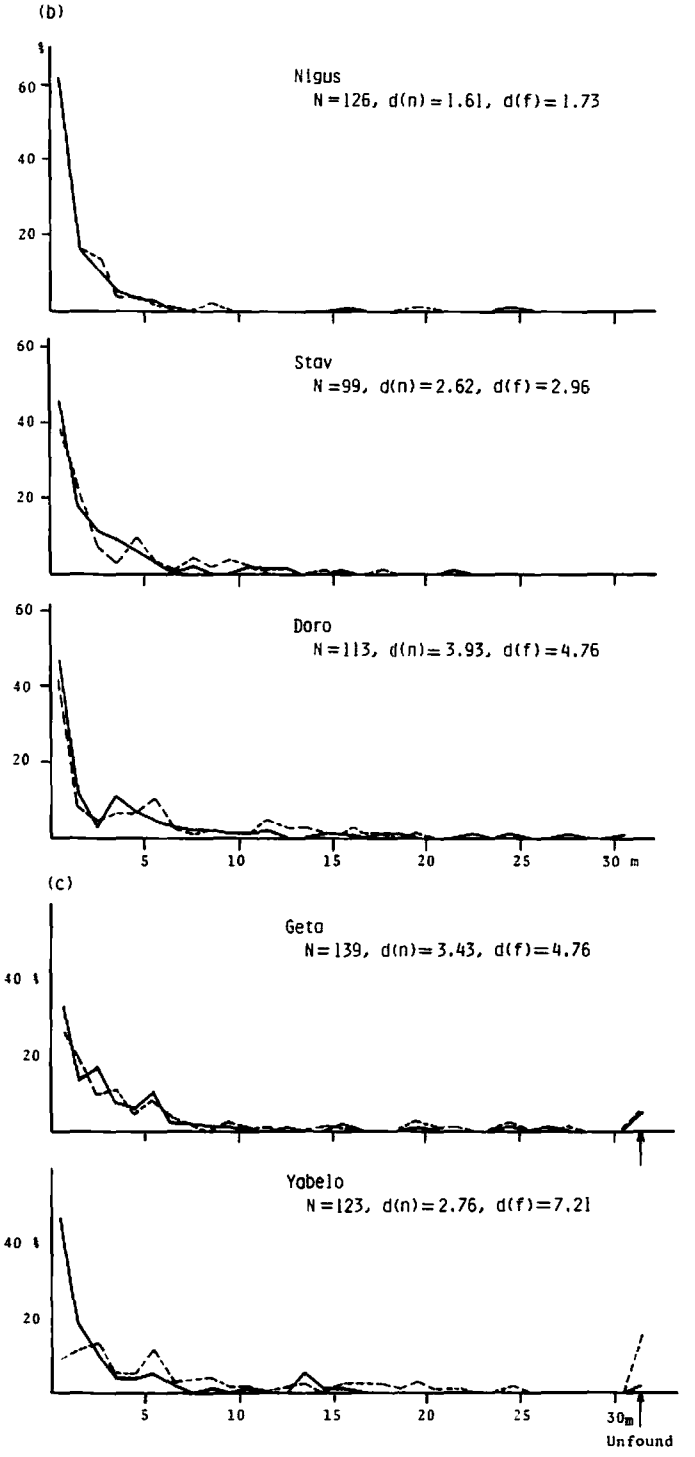


Fig. 12. Variations in distribution patterns of individual distances between male and female within the same unit in the Kerrayu group. (a) Pair units; (b) small one-male units (next page); (c) large one-male units (next page). In pair units, 'd' indicates the mean value of distances between a male and a female. In one-male units, 'd(n)' and 'd(f)' indicates, respectively the mean values of distances for the nearest and the farthest female from the leader male. Solid lines and broken lines represent the nearest and the farthest females, respectively.


(b)
%
60
40
20
Nigus
N=126, d(n)=1.61, d(f)=1.73
Stav
N=99, d(n)=2.62, d(f)=2.96
Doro
N=113, d(n)=3.93, d(f)=4.76
5
10
15
20
25
30 m
(c)
40 %
20
Geta
N=139, d(n)=3.43, d(f)=4.76
Yabelo
N=123, d(n)=2.76, d(f)=7.21
30m
Unfound

other (within 1 m) was a little lower than in the pair unit. The distances between male and female exceeded 20 m on rare occasions. Especially the females possessed by Doro, which revealed relatively many anubis characters in his morphology, showed a tendency to disperse away from him. The common feature among these small one-male units was that the 2 females within each unit showed strikingly similar patterns to each other. In other words, the 2 females respectively maintained proximity to their possessor male almost equally.

Finally, the spacing mechanism within the large one-male unit was examined, analyzing samples from the 2 males, Geta and Yabelo, which possessed from 5 to 6 females. Focal-male samples collected from Yabelo after the breakdown of his one-male unit were excluded from the analysis (Fig.12c). The spacing patterns between male and female in these 2 units made a sharp contrast with each other. In Gt-OMU, the individual distances between male and female tended to be longer than those in any of the infra-units examined above, the exponential curve being very smooth. However, the difference between the patterns shown by the nearest and the farthest female was conspicuously slight. Thus, all of the 5 females respectively maintained almost equivalent levels of spacing from the possessor male to one another. On the other hand, in Yb-OMU the difference between the patterns shown by the nearest and the farthest female was remarkable. The nearest female tended to be very proximate to the male, showing a similar distribution pattern of distances to the pattern in male-female dyads within small one-male units. The farthest female showed an irregular pattern that was not found in any other unit and which could not be approximated to an exponential curve. This suggests that in Yb-OMU a particular female very often stays in proximity to the possessor male while the other females often shift far away from him.

The above comparisons elucidate several points, as follows. In the Kerrayu group, the distribution of individual distances between a male and a female within the same unit reveals an exponential pattern, irrespectively of the number of females which are simultaneously possessed by that male. However, as the number of females increases, each female tends to stay more frequently at long distances from the male. When only 2 females are present within the same unit, this tendency is not so sharply apparent. In large one-male units containing more females, the following two kinds of spacing patterns are possible: 1) the females can be differentiated into 2 groups--those which are extremely proximate to the possessor male, and those which frequently shift from him; and 2) although the respective individual distances of the females from the male become rather long, all of the females maintain an approximately equal degree of proximity to the male.

The spacing pattern under 2) is similar to that which has been found within the large one-male units of gelada baboons, where no great differences were observed in mean values of the individual distances between the leader male and the females (Kawai et al., 1979). As Kawai et al. have pointed out, such a spacing pattern is considered to provide strong proof that the large one-male unit is well integrated. The difference between the spacing patterns 1) and 2) above cannot be attributed to the sexual condition of the females, because only one female was observed to become oestrous in both Gt-OMU and Yb-OMU. Moreover, those females which were sexually active did not coincide with the nearest females in both units. It is considered that such two forms of spacing between a male and his females should be attributed to differences in herding behavior between leader males.

Sugawara (1979) argued that the possessiveness towards females displayed by hamadryas or hybrid males is based on the attitude of

'interest-fixation-on-a-specific-other.' It is expected that the interest of the male becomes dispersed, as the number of females with which he is in contact increases. At the same time, when the interest of the male is focussed on a particular female, the remaining female possessed by him can be expected to acquire increased freedom of movement as a result of a decrease in the male's control over them. In order to verify this, examinations were made of how the spacing between a male and the female previously having been proximate to him was affected by the acquisition of a new female into the unit. Each of the 3 males, Uzo, Zefen, and Jirat, acquired a new female during the sessions of focal-male sampling (see Fig.7). A comparison was made of the distances of the originally nearest females from these males before and after the acquisition of the new females. At the same time, the distribution of distances between these males and the newly-acquired females was also determined (Fig.13). In order to make the size of the samples sufficiently great, the data from these 3 males were combined.

It should be noted that the acquired females were extremely proximate to their new possessors within 1-12 days after acquisition. In fact, they spent as much as 80% of their time within 1 m from the new possessors and were never present at distances of greater than 6 m away from him. In the dyads of Uzo-fossy or Jirat-sonja, frequent mounting by the male or grooming by both of them was observed, whereas in the dyad of Zefen-sasha very frequent and intensive herding behavior by the male was observed.

There was a tendency for the originally nearest female to shift far away from the male while he was in close contact with the new female, but the difference in individual distances of the former from the male before and after the acquisition of a new female was not sufficiently significant (Kolmogorov-Smirnov test: $D_r = 0.147$, $p < 0.10$, two-tailed). This suggests that even if the interest of the male is temporarily focussed on a particular female, the remaining females dare not immediately shift far away from him. In Zf-OMU, it was sometimes observed that the originally farthest female, woly, attempted to interrupt the close interactions between Zefen and the newly-acquired female, sasha, by threatening her, sitting between them, or by grooming Zefen by herself. As has been pointed out by Stammbach (1978: 334), it is considered that the effort of each female to "defend its already established relationship with" the male may contribute to the cohesion of the one-male unit, moderating the effects of concentration or dispersion of the male's interest among females.

GROOMING RELATIONSHIPS

1. Distribution of Grooming Budget among Males and/or Females

Of all the grooming interactions observed, only those which were recorded continuously from start to finish were included in the quantitative data. A bout of grooming was defined as a continuous activity in which one animal initiated and carried out the active role, while another performed the passive role. A mutual grooming interaction consisted of more than 2 bouts, with the active and passive roles interchanging alternately. The distributions of the 'grooming budget,' i.e., the total of the time durations of grooming interactions, in the 3 categories of dyads (male-male, male-female, and female-female) were compared between 2 groups based on the entire data including ad lib. samples (Table 7). Only grooming interactions observed among adult or adolescent members were utilized for this comparison.

It should be noted first that in the Kerrayu group, grooming interactions among adult and/or adolescent males occasionally occurred,

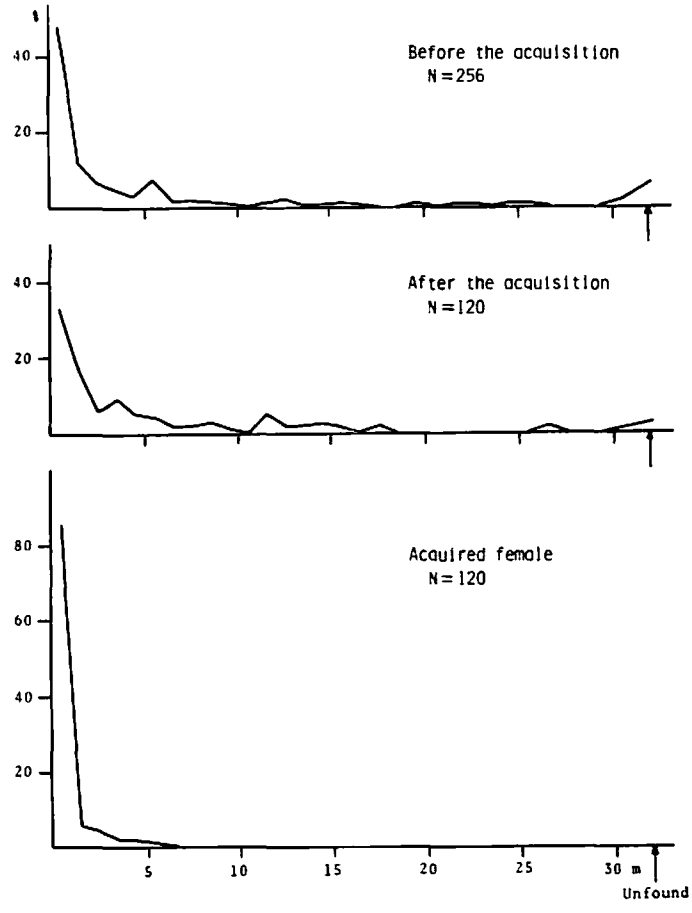


Fig. 13. Effect of acquisition of a new female on the distribution pattern of distances between a possessor male and the originally nearest female in the Kerrayu group. (a) Distances between the possessor male and the nearest female before the acquisition of a new female; (b) after the acquisition of a new female; (c) distances between the possessor male and the acquired female. The data from 3 different males were collected together.

but they were never seen in the Gorge group**. During the previous study period, about 100 hours of grooming interactions had been recorded in the Gorge group, but grooming had never been observed among adult or adolescent males (Sugawara, 1979). In the Kerrayu group, the most frequent grooming was observed between particular bachelor males, Asama and Igir (18 bouts; 65 min). At the same time, relatively frequent grooming was observed in 2 pairs composed of a possessor and a bachelor [Posta-Igir (8 bouts; 28.5 min) and Uzo-Bal (9 bouts; 24.5 min)]. However, grooming between possessor males was very rare, only 1 bout (1.5 min) being observed between Hakeem and Posta throughout the study period. In the Kerrayu group, at least among possessor males, friendly bodily contact such as grooming was clearly avoided. On the other hand,

Table 7. Distribution of grooming budget among male-male, male-female, and female-female dyads

Group		Duration of grooming (a)M↔M	(b)M↔F	(c)F↔M	(d)F↔F	Total	(b)/(c)	(c)/(d)	$\frac{(b)+(c)}{2(d)}$
Kerrayu	Duration	179.5 (5.6)	544.0 (16.9)	1500.0 (46.5)	1000.5 (31.0)	3224.0 (100.0)	0.36	1.50	1.02
	Number of dyads	9	30		38	77			
Gorge	Duration	0 (0.0)	626.5 (28.5)	780.0 (35.4)	795.0 (36.1)	2201.5 (100.0)	0.80	0.98	0.88
	Number of dyads	0	33		30	63			

The data indicate the total minutes of grooming performed by (a) male to male, (b) male to female, (c) female to male, and (d) female to female. Figures in parentheses indicate the percentages of the respective duration in the total grooming budget of each group. Both focal-male sampling and *ad lib.* sampling were used.

in the Gorge group, grooming was strongly restrained from occurring among males which had reached sexual maturity. This suggests that the males of the Kerrayu group may be more affinitive with, or more tolerant to, each other than those of the Gorge group.

The percentages of the amount of grooming between males and females in the grooming budget showed very similar values (about 63%) to each other. However, the 2 groups differed conspicuously from each other in the tendency of the male or female participants to perform active or passive roles in grooming activity. In the Kerrayu group, on the average, one male groomed females only for 1/3 of the time that one female groomed males, whereas in the Gorge group one male performed the active role for 4/5 of the time that one female performed the active role.

Concerning the amount of grooming between males and females as compared to that between females and females, it was found in the Kerrayu group that, on average, one female spent 1.5 times as much time grooming towards males as it did grooming towards other females, whereas the females of the Gorge group devoted approximately equal times to grooming towards other females and grooming towards other males. This appears to suggest that the females of the Kerrayu group are more 'obedient' to the males than those of the Gorge group. However, it has been pointed out that the occurrence of grooming between males and females depends strongly on the sexual condition of the females in savanna baboons (Saayman, 1971: Seyfarth, 1978a).

Here a female was considered to be oestrous, or sexually active, when it showed partial or maximum perineal swelling, and it was considered to be anoestrous, or sexually inactive, when its sexual skin was flat. For respective focal males, the durations of their participation in grooming interactions with oestrous or anoestrous females, as observed during the sessions of focal-male sampling, are shown in Table 8. In both groups, the males display a tendency to spend more time as the groomer in interactions with oestrous females than with anoestrous females.

The eagerness of each male to perform the active role in the grooming interactions was represented by the 'male groomer rate,' i.e., the proprotion of the time spent by each male performing the role of the groomer to the total time duration of the grooming interactions between him and the females. The male groomer rates for the Kerrayu group did not differ significantly from those of the Gorge group for grooming interactions with oestrous females (Mann-Whitney U test: $U_{cal}=12$, $p<0.10$, two-tailed). However, for interactions with anoestrous females, the male groomer rates of the Kerrayu group were significantly lower than those of the Gorge group ($U_{cal}=23$, $p<0.05$, two-tailed).

If it is assumed that the total amount of time that each male can devote to grooming towards females is fixed, the male groomer rate will inevitably decrease as the number of females simultaneously possessed by him increases (cf. Seyfarth, 1977). However, the number of adult or adolescent females per possessor male was 2.30 in the Gorge group, and 2.17 in the Kerrayu group, i.e., the mean number of females possessed by a male was slightly bigger in the Gorge group than in the Kerrayu group. Furthermore, even the males of the Kerrayu group which possessed only one female (Hakeem, Kusil, Villa, and Posta) showed lower values for the male groomer rate than any males of the Gorge group except Chilotta. Thus, the lowness of the male groomer rates in the Kerrayu group cannot be attributed to a great number of females possessed by each male. It is considered either that the males of the Gorge group are more strongly motivated to perform the active role in grooming interactions with females than those of the Kerrayu group or that the females of the Gorge group are more 'inactive' in their grooming interactions with males than those of the Kerrayu group.

Table 8. Percentages of the duration of grooming performed by focal males in the grooming interactions between males and females

Group	Focal male	Anoestrous female		Oestrous female	
		Male groomer	Total duration	Male groomer	Total duration
Kerrayu	*Hakeem*	5.3%	9.5 min	46.3%	34.5 min
	Villa	5.4	74.0	-	0
	Geta	8.8	147.5	8.3	12.0
	Doro	8.9	45.0	-	0
	Zefen	10.6	33.0	56.0	45.5
	Kusil	14.1	39.0	0	21.0
	Uzo	16.1	56.0	44.1	46.5
	Posta	17.1	17.5	-	0
	Stav	31.1	30.5	0	17.0
	Jirat	32.2	45.0	53.0	33.0
	Yabelo	34.4	78.5	0	3.5
	Nigus	40.9	85.5	71.7	26.5
	Total	(19.4)	661.0	(41.5)	239.5
Gorge	*Chilotta*	9.4	53.0	47.3	27.5
	Robes	29.8	65.5	-	0
	Hagos	30.9	40.5	-	0
	Maler	32.1	54.5	64.3	7.0
	Danielle	33.8	32.5	84.6	19.5
	Matiou	35.1	57.0	16.0	12.5
	Baboof	36.9	51.5	94.7	19.0
	Necker	46.7	60.0	-	0
	Zare	51.3	19.5	50.2	114.5
	White	56.9	68.5	-	0
	Total	(36.1)	502.5	(55.5)	200.0

The left and right columns indicate the grooming interactions of each male with anoestrous and oestrous female partners, respectively. The 'male groomer' columns indicate the percentage of duration of grooming performed by each male to his partner female in the total duration of grooming interactions between them. Figures in parentheses indicate average percentages.

As stated earlier, the one-male units of the Kerrayu group were more cohesive than the one-male groups of the Gorge group. At the same time, ethological comparisons clarified that the leader males of the one-male units in the Kerrayu group had in their behavior repertoire far more effective ways of herding females by aggression than the males of the Gorge group (Sugawara, in prep.). Thus, the high male groomer rates in the Gorge group, as well as the persistent following behavior by males towards females (Sugawara, 1979), are considered to represent an indication of a compensatory effort on the part of the males, lacking aggressive herding techniques, to maintain the association with partner females.

2. Grooming Network in the Kerrayu Group

Sociograms representing the grooming relationships in the Kerrayu group and the Gorge group were constructed, based on the grooming interactions observed only during the sessions of focal-male sampling. Grooming interactions observed between focal males and bachelor males were omitted from these sociograms (Fig.14).

In the Kerrayu group, 4 small one-male units each of which contained only 2 females, and 2 pair units were isolated from each other and from the rest of the Kerrayu group in terms of grooming relations (Fig.14a). Of these 4 small one-male units, only Ng-OMU showed a

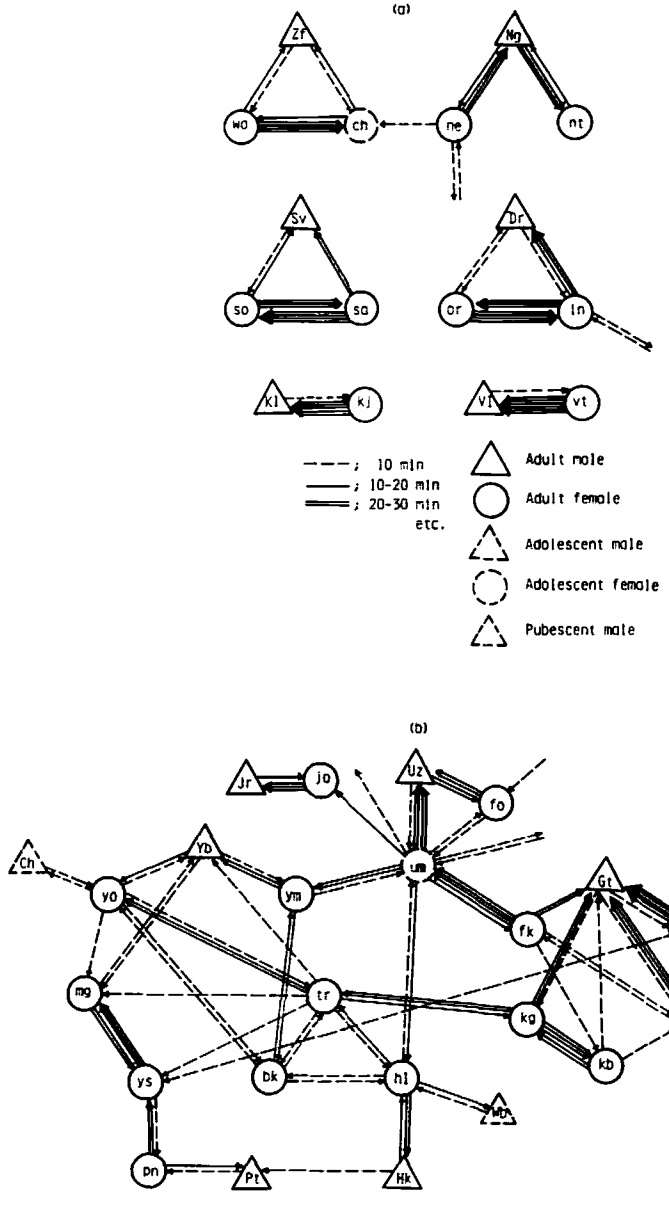


Fig. 14. Grooming network in the Kerrayu group based on focal-male samples. (a) Network including 4 small one-male units and 2 pair units; (b) network including 2 large one-male units, a small one-male unit, and 3 pair units. The arrows point from the groomer to the groomee.

peculiar pattern. That is to say, grooming interactions between the 2 females never occurred in Ng-OMU, while in each of the 3 other one-male units a far larger amount of grooming occurred between the 2 females than between the leader male and the females. Even if ad lib. samples were included, only 1 bout of grooming (0.5 min) was observed between the 2 females in Ng-OMU.

Kummer (1968) stated that within the one-male unit of the hamadryas baboon very little grooming took place among females. The sociogram for Ng-OMU is clearly concordant with the "star-like sociogram" (Stammbach, 1978) of the hamadryas one-male unit. However, the sociograms for most of the one-male units of the Kerrayu group deviated from such a star-like pattern.

Within the grooming network composed of infra-units other than such isolated units as were examined above, 2 large one-male units, Gt-OMU and Yb-OMU, sharply contrasted with each other in their patterns of grooming relationships (Fig.14b). The sociogram of Gt-OMU approximated to a hamadryas star-like pattern, while in Yb-OMU, 6 females were split into 3 dyads in each of which frequent grooming occurred. This contrast between Gt-OMU and Yb-OMU in grooming relationships paralleled to the contrast between these 2 units in the spacing mechanism between the leader male and females, which was described in a previous section.

The second distinctive feature of this grooming network was that frequent grooming occurred between females belonging to different units. Especially the adolescent female, ume (um), had frequent grooming interactions with various females. It may be an age-specific feature in the social behavior for nulliparous females to have variable friendly relations with many females. On the other hand, there were also several couples of adult females, such as yase (ys)-pon (pn) or tare (tr)-kogomi (kg), which frequently groomed each other notwithstanding their belonging to different units.

The origins of the variable grooming relations among females in the Kerrayu group require further examination. Two ways of interpreting are possible: either the grooming relation reflects kinship among these females, or it has been newly established between females which were accidentally possessed by the same male and were forced to become proximate to each other throughout their daily lives. It is possible that woly (wo) and chame (ch) in Zf-OMU or sonja (so) and sasha (sa) in Sv-OMU were mother and daughter, respectively, judging from their relative ages. On the other hand, shortly after Uzo (Uz) acquired a new female, fossy (fo), frequent grooming began to occur between fossy and the female, ume, originally possessed by Uzo. (including ad lib. samples, 13 bouts or 54 min of grooming were observed). Similarly, frequent grooming was observed between a female, ore, which was newly acquired by Doro and another female, ino, which had originally been his partner female. (Only during the focal-male sampling, 22 bouts or 73.5 min of grooming were observed). Such grooming relations can be considered to have been newly established between 2 females which accidentally became possessed by the same male.

It should be noted also that the close grooming relations between females within the same unit immediately disappear when the females come to be separated into different units as a result of breakdown of the original one-male unit. After the breakdown of Sv-OMU, grooming between sonja and sasha, which came to be possessed by different males, was never observed at least during the study period.

It is possible that grooming relations between females belonging to different units are based on kinship beetween them. For example, it is very probable that a female of Gt-OMU, fekelta (fk), and an adolescent female of Uz-PU (or OMU), ume, were mother and daughter. The fact that

the females of the large one-male unit often groom the females of units different from their own suggests that they may have acquired more freedom of interaction with others as a result of dispersion of the interest of the possessor male among them. It is considered that the affinitive bonds between closely related females are immediately cut off after they are possessed by different males, but these bonds may sometimes be revived when the control by the possessor males over such related females decreases.

The fact that even among the Kerrayu group a few one-male units existed which were concordant with the hamadryas star-like sociógram, suggests that the affinitive interactions between females within the unit may be strongly restrained from occurring if the control by the male over the female is sufficiently strict. Thus, the deviation in the sociograms of most one-male units in the Kerrayu group from the ideal star-like pattern may indicate that in this group even the males forming the one-male units suffer some loss of the faculty to control the females persistently under the influence of the hybridization.

3. Grooming Network in the Gorge Group

The grooming network within the Gorge group shows a rather intricate pattern (Fig.15). Such intricacy in grooming pattern is due primarily to the occurrence of infrequent but variable grooming episodes among females of different subgroups. Each of the clusters emerging from this network almost coincides with the respective subgroups, each of which usually moves in a body through the process of joining and parting. In other words, the network is basically composed of 10 'one-male groups,' which are connected with each other by the grooming relations among females. However, some of the females which were linked with their partner males at only a low level of similarity (see Fig.5) had grooming interactions with 2 or more males.

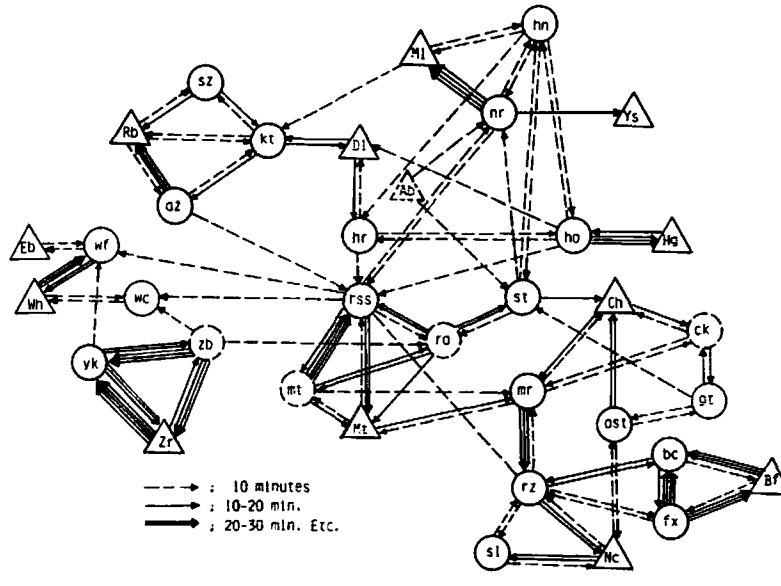


Fig. 15. Grooming network in the Gorge group based on the focal-male sampling.

In the previous study, it was elucidated that affinitive bonds existed among females within each of the subgroups and that femles often groomed one another even if they belonged to different subgroups. Such features of the grooming relations among females in the Gorge group were again recognized in the present study. Since there was a great difference in both the hour lengths of observation and sampling methods between the previous and present study, it is difficult to make direct comparisons between the closeness and the variety of the affinitive bonds among females between the two research periods. At least within the subgroups the affinitive bonds among females, as they are read from the sociograms, are not so conspicuous in the present study as was recognized in the previous study.

It has been pointed out that the male-female relations in the Gorge group undergo great transformations year by year. On the other hand it is necessary to determine the degree of continuity with which the affinitive bonds among females are maintained. In order to elucidate this point, examinations were made of the transformations in the grooming relations which had existed among the femles within the same subgroups 2.5 years previously, based on the total data including ad lib. samples (Table 9). Only 2 dyads of females, roze-rossa (rz-rss) and kitsune-nureme (kt-nr),

Table 9. Changes of grooming relationships in female-female dyads found within the same subgroup from the previous study period (1975-76)

	1975-76		1978-79	
Subgroup	Dyad	Closeness	Within the same subgroup?	Closeness
	sz-stl	++	No	-
St-OMG	*sz-sl*	+	No	-
	stl-sl	++	No	-
	rz-rss	++	No	+
Rb-OMG	*rz-az*	(+)	No	-
	rss-az	-	No	(+)
	hn-hr	++	No	(+)
Hg-OMG	*hn-ho*	-	No	(+)
	hr-ho	++	Yes	+
Wh-OMG	*wf-wc*	+	Yes	-
	ast-bc	(+)	Yes?	-
	ast-fx	++	Yes?	-
Bf-MMG	*ast-gt*	+	No	(+)
	bc-fx	(+)	Yes	++
	bc-gt	+	No	-
	fx-gt	+	No	-
	kt-mr	+	No	-
Gr-MMG	*kt-nr*	+	No	+
	mr-nr	-	No	-

The symboles in the second column from the left indicate female-female dyads found within the same subgroup during the previous study period (1975-76). The closeness of the grooming relationships is represented by the following 4 grades: ++, very close; +, close; (+), weak; -, grooming never observed. Both focal male-samples and *ad lib.* sampling were used.

Table 10. Existence of grooming relationships during the study period (1978-1979) in female-female dyads which were or were not found within the same subgroup during the previous study period (1975-76)

Grooming (1978-79)	Different subgroups	Same subgroup	Total
Not observed	131 (127.6)	10 (13.4)	141
Observed	21 (24.4)	6 (2.6)	27
Total	152	16	168

The data indicate the numbers of dyads of females which belonged to the same subgroup (right column) or to different subgroups (left column) during the previous study period (1975-76). Figures in parentheses indicate expected values calculated from the total numbers. Three dyads found within the same sybgroup during both the previous and the present study period were excluded.

still had close grooming relations in 1978-79, although these females had been separated into different subgroups. In particular, the latter dyad of females, kitsune and nureme, had been thought to be mother and daughter in the previous study period. Only 3 dyads of females, haru-honey (hr-ho), bayech-fox (bc-fx), and wufarem-witch (wf-wc), remained together within the same subgroup in 1978-79. Of all these dyads, the first 2 still had close grooming relations, but no grooming was observed between wufarem and witch. The first dyad of females, haru and honey, had been considered as siblings in the previous study period.

Next, disregarding the time duration of grooming, examinations were made of whether or not at least one bout of grooming occurred in each dyad of females in 1978-79. Excluding 4 adolescent females which had not been identified 3 years previously, grooming was observed in 29 dyads among 19 females, about 17% of the possible combinations between any 2 females (171 dyads). Of these 29 grooming dyads, 8 were present within the same subgroup 3 years previously. However, 2 of these 8 dyads, haru-honey and bayech-fox, were found within the same subgroup in the present study period as well as in the previous study period. Even when these 2 dyads are excluded from the grooming dyads (Table 10), it can be concluded that grooming between females which had belonged to the same subgroup 3 years previously, was more likely to occur than grooming between females which had belonged to different subgroups (chi-square test for 2 independent samples corrected for discontinuity: $\chi^2=4.3923$, df=1, $p<0.05$). This suggests that the affinitive bonds among females are continuously retained by themselves over the rather long term in the Gorge group. However, such persistent bonds among females are not necessarily embodied in any distinct social structure of this group. The affinitive bonds among females, often prevented from developing into a stable relationship due to the males' attempts to possess them, barely exist as thin strings in the social network of the Gorge group.

AGONISTIC INTERACTIONS AND DOMINANCE RELATIONSHIPS AMONG MALES

In this section, the dominance relationships among males of the 2 groups will first be compared, based on an analysis of the agonistic interactions between males which were recorded during the artificial

feeding sessions. Secondly, within the Kerrayu group, the correlation between the neighborhood relationships among males and the occurrence of agonistic interactions will be discussed.

The results of the previous study demonstrated that in the Gorge group the dominance relationships among males were organized into a hierarchy, where males with the closest appearance to hamadryas baboons occupied the uppermost level. At the same time, males with closer appearance to anubis baboons were arranged into an almost linear dominance order (Sugawara, 1979). This analysis was carried out on the basis of one-sided attacks or preferential access to food or location. However, every agonistic interaction between males will now be analyzed into smaller behavioral elements, and the rates of appearance of each element or the manners of association between any 2 elements will be compared between the 2 groups.

A series of agonistic episodes was divided into discrete bouts, where an agonistic bout was defined as follows. It was considered to have started just when one of the behavioral elements to be described below was addressed by one male to another male. If the emission of some agonistic behavioral elements by a male towards a female or a juvenile ignited subsequent agonistic interaction with another male, this agonistic bout was considered to have started when the first element was addressed to the female or the juvenile. While either of the 2 (or more) male participants continued to present any of the behavioral elements, the bout was considered to be lasting. When both participants stopped presenting agonistic behavioral elements and began to perform some other activity (e.g., feeding, grooming a female, etc.), the bout was considered to have terminated. However, if both participants, interacting aggressively with each other, disappeared from the observer's sight, the bout was taken to have closed at that moment. In all, 161 agonistic bouts were recorded in the Gorge group, and 355 bouts in the Kerrayu group.

1. Organization of Behavior in Agonistic Interactions

The agonistic interactions between males often developed from dyadic interactions, in which only 2 males participated, into triadic or polyadic ones in which further animals participated. Pure dyadic interactions can be considered to comprise 7 behavioral elements. On the other hand, there are 10 elements/subcategories which are directed to animals other than the 2 male participants. These elements are described below, where P and Q are the male participants in the agonistic interactions and indicate, respectively, the addresser and the addressee of each behavioral element.

I. Behavioral elements composing pure dyadic interactions.

(1) 'Supplanting' (SP): P approaches and supplants Q to annex food.
(2) 'Attacking' (AT): P springs on Q with his mouth opened, or slaps (or attempts to slap) Q with his hands.
(3) 'Chasing' (CH): P chases Q at a full gallop.
(4) 'Harassing' (HA): P quadrapedally stands near Q, who is sitting and usually looking away from P, and repeatedly directs yawning or "pumping-cheeks" (Kummer, 1968) towards Q (cf. Hall et al., 1965: 65).
(5) 'Counter-attacking and chasing' (CU): P, who has been chased by Q, turns round and leaps on Q and conversely chases Q.
(6) 'Confronting' (CO): Two males stand quadrapedally in front of each other and repeatedly direct yawning or pumping-cheeks towards each other.
(7) 'Fighting' (FI): Two males simultaneously aim to bite at each other's open mouth or shoulder with exposed canines or to slap each other's face or shoulder with their hands (cf. Kummer, 1968: 47).

II. Behavioral elements directed to a third animal.

(1) 'Attacking a female possessed by another male' (ATF): A male attacks a female which is possessed by another male.
(2) 'Possessive behavior to his own female' (POF): A male participating in any agonistic interactions with another male directs one of the following 4 kinds of possessive behavior towards his own female: embracing, crouching over, mounting, and biting.
(3) 'Redirected aggression': A male who has received some agonistic behavioral element from another male attacks or harasses the third animal. Such behavior can be divided into the following 3 subcategories according to the sex or age of the third animal concerned: (a) 'towards a male' (RDM), (b) 'towards a female other than his own', (RDF), and (c) 'towards a juvenile' (RDJ).
(4) 'Alliance' (AL): A male intervenes in an agonistic interaction between 2 other males and attacks one of them (cf. De Waal et al., 1976).
(5) 'Skipping attack' (SK): A male attacks another male and subsequently attacks a different male from the latter.
(6) 'Embracing a juvenile' (EBJ): A male participating in some agonistic interaction with another male embraces a juvenile.
(7) 'Carrying an infant' (CAI): A male participating in some agonistic interaction with another male carries an infant on his belly or back.
(8) 'Attacking a juvenile' (ATJ): This element is distinguishable from the behavior described under (3)-(c) above in that a male attacks a juvenile although he has received no agonistic behavior from another male. Only cases where this behavior was succeeded by agonistic interactions between males were included in the present analysis.

The patterns of dyadic interactions between males in conflict can be divided into 2 categories: asymmetrical and symmetrical. If some action is addressed by one participant to another in a one-sided manner, it can be said that this interaction has an asymmetrical pattern. If the same kind of action is addressed by both participants to each other, this interaction has a symmetrical pattern. It can be considered that behavioral elements such as 'supplanting' (SP), 'attacking' (AT), 'chasing' (CH), and 'harassing' (HA) compose asymmetrical patterns of agonistic interactions, while elements such as 'fighting' (FI) and 'confronting' (CO) compose symmetrical patterns. 'counter-attacking' (CU) also contributes to symmetrical patterns of interaction, since in this behavior the animal which has received an agonistic behavioral element (CH) in turn comes to address the same element towards the previous addresser.

The dominance relationships among indivifuals within a group of primate species have generally been measured according to the asymmetrical interactions in agonistic situations such as preferential access to food (Kawai, 1958), threatening (Sade, 1967), or approach-retreat interactions (Rowell, 1966). If there is a stable linear dominance order among members in any primate group, at least in dyadic situation involving conflict the dominant animal can always assert himself (by attacking, threatening, or supplanting) while the subordinate responds in other ways (by fleeing, screaming, retreating, etc.). The appearance of symmetrical patterns of agonistic interactions should therefore, in itself, be regarded as evidence of inconsistency with the linear dominance order.

The percentage of the number of agonistic bouts in which some behavioral element appeared at least once in the total number of agonistic bouts was designated as the 'appearance rate' of that element. The appearance rates of behavioral elements composing dyadic interactions were compared between the Gorge and Kerrayu groups (Table 11). Concerning the agonistic bouts composed only of dyadic interactions, the appearance rate of 'supplanting' was far higher in the Gorge group than in the Kerrayu group (chi-spuare test for 2 independent samples: $\chi^2=56.796$, df=1,

Table 11. Numbers and percentages of agonistic bouts in which respective behavioral elements of pure dyadic interactions appeared at least once

Behavioral elements	Dyads			Triads & Polyads		
	G		K	G		K
SP	40 (47.6)	>>>	8 (5.6)	17 (22.1)	>>>	1 (0.5)
AT	21 (25.0)		43 (29.9)	24 (31.2)		60 (28.4)
HA	10 (11.9)	<	37 (25.7)	18 (23.4)		70 (33.2)
CH	21 (25.0)		27 (18.8)	16 (20.8)		41 (19.4)
CU	1 (1.2)	<	10 (6.9)	5 (6.5)		6 (2.8)
CO	4 (4.8)	<<<	37 (25.7)	3 (3.9)	<<	38 (18.0)
FI	13 (15.5)	<	39 (27.1)	14 (18.2)		47 (22.3)
Total bouts	84		144	77		211

G and K indicate the Gorge group and the Kerrayu group, respectively. The data in each cell indicate the number of times of occurrence of agonistic bouts in which each behavioral element appeared at least once. Figures in parentheses indicate the 'appearance rate' of each element, i.e., the percentage of those bouts to the total number of agonistic bouts. 'Dyads' indicate the agonistic bouts in which only 2 males participated from the beginning to the close. 'Triads & Polyads' indicate those in which 3 or more males participated. SP, 'Supplanting'; AT, 'Attacking'; HA, 'Harassing'; CH, 'Chasing'; CU, 'Counteracttacking and chasing'; CO, 'Confronting'; FI, 'Fighting'. >>>, $p<0.001$; >>, $p<0.01$; >, $p<0.05$ (χ^2-test for 2 independent samples, df=1)

$p<0.001$), while the appearance rate of 'confronting' was far higher in the Kerrayu group than in the Gorge group ($\chi^2=15.748$, $p<0.01$). The appearance rates of 'harassing' ($\chi^2=6.140$, $p<0.02$), 'counterattacking' ($\chi^2=3.929$, $p<0.05$), and 'fighting' ($\chi^2=4.113$, $p<0.05$) were also higher in the Kerrayu group than in the Gorge group. Concerning agonistic bouts including triadic or polyadic interactions, there was again a tendency for 'supplanting' to occur more frequently in the Gorge group ($\chi^2=45.098$, $p<0.001$) and for 'confronting' to occur more frequently in the Kerrayu group ($\chi^2=9.275$, $p<0.01$). In other words, in the Kerrayu group, symmetrical or reciprocal pattern of agonistic behavior is commoner than in the Gorge group, while it is by far rarer in the Kerrayu group for a male who is approached by another male in a competitive situation for food to retreat with no sign of aggression. This finding is corroborated by general observations. If the artificial food was not widely scattered but placed in a number of patches, several 'supplanting' interactions arose one after another around the respective patches in the case of the Gorge group, whereas in the Kerrayu group many violent fights occurred here and there, which led to terrible confusion involving the entire group. On the basis of such observations, it can be said that the dominance

order among males is probably far vaguer in the Kerrayu group than in the Gorge group.

The dominance order among males will actually be deduced below from those agonistic interactions in which the active and passive roles could be distinguished from each other. It has been pointed out by several authors that the frequency of supplanting or of attacking and chasing in a one-sided manner is relatively well-correlated with dominance (Rowell, 1966; Sade, 1967; Kaufmann, 1967). Here, the frequencies of the 3 kinds of behavioral element, i.e., 'supplanting', 'attacking', and 'chasing', were summed together, and all the males in the same group were arranged in a single matrix according to the frequency of these elements addressed or received by each male*5. In order to approximate this arrangement as far as possible to a linear order, the following procedures were adopted. (1) All males were arranged according to the ratio of the frequency of the 3 behavioral elements addressed by each male to the frequency of these elements received by each male. (2) If 2 or more males showed the same values for this ratio, the one with the highest frequency of addressing these elements was placed in a higher position than the other. (3) Finally, the order so obtained was modified so that the total frequency of the elements found under the diagonal of the matrix became the least.

The ranking order among males constructed according to the above procedures is now designated as the hypothetical rank (HR) among males (Fig.16). In such matrices, the score under the diagonal represents the number of interactions in which the 'lower' male in the HR supplanted, attacked, or chased the 'higher' male. It can be considered therefore that the percentage of this score to the total number of times gives a measure of the inconsistency with linearity, or completeness, of the HR. Since this percentage is a version of Rowell's "direction consistency index" (Rowell, 1966), it is here designated as the 'inconsistency index.' In the Kerrayu group, the inconsistency index was estimated to be only 13.4%, which was somewhat smaller than that in the Gorge group (17.4%). The assumption that the dominance order among males is vaguer in the Kerrayu group than in the Gorge group is thus not supported by this result.

However, there are other forms of agonistic behavior which manifest aggression by one male towards another male in a one-sided manner. The most frequent was 'attacking a female possessed by another male' (ATF) or 'harassing' (HA). Although these 2 kinds of behavior performed by one male do not directly or physically injure his opponent, they can function to menace the opponent. The frequency of 'harassing' was represented by the number of times of yawning and pumping-cheeks actually addressed. The number of times of these kinds of behavior were arranged in the HR matrix. The inconsistency index of ATF was found to be more than 70% and that of HA close to 60% in the Kerrayu group, whereas both indices were less than 20% in the Gorge group (Table 12). In other words, in the Kerrayu group it is more frequent for ATF or HA to be addressed by 'lower' males in the HR to 'higher' ones, while in the Gorge group the direction of addressing such behavior is usually consistent with the HR (χ^2=30.806 for ATF, χ^2=41.694 for HA, df=1, $p<0.001$ for both).

Furthermore, examinations were made in the Kerrayu group of the correlation between the HR and the rank order in which males were arranged according to the number of occasions on which each of them addressed or received ATF or HA by the same method as that used in the construction of the HR (Table 13). A significant negative correlation was obtained between the HR and the rank order based on the frequency of HA (Spearman rank correlation coefficient: r_s=-0.4872, $p<0.05$, two-tailed). At the same time, there was a weak negative correlation between the HR and the rank order based on the frequency of ATF (r_s=-0.3549, $p<0.20$),

(a) Kerrayu group

ACTOR \ REACTOR	Uz	Hk	Gt	Zf	Kl	Sv	TJ	Yb	DJ	Jr	Ng	Vl	As	Fs	Ig	Pt	Dr	Ch	Qt	Bl	Em	Ls	TOTAL
Uz		2										1	1		2		1		1				8
Hk			1	1	1							2	4					1	2	2			14
Gt	1					5	1	1		5		7	6	2			2	2	2	3			37
Zf					1		1	5	6	3	1		5		1		7	2		5			37
Kl				1				1		1		1	1	1	3	3							12
Sv								1		2	1	1	1	1				1		1			9
TJ								1		1										1			3
Yb										2			1						3	3			9
DJ								1		1		2	1	1	1					2			9
Jr						1					3	1					1		5	4			15
Ng		1		2		1							3	1	3		1		1	3			16
Vl			2										3	1			1		3	2		1	13
As									1			2		1		1	8		2	1			16
Fs					1	3		1									2			8	1		16
Ig	2			1												1	1						5
Pt					1			1					1							1			4
Dr				1			1						1	1				2	1				7
Ch			1																				1
Qt								1															1
Bl																							0
Em																							0
Ls																							0
TOTAL	2	4	4	6	4	10	3	13	7	15	5	17	28	9	10	5	24	8	20	36	1	1	232

(b) Gorge group

ACTOR \ REACTOR	Rb	Bf	Wh	Zr	Dl	Ch	Mt	Ml	Ys	Nc	Gr	Kr	Hg	Eb	Al	TOTAL
Rb				1	9	4	5	1	1	2	1		1			25
Bf			1		4			5				2	1		1	14
Wh				1			1	3		1			1			7
Zr					1		4	4		1	1		1			12
Dl	1	1				2	2	6	8		2		6	3	2	33
Ch		1		1	1		3	3		1						10
Mt					1	3		5	1			1	1			12
Ml			1		3	1	2		3		2		2	1	1	16
Ys				1	1		2			2	1	1	2		2	12
Nc						1	1					1				3
Gr							1								1	2
Kr									1							1
Hg	1							1								2
Eb																0
Al																0
TOTAL	2	2	2	4	20	11	21	28	14	7	7	5	15	4	7	149

Fig. 16. Hypothetical rank matrices among males in 2 hybrid groups. The frequencies of 'Supplanting', 'Attacking', and 'Chasing' were collected together. The males are arranged from top to bottom according to rank. The matrices were constructed so that the total frequency under the diagonal was the minimum.

Table 12. Inconsistency indices for 4 kinds of agonistic behavioral elements addressed in a one-sided manner

Group	Behavioral elements			
	AT+CH+SP	ATF	HA	RDM
K	13.4 (232)	73.1 (104)	59.4 (219)	48.5 (33)
		v	v	
G	17.4 (149)	16.7 (30)	13.1 (61)	26.7 (15)

The inconsistency index is the percentage of the numbers of each behavioral element addressed by the 'lower' males to the 'higher' males in the hypothetical rank. Figures in parentheses indicate the total frequency of each element. The frequencies of AT, CH, and SP were summed together. >, $P<0.001$ (χ^2-test, df=1). AT, 'Attacking'; CH, 'Chasing'; SP, 'Supplanting'; ATF, 'Attack a female possessed by another male'; HA, 'Harassing'; RDM, 'Redirected aggression towards a male'.

Table 13. Correlations among rank orders based on 3 kinds of behavioral elements

Rank	AT+CH+SP	HA	ATF
1	*Uzo*	*(Chatto)*	*(Bal)*
2	*Hakeem*	*(Quonta)*	*(Djoro)*
3	*Geta*	*(Bal)*	*(Igir)*
4	*Zefen*	*(Tadji)*	*(Asama)*
5	*Kusil*	*(Igir)*	*(Tadji)*
6	*Stav*	*Zefen*	*(Quonta)*
7	*(Tadji)*	*Jirat*	*Posta*
8	*Yabelo*	*Doro*	*Feres*
9	*(Djoro)*	*Uzo*	*Uzo*
10	*Jirat*	*Feres*	*Hakeem*
11	*Nigus*	*(Djoro)*	*Doro*
12	*Villa*	*(Asama)*	*Villa*
13	*(Asama)*	*Geta*	*Jirat*
14	*Feres*	*Villa*	*Stav*
15	*(Igir)*	*Posta*	*Yabelo*
16	*Posta*	*Yabelo*	*Geta*
17	*Doro*	*Hakeem*	*Kusil*
18	*(Chatto)*	*Kusil*	*Nigus*
19	*(Quonta)*	*Nigus*	*Zefen*
20	*(Bal)*	*Stav*	*(Chatto)*
Correlation	−0.4875	−0.3549	0.3128

Adult and adolescent males of the Kerrayu group are arranged as linearly as possible according to the frequencies with which each of them addressed or received respective behavioral elements. Two males, *Louis* and *Emoly*, were excluded, since they rarely participated in agonistic interactions at the feeding site. Names in the parentheses indicate bachelors. 'Correlation' shows the value of the Spearman rank correlation coefficient. AT, 'Attacking'; CH, 'Chasing'; SP, 'Supplanting'; HA, 'Harassing'; ATF, 'Attacking a female possessed by another male'.

while the rank orders of HA and ATF were positively correlated with each other (r_s=0.3128, $p<0.20$). In other words, in the Kerrayu group, the 'lower' a male is in the hypothetical rank constructed according to the frequency of direct attacking or supplanting, the more frequently does he menace the males of 'higher' ranks by means of indirect manifestations of aggression.

If one assumes that addressing such behavioral elements as HA or ATF is equivalent to a manifestation of subordination, the above results could be interpreted as evidence that a quite linear rank order exists among the males in the Kerrayu group. However, it is probably more accurate to say that the agonistic interactions among males in the Kerrayu group are very often intensified to develop into symmetrical patterns such as a confrontation or fight just because the 'subordinate' male in the usual meaning is not willing to retreat obediently from the 'dominant' male but dares to menace his 'dominant' opponent by means of indirect manifestations of aggression. If this is a correct assessment, then a linear dominance order in its usual meaning, i.e., a system which always enables the dominant animal to drive away a subordinate from some incentive, is not in fact established among the males of the Kerrayu group.

Next, the tendency of each behavioral element to appear together with any other element in the same agonistic bout was examined in the 2 groups. It was determined whether each behavioral element appeared at least once or did not appear at all in each agonistic bout, taking no account of the frequency of those behavioral elements which were repeatedly addressed in the same agonistic bout. The likelihood of any 2 behavioral elements being associated with each other in the same bout, i.e., the association rate (A.R.), was obtained from the following formula:

$$A.R.= \frac{N(A,B)}{N(A)+N(B)-N(A.B)} \times 100 \ (\%)$$

where N(A) or N(B), respectively, indicates the number of bouts in which the element A or B appeared at least once, and N(A.B) indicates the number of bouts in which both A and B appeared. The association rates for all combinations between any 2 elements were calculated for both groups, and SLCA-dendrograms (Morgan et al., 1976) were constructed (Fig.17).

The common features of the 2 dendrograms may be summarized as follows: (1) 'Attacking to a female' (ATF), 'possessive behavior' (POF), and 'harassing' (HA) are associated with one another at a high rate. (2) 'Attacking' (AT), 'fighting' (FI), and 'chasing' (CH) are also associated with one another at a high rate. (3) 'Confronting' (CO) is associated with the major cluster including the 2 subclusters described under (1) and (2) above. On the other hand, the most striking difference between the 2 groups is that in the Kerrayu group, 'alliance' (AL) is frequently associated with the cluster of 3 behavioral elements (AT, FI, CH) which comprise physical conflicts between males, while in the Gorge group, 'redirected aggression towards a male' (RDM) is associated with such physical conflicts at a high rate. At the same time, it should be noted that in the Gorge group, 'supplanting' (SP) and 'redirected aggression towards a juvenile' (RDJ) are associated with each other at a high rate.

The above results indicate that the males in the Kerrayu group have a strong tendency to intervene in physical conflicts occurring between 2 other males and to cooperate with one of them in the attack upon another, while in the Gorge group it is frequent for one of the 2 participants in physical conflicts to redirect his aggression towards a male other than his

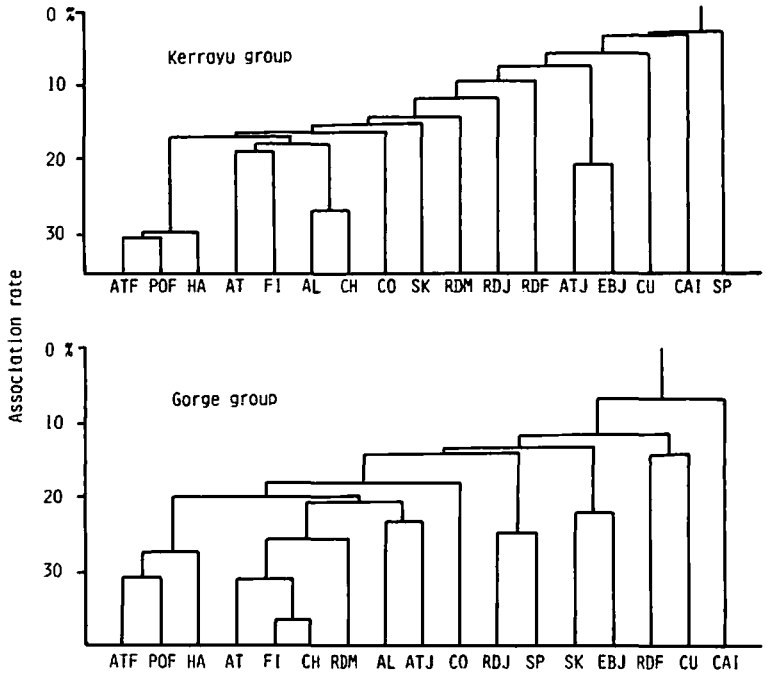


Fig. 17. SLCA-dendrograms representing the tendency for any 2 behavioral elements to be associated with each other in the same bout. (cf. Fig.5). The association rate (A.R.) for any 2 behavioral elements was obtained from the following formula; A.R.=100xN(A,B)/[N(A)+N(B)-N(A,B)] where N(A) or N(B) indicates the number of bouts in which the element A or B appeared at least once, and N(A,B) indicates the number of bouts in which both A and B appeared. SP, 'Supplanting'; AT, 'Attacking'; CH, 'Chasing'; HA, 'Harassing'; CU,'Counterattack and chasing'; CO, 'Confronting'; FI, 'Fighting'; ATF, 'Attacking a female possessed by another male'; POF, 'Possessive behavior to his own female'; RDM, 'Redirected aggression towards a male'; RDF, 'Redirected aggression towards a female other than his own'; RDJ, 'Redirected aggression towards a juvenile'; AL, 'Alliance'; SK, 'Skipping attack'; EBJ, 'Embracing a juvenile'; CA, 'Carrying an infant'; ATJ, 'Attacking a juvenile'.

opponent. Judging from the fact that in the Gorge group, indirect aggression such as 'harassing' (HA) and 'attacking a female possessed by another male' (ATF) usually occurs in a downward direction in the hypothetical rank, it can be concluded that the dominance relationships among males in this group more nearly approximate to a linear rank order than those in the Kerrayu group. It can be said therefore that the linearity of rank order in this group may be reflected in a distinct feature of the organization of the agonistic interactions, that dyadic physical conflicts between males often lead to attacks redirected towards another male. In general, in a society where a single linear dominance order is perceived by its members, a 'subordinate' which has been attacked by a 'dominant' can readily find a 'more subordinate' than itself to which its aggression can be redirected. Furthermore, in the

Gorge group, a 'subordinate' male supplanted by a 'dominant' male often attacked a juvenile immediately. This also suggests that the males of the Gorge group are more strongly motivated to redirect their aggression towards a third animal than are the males of the Kerrayu group. The inconsistency index of RDM was almost 50% in the Kerrayu group, while it was less than 27% in the Gorge group (see Table 12), although this difference was not statistically significant ($\chi^2=2.048$, $p<0.20$). However, the assumption that redirection towards a third animal may be closely correlated with linearity of the dominance order, has a particular significance in the examination of the spacing mechanism among males, as will be discussed later.

2. Correlation between Neighborhood Relationships and the Occurrence of Agonistic Bouts in the Kerrayu Group

In a preliminary report on correlations between grooming relationships and object competition among hamadryas baboons, Kummer et al. (1978: 37) stated that a conflict over an incentive was more likely to occur among grooming companions, and assumed that "the rival can predict his chances against a grooming companion more precisely than against a less intimate opponent..." (italics in original). At the same time, they remarked that this hypothesis is inconsistent with the fact that purely dyadic objectless fighting is most common among dyads that have not reached the grooming stage.

Although grooming among males was not so frequent in the Kerrayu group, conspicuous partnerships were recognized among certain male-male dyads when the spatial relationships among them were analyzed. An examination will now be given of how the intensity of the neighborhood relationships among males is correlated with the frequency of agonistic bouts occurring among male-male dyads. The intensity of neighborhood relationships is represented by the neighborhood index as defined in a previous section (see Fig.10). Since no bachelor male was traced as a focal male, the neighborhood index for possessor-bachelor dyads was represented by the percentage of the number of scans in which each bachelor male was at the shortest distance from the possessor in the total number of measurements during focal-male sampling of the latter. Bachelor-bachelor dyads are excluded as subjects of this analysis.

All dyads were divided into 7 or 8 grades according to the frequency of agonistic bouts which occurred in each dyad, and the range and mean value of the neighborhood index for the dyads included in each grade are shown in Fig. 18. On occasions where 3 or more males simultaneously participated in an agonistic bout, e.g. P and Q cooperated with each other in an attack upon R, it was considered that two different agonistic bouts independently occurred in the 2 dyads, P-R and Q-R. Figure 18 shows that the neighborhood index correlates almost positively with the frequency of agonistic bouts among possessor-possessor dyads, whereas there is a negative correlation among possessor-bachelor dyads. In general, agonistic bouts are more likely to occur among possessors who are in close partnership with each other during the daily nomadic movements, whereas conflicts tend to occur less often between a possessor and a bachelor who are usually in close proximity to each other.

However, among possessor-possessor dyads the neighborhood index drops conspicuously at the tail of the graph, corresponding to the highest frequency (more than 7 times) of agonistic bouts. Of the 7 dyads with the highest frequency of agonistic bouts, 4 included a particular male, Geta, and 2 other dyads included another male, Zefen. Since both of these males were the most active in addressing direct aggressive behavior in a one-sided manner (AT, CH, and SP), they were considered to be especially quarrelsome animals (see Fig.16). The drop in neighborhood index at the

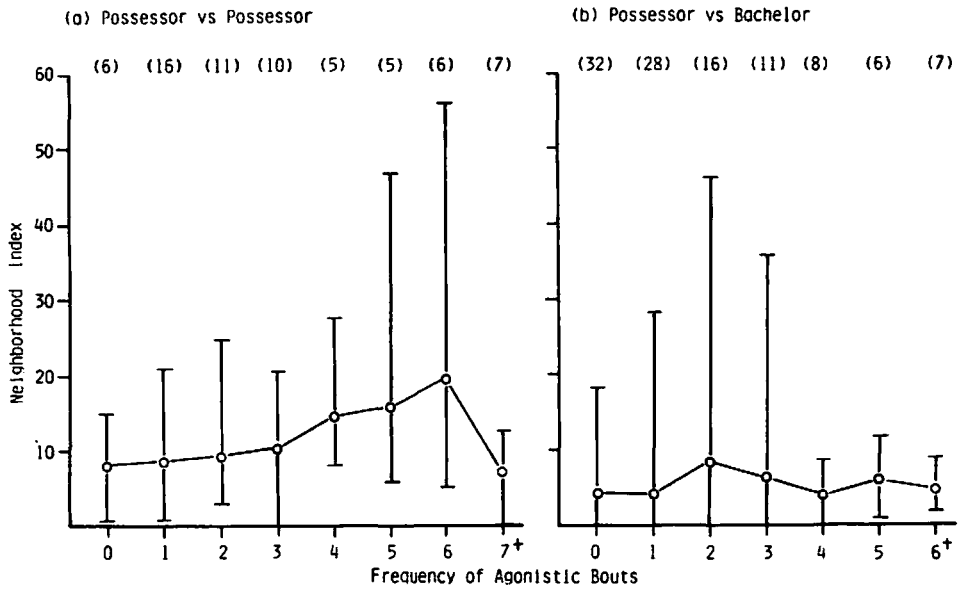


Fig. 18. Correlation between the neighborhood index and the likelihood of agonistic bouts occurring in (a) possessor-possessor and (b) possessor-bachelor dyads in the Kerrayu group. The figures in the parentheses above the graphs indicate the number of dyads. White dots represent mean values for neighborhood indices of the dyads included in each grade of bout frequencies. Vertical lines represent the range of neighborhood indices.

tail of the graph can thus be attributed to the peculiarity of behavior of these 2 males.

Concerning possessor-bachelor dyads, it was found that the neighborhood index was not so high among dyads in which rare or no agonistic bouts occurred. Such an inconsistency with the negative correlation between the neighborhood index and frequency of agonistic bouts among possessor-bachelor dyads can be attributed to the fact that there are several bachelor males who occupy peripheral positions in the group and rarely participate in the agonistic interactions at the feeding site. With the reservations outlined above, it can be concluded that in a competitive situation over food, possessor males tend to open conflicts against other possessors with whom they have distinct partnerships in their everyday life, whereas conflicts are strongly restrained from occurring between possessors and their bachelor partners such as the followers of one-male units. These results appear to support the assumption of Kummer et al. (1978: 37-38) that "a hamadryas baboon's tendency to risk an open conflict may depend on...the precision with which he can predict the chance of success...." In addition, it should be emphasized that whether he dares to open conflicts or not may depend strongly on whether he is actually in possession of any female or not. The ambiguous correlation between partnership and rivalry among hamadryas males within the same band should be examined further, based on the factors elucidated above.

DISCUSSION

1. Origins of the Two Hybrid Groups

Nagel (1973) hypothesized that the hybridization in the Awash Valley had been caused mainly by the abduction of anubis females from their native troops by hamadryas males, resulting in a one-way gene flow from the anubis to hamadryas side. Kawai and Sugawara (1976) pointed out that the "abduction story" described by Nagel (Nagel, 1973: 115-116) was lacking in adequate supportive evidence because his observations of the process of abduction were fragmentary, not being based on complete individual identification. They assumed that the hybridization in the region might have been caused mainly by two other processes: immigration of anubis males into hamadryas bands, and immigration of hamadryas males into anubis troops. Further, Sugawara (1979) concluded that the Gorge group had originated from an anubis troop through the latter process.

On the other hand, it can be said that the Kerrayu group must have originated from a hamadryas band. Shotake et al. (1977) had estimated that 74.1% of the genes in the Gorge group had originated from anubis baboons. At the end of the present study period, Shotake collected blood samples from 43 animals of the Kerrayu group, and estimated that about 70% of the genes in the Kerrayu group originated from hamadryas baboons (Shotake, in prep.). During the study period, copulation of anubis males with the females was never observed in the Kerrayu group. Furthermore, the 2 males with pure anubis appearance in the Kerrayu group often traveled alone away from the main body of the group and appeared "socially isolated" as described by Nagel (1973). Thus, no evidence was gained to support the assumption of Kawai and Sugawara that the hybridization of hamadryas bands might have been caused by the copulation of anubis males, which had immigrated into hamadryas bands, with hamadryas females. However, it cannot be said that copulations between anubis males and hamadryas females are entirely impossible over longer periods of time. As mentioned, it was observed that a pubescent male transferred from the Gorge group into the Kerrayu group and temporarily stayed there, peacefully interacting with the pubescent males and juveniles of the Kerrayu group. Thus, if anubis males immigrate into hamadryas bands at a very early stage of their life, it seems probable that they would be more easily accepted by the band members and enjoy a greater chance of copulations as they grow older, than anubis males which immigrate at later stages.

It can be considered therefore that in the Awash Valley, there is probably not just a one-way gene flow from the anubis to hamadryas side but a mutual gene flow between both populations. This raises the question of why both the anubis and hamadryas populations in the region have not been reduced to homogeneous hybrid populations as a result of perpetuated intergradation. Three factors should be considered as possible reasons. First, as suggested by Nagel (1973), anubis males which have transferred from an anubis troop into a hamadryas band probably do have only a very small chance of copulating with hamadryas females which are usually protected by the leaders of the one-male units. Thus the rate of gene flow from the anubis to hamadryas population due to anubis male immigrants must be very low. Second, there may be a difference in the male's tendency to secede from their natal troop, or band, between anubis and hamadryas baboons. According to Packer (1977), all the males in anubis baboons transfer from their natal troop into other troops. It has also been confirmed that most males desert their natal troop in rhesus monkeys (Drickamer, 1974) and in Japanese monkeys (Sugiyama, 1976). Such a tendency of males to desert their natal troop has been considered

to represent a common character of the troop-type social structure found in Macaca or Papio species (Itani, 1977). On the other hand, it can be assumed that secession of hamadryas males from their natal band is not so usual as was ascertained for anubis baboons, since the 'bonds' (or mutual attraction) among hamadryas males are very strong within the same band (Kummer, 1968). Distinctive 'bonds' were also found among males of the Kerrayu group, and it was thought that the social structure of this group had a fundamental affinity with that of the hamadryas band. The socionomic sex ratio was also strikingly high in the Kerrayu group, suggesting that secession of males from the group may not be so frequent. Nagel (1973: 139) pointed out that 2 hamadryas groups inhabiting the downstream region near Awash Station (C5 and C6) included a remarkably high percentage of adult and subadult males, 50% of whom had no access to females, and suggested that "having no possibility of getting an adult female in their home group, may be a reason for young hamadryas males to emigrate...." However, the fact that many bachelor males are present in the present group should rather be regarded as evidence that secession of males from this group only rarely occurs. Further, it was elucidated in the present study that males with a close appearance to anubis were apt to shift from group to group with a short cycle. It is considered therefore that a lot of anubis males may have continued to immigrate into the hamadryas population, while far less hamadryas males have immigrated into the anubis population.

The third possible factor suppressing the flow of hamadryas genes into the upstream anubis population is that the nomadic life of the hamadryas baboons depends strongly on the cliff. Retaining the habit of sleeping on or taking refuge on the ledges of the steep cliff, most hamadryas male immigrants into the anubis population above the Awash Fall would probably not relish a long stay in the plain habitat which lacks available cliff. If abduction of anubis females by hamadryas males into the downstream region actually occurred as Nagel suggested, it could have been the preference of the hamadryas males for a habitat providing an abundance of cliffs that prompted them to return to the canyon below the Awash Fall. Thus, the rate of flow of hamadryas genes into the anubis population above the Awash Fall may also be very low. The three above factors may have cooperated to retard any rapid expansion of the hybrid zone.

2. Influence of Hybridization on the Social Structures of the Original Species

Based on the sociological features of the Kerrayu group elucidated in this paper, a discussion will now be given of how the social structure of the hamadryas band was influenced by the inflow of anubis genes. From the viewpoint of male-female relationships, the most remarkable feature of the Kerrayu group was that at one extreme a few males formed very large one-male units and at the other extreme many males formed small one-male units or pair units. At the same time, there were many bachelor males without any access to females. The main cause of such features may be a wide variation among the males in their ability to herd females effectively. Sequential analysis of the male social behavior proved that the pathway from 'directing visual attention towards a female' to 'giving neck-bites to a female' was missing from the "principal pathways" (van Hooff, 1971) of the social behavior of the males which formed pair units (Sugawara, in prep.). This means that the inflow of anubis genes must have dealt a severe blow to a key link in the chains of possessive behavior of males towards females.

On the other hand, another remarkable feature of the social structure of the Kerrayu group was that the cohesion of the entire group was

usually very high. It is considered that such a high degree of cohesiveness within the group must be supported by the tendency of males to be proximate to each other or, to use Kummer's words, by a mutual attraction among males (Kummer, 1968). According to Mason (1978), the basic social structure of any primate species can be more usefully characterized in terms of social dispositions than in terms of specific patterns, frequencies, and directions of social behavior, which may be viewed as agents for the expression of the underlying social dispositions. In the context of Mason's concept, the males of the Kerrayu group clearly have a far stronger social disposition to be proximate to each other than do the males of the Gorge group. Such a disposition towards proximity among males should be regarded as the most fundamental basis on which the integration of the hamadryas bands depends. It is concluded therefore that the inflow of anubis genes into the hamadryas band has brought about a great disturbance of the possessive behavior of males towards females, but it has exerted little effect on the social disposition of males to be proximate to each other.

Next, the effect of inflow of hamadryas genes on the social structure of the anubis troop will be discussed. The most distinctive features of the social structure of the Gorge group were: 1) that the group was segmented into subgroups each of which had a stable membership from a short-term point of view, and 2) that these subgroups repeatedly joined and parted from each other.

It is possible that the most important factor determining the forms and compositions of the subgroups could be how many females in this group have been in exclusive contact with hamadryas-like males. During the previous study period, 4 males with closer appearance to hamadryas each formed one-male group, monopolizing 12 (54.5%) of 22 females over the age of adolescence. However, of these 4 males at 2.5 years after the end of the study period, one (Saint) who had formed a cohesive one-male group had disappeared and the other 3 males had suffered a decrease in their ability to herd females effectively because of their old age. On the other hand, 3 males with closer appearance to hamadryas (Zare, Ain, and Chilotta) had immigrated into the Gorge group. Of these 3 immigrants, only Zare appeared to be able to establish an exclusive bond with females by means of aggressive herding techniques. Thus, during the present study period, only 6 (26.1%) of 23 females over the age of adolescence formed stable partners for males with a closer appearance to hamadryas[*6]. It follows in such a situation that males closer to anubis baboons have not only gained more chance of access to females but have also been able to maintain their associations with females more easily.

Based on the previous study, the author argued that "the persistent following by a male of a female could arouse a tendency to remain close to the male on the female's side" (Sugawara, 1979: 46). In the present study period, 4 anubis-like males (Baboof, Necker, Maler, and Matiou) each formed loose 'one-male groups'. The formation of one-male groups by such anubis-like males may have resulted from both the present effort of males to follow some females and the tendency of other females to be close to the male which had been following the latter females in the past. Thus, if more hamadryas-like males immigrate into the Gorge group and try to possess more females in the future, the form of the bond which anubis-like males can have with the females will probably be reduced to the dyadic one.

On the other hand, an irreversible change was initiated in the structure of the Gorge group between 1976 and 1978. Bf-MMG, which had been the largest subgroup in 1975, revealed a strong tendency to split into 2 'one-male groups' in 1978. The multi-male groups found in the Gorge group represent, so to speak, a remnant of the social structure of

the troop of anubis baboons. The tendency of the multi-male group towards breakdown may indicate that this group is progressively losing more and more of its integration which characterizes the troop society of anubis baboons.

The most important problem for discussion in relation to the influence of the hybridization on the social structure of the anubis troop is why the Gorge group displays a grouping pattern of joining and parting. In the previous study, the author stated that the joining and parting of subgroups in the Gorge group was made possible by the stability and independence of each of the subgroups (Sugawara, 1979: 50). However, the cohesiveness of the Kerrayu group indicated that the formation of cohesive infra-units within a group does not necessarily result in dispersion of the group. Comparison of the spatial relationships among males between the 2 groups revealed that the males of the Gorge group did not have such a strong social disposition to be proximate to each other as did those of the Kerrayu group. It appears likely that hamadryas males originally have by far the stronger social disposition towards each other's proximity, compared to anubis males. Furthermore, the most fundamental bonds supporting the cohesion of the troop of anubis baboons may be the consanguineous ties among females.

The two above assumptions would tend to make the fluid grouping pattern of the Gorge group comprehensive. Analysis of the grooming network in the Gorge group demonstrated that affinitive relationships exist based on the long-term recognition among females but these bonds among females became gradually weakened, being intervened or severed by the ever-changing male-female associations. It can be considered therefore that the consanguineous ties among females on which the integration of the original anubis troop was based, have been loosened through the process of segmentation into several subgroups, which was probably induced by the flow of hamadryas genes into the anubis troop. Moreover, if the anubis males were not originally disposed to be close to each other, it might have been very difficult for the independent subgroups, which had thus been formed, to be persistently associated with each other. It follows therefore that the hybridization has dealt a crucial blow to the integration of the anubis troop.

3. Speculation on the Evolution of the Multi-Level Society in Hamadryas Baboons

Kummer (1968) stated that within a hamadryas one-male unit there is no evidence of affinitive bonds among females and that the cohesion of the one-male unit is primarily enforced by the aggressive herding behavior of its leader male. In contrast, when discussing the social structure of the one-male unit of gelada baboons, Mori (1979b: 244) wrote that "the unit females are held together by strong mutual bonds and form a strong social system in their own right." Itani (1977), proposing an inclusive theory for the evolution of the primate social structure, made a comparison of the social structures of gelada and hamadryas baboons and concluded that the basic social unit of the gelada baboons is the one-male unit whereas that of the hamadryas baboons is the band.

The distinctive feature of the grooming relations in the Kerrayu group was that within most one-male units frequent grooming occurred among females, the amount of which exceeded even the amount of male-female grooming in some instances. As read from the sociograms, the proportion of the amount of female-female grooming to that of male-female grooming within most of the one-male units in the Kerrayu group, was by far higher than that within the one-male units of gelada baboons observed by Mori (1979a). Furthermore, some females in the Kerrayu group, especially the members of the large one-male units, often groomed females

belonging to different units from their own. These features of the grooming relations among females in the Kerrayu group presumably indicate that the control of the leader males over their unit females may not be sufficiently strict to restrain them entirely from having friendly interactions with each other. Furthermore, through the process of breakdown of the one-male unit, females which had been possessed by the male were individually divided among different males, and the affinitive bonds among them immediately ceased to exist. This process contrasts sharply with the process of alternation of leaders of one-male units in the gelada society, where a free-lance male or a male from an all-male group can challenge the leader of a one-male unit and take over the whole unit (Mori, 1976). It is considered therefore that the grooming relations among females within the same unit in the Kerrayu group, do not represent evidence that they "form a strong social system in their own right" but are based primarily on rather temporay bonds which may derive from the usual spatial proximity among them.

The above arguments, as well as the cohesiveness of the Kerrayu group during its nomadic movements, appear to support Itani's view that the band, rather than the one-male unit, should be regarded as the basic social unit of hamadryas baboons, since in spite of the modification of the male-female associations caused by the hybridization, the Kerrayu group can be considered to have preserved the basic structure of hamadryas baboons.

Kummer (1971) ascribed the formation of the multi-level organization of the hamadryas society to an adaptation to scarcity of food and sleeping sites, and argued that hamadryas one-male units are primarily functioning as a foraging unit which can effectively make use of scattered food resources. In other words, insofar as the formation of one-male units is concerned, he placed emphasis on the fact that the band can subdivide into one-male units and the band members can thus disperse as widely as possible.

However, tracing the nomadic movements of the Kerrayu group, the author was impressed by the observation that many individuals were very often concentrated in a narrow area. On the savanna, such concentration of many animals occurred during resting in the shade of a tree or feeding on crowns of Acacia tortilis which bore abundant beans, while in the riverine forest such concentration was often observed when the baboons were eating pods of Tamarindus indica on the tree or while they were taking a long rest or an afternoon nap on the ground. It is apparently paradoxical that the subdivision of the group into cohesive infra-units does not result in breakdown or dispersion of the basic social unit, the band, but rather results in the formation of 'crowding space.' It is considered that the factor which enables 'crowding space' to be formed is the disposition of the males toward each other's proximity, and this disposition is profoundly correlated with the breakdown of the linear dominance order among the males.

The author has analyzed the structure of social encounters among non-troop males (hanarezaru; Sugiyama, 1976) of Japanese monkeys on Koshima Islet. He pointed out that in the polyadic encounters including non-troop males, entry of the dominant male into a situation already maintained often prompted one attendant to attack other attendant, and such "redirection" (Kaufmann, 1967) had the effect of making one of the attendants leave the situation (Sugawara, 1980). This result permits the assumption that the linear dominance order among males might have the function of accelerating their spatial dispersion. In the present paper, the following three points have been demonstrated for the Gorge group: 1) linearity of dominance order among the males is more distinctly established than in the Kerrayu group, 2) physical conflicts between males are

associated with redirected aggression towards a third male at a high rate, and 3) the males tend to sit at longer distances from each other in the resting situation than in the Kerrayu group. These three points together strongly support the above assumption.

Furthermore, the breakdown of a linear dominance order among males may be strongly correlated with the possession of females by males. Kummer (1973) argued that the competitor is inhibited from interacting with two animals which are in close contact or proximity by perceiving the "pair gestalt," and thus "pair gestalt inhibition" moderates the effects of dominance. However, the author considers that in a multi-level society, the concept of 'dominance' itself must be reconsidered, since this concept was originally elaborated from studies on inter-individual relationships in one-level societies and is so likely to involve essentially different implications in a multi-level society from those in one-level societies. If it is true that the most effective way to manifest dominance is through access to incentives without hesitation, access to females, a highly desired incentive, performed without hesitation by respective possessor males may properly regulate the effects of other performances manifesting dominance which occur in relation to other incentives, such as food or location.

The formation of the 'crowding space' may have a strong effect on the possession of females. Citing the observations of Abegglen and Abegglen, Kummer et al. (1978) pointed out that the most dangerous rivals of the harem leader are the young followers with whom he has been most closely associated. In the Kerrayu group, the adult followers were inhibited from engaging in conflicts with the unit leaders whom they followed, but the possessor males in close neighborhood relationships tended to be in conflict with each other. Thus, in the Kerrayu group, the nearest neighbor is potentially the most dangerous rival to any possessor male. On the other hand, the crowding space provides males possessing no or few females with an opportunity to observe in detail the disturbance of the performance of their neighbors and to predict his chances of success more precisely (Kummer et al., 1978). In other words, the 'crowding space' constitutes a social field where the motivations of individual males to possess more of the females can be reinforced.

Aldrich-Blake et al. (1971) argued that the selection pressure which led to the initial formation of one-male units in hamadryas baboons cannot necessarily be confined to food scarcity. If one attempts to enumerate the factors which have favored the formation of a multi-level social organization in the context of adaptation to an arid habitat, it is necessary to emphasize not only the need for exploiting scattered resources but also the urgency of concentrating on restricted resources, such as food, water, or shade. The 'crowding space' so formed may well have affected the dominance relationships among males or relationships between males and females within the same basic social unit. It is too early to attempt to identify the causal relationships among these three aspects [i.e., (1) formation of the 'crowding space,' (2) breakdown of the linear dominance order among males, and (3) possession of females by males], but special emphasis should be attached to the complex of these three aspects as the likely base on which the multi-level system of the hamadryas society is organized.

4. The Basic Social Structure of Hybrid Baboons

At the conclusion of this paper, the author attempts to compare the basic social structure of hybrid baboons with that of anubis or hamadryas baboons and to make some speculation on the likelihood for the 'hybrid-specific' patterns of social structure to be permanently fixed. It is suggested that in the troop of anubis baboons there is long-term and relatively consistent division into major subgroups the composition and

stability of which depend in part upon kinships of females. Furthermore pair-bonds or long-lasting relationships between adult males and females are existing within major subgroups (Ransom & Ransom, 1971; Seyfarth, 1978b). But, on the other hand, in the captive baboon colony (Papio cynocephalus) it is pointed out that subgroups are relatively flexible and particularly influenced by the birth of an infant (Fairbanks, 1976). Taking account of these structural features, basic social structure of savanna baboons can be schematized as shown in Fig.19a. Here, each subgroup includes female close relatives and one or more males which have pair-bonds with specific females. Males are arranged in a single linear dominance order, but here it is assumed that there is no specific attraction among males. As was pointed out by Fairbanks (1976), subgroups are relatively artificial breaks in a continuum of overlapping associations between females. In addition, males have occasional consort relations with various females which last only during less than two weeks (Saayman, 1971).

The basic structure of hamadryas band is illustrated in Fig.19b. Here, one-male units are discrete entities. There is no affinitive bond among females within or between the units, but males are connected with each other by mutual attraction, or 'male bond' (Kummer, 1968).

The basic pattern of social structure of a group composed of anubis-hamadryas hybrids should be represented in two different ways according to the degree of the hybridization in that group. If this group has originated from an anubis troop and genes from anubis baboons predominate in it, its basic social structure can be represented by the schema in Fig.19c. If it has originated from a hamadryas band, its basic social structure can be schematized as shown in Fig.19d. These two basic patterns, c and d, are similar with each other in that within each unit, or subgroup, females are connected with each other by affinitive bonds even though these bonds may be relatively temporary. The most

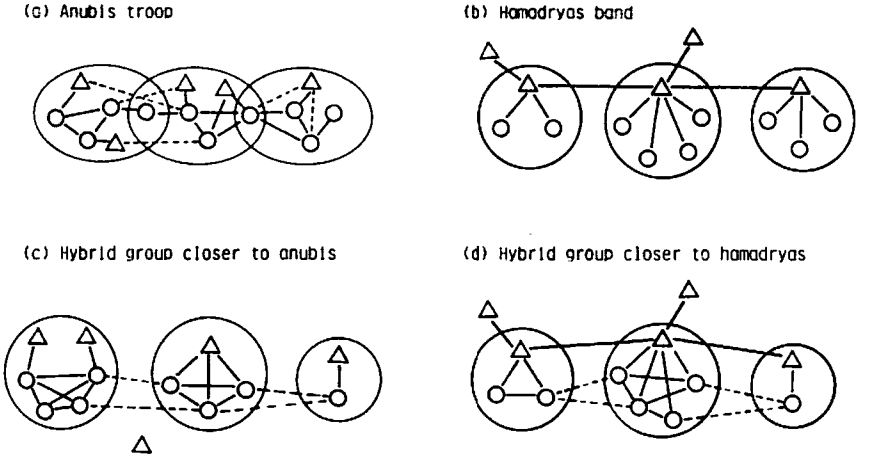


Fig. 19. Schematic representations of basic patterns of social structure of the anubis baboons, hamadryas baboons, and their hybrids. Triangles and circles respectively represent adult males and females. Solid lines indicate long-lasting affinitive bonds between individuals, and broken lines indicate temporary consort relations between males and females, or infrequent friendly interactions between females.

conspicuous difference between the structures of 'anubis-like' and 'hamadryas-like' hybrid groups is that in the former there is little affinitive bond among males, while in the latter males are connected with each other by specific partnerships, or neighborhood relationships. During nomadic movements the anubis-like hybrid group is very likely to split into several temporary parties which repeatedly join and part each other. In both anubis-like and hamadryas-like hybrid groups, the infra-units, or subgroups, do not coincide with female kinship groups. Female belonging to different units, or subgroups, may occasionally interact with each other, which is suggestive of the existence of latent consanguineous ties among them.

Thus the hybridization between anubis and hamadryas baboons has bred unique social structures which show clear deviations from those of both species. However, at present, no single pattern of basic structure specific to hybrid groups cannot be identified. In accordance with Nagel's conclusion (1973), Gabow (1975) elaborated the behavioral mechanism through which the hybrid zone between anubis and hamadryas along the Awash River is stabilized. However, in their population genetical study on the blood protein variations in baboons, Shotake et al. (1977) concluded that the hybrid zone is fairly wide and still expanding now. The results of this article also support the latter conclusion. It therefore cannot be considered that at present the social structure of all hybrid groups may converge on a single basic pattern.

Grubb (1978) demonstrates that there are nearly 20 examples of secondary contact between species or subspecies of African mammals, most of which being among the primates and ungulates. He also argues that the primates have been subjected to isolation and differentiation, associated with Quaternary climatic and vegetational changes, so that they have speciated very frequently but have not been able to complete later stages of sympatry. Shotake et al. (1977) calculated the divergence time between anubis and hamadryas baboons as being 337,000 years, and suggested that the peculiar characters of hamadryas social organization have evolved in a relatively short time. Such a shortness of divergence time between these two species thus calculated appears to reflect the features of speciation among African primates demonstrated by Grubb (1978). If the definition of species should be rigorously based only on a single genetic criterion such as the genetic distance or divergence time, the genus Papio might have to be considered as a single species, as have been proposed by Shotake et al. (1977). However, in order to refine the concept of species into an ecological entity, it is necessary to make much of the unique character of the social structure revealed by any primate 'species.' There have been some attempts to reconsider the taxonomic classification or to reconstruct the phylogeny and evolution among the primate order in terms of the types and characters of the social structure (Petter, 1965; Itani, 1972). From such a point of view, it is of special interest that the hybridization between anubis and hamadryas baboons has bred unique social structures. It is however very difficult to predict the fate of the hybrid population along the Awash River, since there remains several factors to be quantified and identified. The most important of which is the rate of flow of genes due to anubis or hamadryas immigrants into bands or troops of another species. It is possible that in the future some changes of environment caused by climatic changes, as well as human influences, will isolate the baboon population along the Awash River. It will be only after some genetic equilibrium is attained within such an isolated population that a single pattern of social structure specific to hybrid is fixed and stabilized.

SUMMARY

In the Awash Valley, Ethiopia, social organizations of two groups of hybrid baboons between Papio anubis and P. hamadryas were compared with each other, based on the quantitative data collected for about 4 months. The purpose of making these sociological comparisons are 1) to elucidate the social structure of hybrid groups, 2) to elucidate both the essential difference and common elements in the social structure of anubis baboons and hamadryas baboons, and 3) to confirm the social process by which hybridization can progress between the 2 species. Morphological hybrid indices were calculated for all the adult males and females of the 2 groups. In one group, the Gorge group (composed of 69 animals), anubis features were prevalent, while in the other group, the Kerrayu group (composed of 84 animals), hamadryas features were prevalent. The 2 groups, sharing a small area with each other, maintained antagonistic relationships between each other, while the Kerrayu group maintained more tolerant relationships with another neighboring group downstream, the Shelko group, than with the Gorge group. The tolerant relationships between the Kerrayu and the Shelko groups were comparable to those between different hamadryas bands, though they rarely formed a troop at the sleeping cliffs. All the members of the Kerrayu group were usually united in a single group during its nomadic movements, whereas the Gorge group often splitted into several parties, without stable membership, which repeatedly joined and parted each other.

The results of the comparisons of male-female, female-female, and male-male relationships between 2 groups are as follows:

(a) Male-Female Relationships

In the Gorge group, 8 subgroups were distinguished: 3 multi-male groups and 5 one-male groups. Comparing the memberships of subgroups with those ascertained in the previous study 3 years ago, it was found that the membership of the Gorge group, as a whole, had been stable, but the male-female associations had undergone great transformations. In the Kerrayu group, there were 2 large one-male units, 3 small one-male units, and 9 pair units at the beginning of the study period. Although these infra-units within the Kerrayu group were spatially more cohesive than the subgroups within the Gorge group, 4 cases of the alterations in possession of females by males occurred during the study period. In the Kerrayu group, there was a significant correlation between the males' tendency to possess females and their morphological features, which suggests that the males' ability to herd many females is genetically determined. It was concluded that there were far more persistent male-female bonds in both hybrid groups than those found in the anubis society. Especially, the analysis of the spacing mechanism between males and females within the same unit in the Kerrayu group proved that the large one-male units of this group were well integrated. However, in the Gorge group, and probably in the Kerrayu group, the male-female bonds were unstable from long-term point of view.

(b) Female-Female Relationships

The female-female relationships in both groups were very different from those in the hamadryas society. In both groups frequent grooming were occurring between females within the same unit or subgroup. This indicates that even the males forming cohesive one-male units in the Kerrayu group suffer some loss of the faculty to control the females. Affinitive relations were also existing between females of different units or subgroups. Especially, in the Gorge group, it was proved that affinitive bonds among females had been continuously retained over the rather long term. It was considered that such affinitive bonds among females were based on kinship among them. But it was also emphasized that the

female-female affinitive relationships were strongly affected by the transformations of male-female associations in both groups.

(c) Male-Male Relationships

The difference in the male-male relationships between the 2 groups was very distinct. The males of the Kerrayu group had a far stronger social disposition towards each other's spatial proximity than do the males of the Gorge group. In the Kerrayu group the occasional grooming was occurring among some bachelor-bachelor or possessor-bachelor dyads, whereas the grooming never occurred among adult or adolescent males in the Gorge group. It was concluded that there was far more stronger mutual attraction among males of the Kerrayu group than those of the Gorge group. The analysis of agonistic interactions between males revealed that the linearity of dominance order among the males in the Gorge group was more distinctly established than in the Kerrayu group. It was considered that such differences in male-male relationships between the 2 groups revealed the difference between original species. It was therefore concluded that the inflow of anubis genes into the hamadryas band had brought about a great disturbance of the possessive behavior of males towards females, but it had exerted little effect on the mutual bonds among males within the band.

The fluid grouping pattern of the Gorge group was considered to be mainly caused by the following 3 factors: (1) the segmentation of the group into independent subgroups, (2) lack of the mutual attraction among males, and (3) the breakdown of the consanguineous ties among females. Thus the inflow of hamadryas genes into the anubis troop had severely affected the integration of the anubis troop. It was argued that the multi-level system of the hamadryas society is based on the complex of the following 3 aspects: (1) the disposition of males towards each other's proximity, (2) breakdown of the linear dominance order among males, and (3) possession of females by males. The formation of this sociological complex was related to the need for concentrating on restricted resources in the arid habitat.

It was concluded that the Gorge group had originated from the anubis troop, and the Kerrayu group from the hamadryas band. Therefore the hypothesis proposed by Nagel that the hybridization was caused by the abduction of anubis females by hamadryas males cannot be supported. It was considered that the hybridization was mainly caused by immigration of anubis males into hamadryas bands, and immigration of hamadryas males into anubis troops. It was therefore considered that in the Awash Valley there was a mutual gene flow between anubis and hamadryas populations. Following 3 factors suppressing the rapid expansion of the hybrid zone were pointed out: (1) a small chance for anubis males of copulationg with hamadryas females within the hamadryas band, (2) rare secessions of hamadryas males from their natal bands, and (3) the dependence of the hamadryas nomadic life on the cliffs. It was concluded that the hybridization between anubis and hamadryas baboons had bred unique social structures which showed clear deviations from those of both species, but a single pattern of basic social structure specific to hybrid baboons had not yet fixed or stabilized.

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NOTES

*[1] N and G.H.I. indicate the size and the group hybrid index of each group, respectively (from Nagel, 1973). The group hybrid index is represented by an approximate value which was read from the relevant graph.

*[2] From February 22 to March 2, no observations were made of the Kerrayu group, since the author focussed his attention on the Gorge group during this period.

*[3] N indicates the number of measurements of the distances between each male and his partner females at 5-min intervals in the resting situation.

*[4] In the Gorge group, grooming interactions between adult males and 2 pubescent males (Tara and Ambassa) were sometimes observed.

*[5] The cases where a male attacked or chased another male with screaming, were excluded from this analysis.

*[6] A partner female of Hagos (honey) was excluded from the stable partners, since she copulated with Danielle when she showed maximum swelling of her perineum.

REFERENCES

Abramovich, R., 1976. The relation of attention and proximity to rank in preschool children. In: The Social Structure of Attention, M.R.A.Chance & R.R.Larsen (eds.), John Wiley & Sons, London, pp. 153-176.

Aldrich-Blake, F.P.G., T.Bunn, R.Dunbar & P.Headley, 1971. Observations on baboons, Papio anubis, in an arid region in Ethiopia. Folia primat., 15: 1-35.

Altmann, J., 1974. Observational study of behavior: Sampling methods. Behaviour, 49: 227-267.

De Waal, F.B.M., J.A.R.A.M.van Hooff & W.J.Netto, 1976. An ethological analysis of types of agonistic interaction in a captive group of Java-monkeys (Macaca fascicularis). Primates, 17(3): 257-290.

Drickamer, L.C., 1974. A ten-year summary of reproductive data for free-ranging Macaca mulatta. Folia primat., 31: 61-80.

Fairbanks, L., 1976. A comparative analysis of subgroup structure and spatial relationships in captive baboons and squirrel monkeys. Primates, 17(3): 291-300.

Gabow, S.A., 1975. Behavioral stabilization of a baboon hybrid zone. Amer. Natural., 109(970): 701-712.

Grubb, P., 1978. Patterns of speciation in African mammals. In: Bulletin

of Carnegie Museum of Natural History, No. 6: Ecology and Taxonomy of African Small Mammals, D.A.Schilitter (ed.), Carnegie Museum of Natural History, Pittsburgh, pp. 152-167.

Hall, K.R.L. & I.DeVore, 1965. Baboon social behavior. In: Primate Behavior: Field Study of Monkeys and Apes, I.DeVore (ed.), Holt, Rinehart & Winston, New York, pp. 53-110.

Itani, J., 1972. Social Structure of Primates. Seitaigaku-Koza, Kyoritsu-Publ., Tokyo. (in Japanese)

_____, 1977. Evolution of primates social structure. J. Human Evol., 6: 235-243.

Kaufmann, J.H., 1967. Social relations of adult males in a free-ranging band of rhesus monkeys. In: Social Communication among Primates, S.A.Altmann (ed.), Univ. of Chicago Press, Chicago, pp. 73-98.

Kawai, M., 1958. On the rank system in a natural group of Japanese monkey (I): The basic and dependent rank. Primates, 1: 111-130.

_____ & K.Sugawara, 1976. Hybridization and evolution of primates (II): Speciation and hominization. Shizen, 31(12): 64-73. (in Japanese)

_____ & U.Mori, 1979. Spacing within units and unit integrity. In: Ecological and Sociological Studies of Gelada Baboons, M.Kawai (ed.), Kodansha Ltd., Tokyo and S. Karger, Basel, pp. 199-217.

Kummer, H., 1968. Social Organization of Hamadryas Baboons: A Field Study. S.Karger, Basel and Univ. of Chicago Press, Chicago.

_____, 1971. Primate Societies: Group Techniques of Ecological Adaptation. Aldine-Atherton, Inc., Chicago.

_____, 1973. Dominance versus possession: An experiment on hamadryas baboons. Proceed. 4th Int. Congr. Primat., Vol. 1: Precultural Primate Behavior, Karger, Basel, pp. 226-231.

_____, 1974. Distribution of individual distances in patas monkeys and gelada baboons. Folia primat., 21: 153-160.

_____, J.J.Abegglen, Ch.Bachmann, J.Falett, & H.Sigg, 1978. Grooming relationship and object competition among hamadryas baboons. In: Recent Advances in Primatology, Vol. 1: Behaviour, D.J.Chivers & J.Herbert (eds.), Academic Press, London, pp. 31-38.

Mason, W.A., 1978. Ontogeny of social systems. In: Recent Advances in Primatology, Vol. 1: Behaviour, D.J.Chivers & J.Herbert (eds.), Academic Press, London, pp. 5-14.

Morgan, B.J.T., M.J.A.Simpson, J.P.Hanby, & J.Hall-Craggs, 1976. Visualizing interaction and sequential data in animal behavior: Theory and application of cluster-analysis methods. Behaviour, 59: 1-43.

Mori, U., 1976. Alternation of leaders of one-male units and formation of initial unit in gelada society. (Proceeding of the 30th Joint Meeting of the Anthropological Society of Nippon and the Japanese Society of Ethnology) J. Anthrop. Soc. Nippon, 84(4): 308. (in Japanese)

Mori, U., 1979a. Individual relationships within a unit. In: Ecological and Sociological Studies of Gelada Baboons, M.Kawai (ed.), Kodansha Ltd., Tokyo and S. Karger, Basel, pp. 93-124.

_____, 1979b. Social structure of gelada baboons. In: Ecological and Sociological Studies of Gelada Baboons, M.Kawai (ed.), Kodansha Ltd., Tokyo and S. Karger, Basel, pp. 243-247.

Nagel, U., 1971. Social organization in a baboon hybrid zone. Proceed. 3rd Int. Congr. Primat., Vol. 3, S. Karger, Basel, pp. 48-57.

_____, 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. Folia primat., 19: 104-165.

Packer, C., 1977. Intertroop transfer and inbreeding avoidance in Papio anubis. Doct. Disertation, Univ. of Sussex.

Petter, J.J., 1965. The lemur of Madagascar. In: Primate Behavior: Field Study of Monkeys and Apes, I.DeVore (ed.), Holt, Rinehart & Winston, New York, pp. 292-319.

Ransom, T.W. & B.S.Ransom, 1971. Adult male-infant relations among baboons (Papio anubis). Folia primat., 16: 179-195.

Rowell, T.E., 1966. Hierarchy in organization of a captive baboon group. Anim. Behav., 14: 430-443.

Saayman, G.S., 1971. Grooming behaviour in a troop of free-fanging chacma baboons (Papio ursinus). Folia primat., 16: 161-178.

Sade, D.S., 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: Social Communication among Primates, S.A. Altmann (ed.), Univ. of Chicago Press, Chicago, pp. 99-114.

Seyfarth, R.M., 1977. A model of social grooming among adult female monkeys. J. theor. Biol., 65: 671-698.

_____, 1978a. Social relationships among adult male and female baboons: I. Behaviour during sexual consortship. Behaviour, 64: 204-226.

_____, 1978b. Social relationships among adult male and female baboons: II. Behaviour throughout the female reproductive cycle. Behaviour, 64: 227-247.

Shotake, T., in preperation. Blood protein variations in baboons: II. Population genetical study of natural hybridization between Papio anubis and P. hamadryas.

_____. K.Nozawa & Y.Tanabe, 1977. Blood protein variations in baboons: I. Gene exchange and genetic distance betweenPapio anubis, Papio hamadryas, and their hybrid. Japan J. Genetics. 52(3): 223-237.

Siegel, S., 1956. Nonparametric Statistics: For the Behavioral Science. McGraw-Hill, London and Kogakusha, Tokyo.

Stammbach, E., 1978. On social differentiation in groups of captive female hamadryas baboons. Behaviour, 67: 322-338.

Sugawara, K., 1979. Sociological study of a wild group of hybrid baboons between Papio anubis and P. hamadryas in the Awash Valley, Ethiopia. Primates, 20(1): 21-56.

_____, 1980. Structure of social encounters among non-troop males of Japanese monkeys. Kikan Jinruigaku, 11(1): 3-70. (in Japanese)

_____, in preperation. Ethological analysis of social behavior in wild hybrid baboons between Papio anubis and P. hamadryas.

Sugiyama, Y., 1976. Life history of male Japanese monkeys. In: Advances in the Study of Behavior, Vol. 7, Academic Press, New York, pp. 255-283.

Van Hooff, J.A.R.A.M., 1971. Aspecten van het Sociale Gedrag en de Communicatie bij Humane en Hogere Niet-Humane Primaten (Aspects of the Social Behavior and Communication in Human and Higher Non-Human Primates). Bronder-Offset n.v.,Rotterdam.