# Sociological Study of a Wild Group of Hybrid Baboons Between *Papio anubis* and *P. hamadryas* in the Awash Valley, Ethiopia

KAZUYOSHI SUGAWARA
*Kyoto University*

ABSTRACT. A group of hybrid baboons between anubis and hamadryas named the Gorge group was studied for five months in the Awash Valley, Ethiopia. Both morphologically and genetically, anubis features were prevalent in the Gorge group. Three types of subgroups within the group were distinguished: one-male groups, pair groups, and multi-male groups. The joining and parting of subgroups is examined by cluster-analysis. The Gorge group is concluded to be a single social unit, though it was composed of two main clusters. Grooming relations, spacing mechanisms, and sexual relations among its members were analyzed in detail. The dominance relationships among males are clarified in order to be related with their social interactions. Various aspects of the social organization are compared with those of anubis or hamadryas. It is demonstrated that the social structure of the Gorge group showed an intricate mixture of anubis and hamadryas characteristics. It is discussed how such a structure had been formed through hybridization, and what were the factors causing the differences among three types of subgroups.

## INTRODUCTION

Recently, some cases of hybridization under natural conditions have been reported by several authors in three or four genera of Cercopithecoidea, i.e., *Macaca* (FOODEN, 1964; BERNSTEIN, 1968), *Cercopithecus* (STRUHSAKER, 1970), and *Papio*. Especially among baboons, hybridization is not an exceptional phenomenon, because it occurs in various combinations such as *Papio anubis* × *P. hamadryas* (NAGEL, 1971, 1973), *P. anubis* × *P. cynocephalus* (MAPLES, 1972) and *P. cynocephalus* × *P. ursinus* (JOLLY, unpublished, cited by NAGEL, 1973). Moreover possible case of hybridization was reported to occur between *P. anubis* and *Theropithecus gelada* (DUNBAR & DUNBAR, 1974). Of all these cases, those occurring between anubis and hamadryas are worthy of notice, for the social organizations of these two species differ drastically (KUMMER et al., 1970).

The social unit of hamadryas baboons, the band, consists of several one-male units each of which has a stable membership and usually maintains spatial cohesion. At the cliff used for their sleeping site, two or more bands form a large sleeping group called a troop (KUMMER, 1968). On the other hand, the social unit of anubis baboons is a group varying in number from 30 to 150 animals and containing several males, more females, and their offspring. Anubis baboons form a one-level society very common among *Papio* species, whereas hamadryas baboons have a multi-level society, representing an idiosyncratic social organization among primates (KUMMER, 1971).

NAGEL found an anubis-hamadryas hybrid zone in the Awash Valley in Ethiopia, and made a sociological and an ecological comparison between anubis baboons, hamadryas baboons, and their hybrids (NAGEL, ibid.). According to NAGEL, hybridization in the Awash Valley is mainly caused by the abduction of anubis females from their native groups by hamadryas or hybrid males, which must result in a one-way gene flow from the anubis to the hamadryas side. But two other ways of hybridization can be supposed. One is the immigration of solitary anubis males into the hamadryas bands. The other is the reverse process through which hamadryas males intrude into anubis troops and stay there, copulating with anubis females. The possibility of the occurrence of these two processes was denied by NAGEL, but the latter process was actually observed to occur by the author and coworkers (KAWAI & SUGAWARA, 1976). Further, it was found by the study of population genetics that the anubis genes were present, though the frequency was very low, in a population of hamadryas baboons living outside the basin of the Awash River (SHOTAKE et al., 1977). Therefore NAGEL's conclusion that the hybrid zone is stable and limited to the narrow area of about 20 km along the Awash River cannot be supported. This problem was discussed in more detail in another article (KAWAI & SUGAWARA, ibid.). This report is focussed on the internal structure of the hybrid group.

The most important sociological problem concerning the anubis-hamadryas hybrid society is what kind of basic social structure it has. Especially, it should be clarified which characters of anubis and of hamadryas predominate, or whether characters unique to hybrids can be found. For example, do there exist in the hybrid society such male-female bonds as are found in the hamadryas society? If so, what are the behavioral and social mechanisms that maintain them? In order to solve these problems the author chose one hybrid group from the groups inhabiting the Awash Valley and investigated its internal social structure.

## MATERIALS AND METHODS

### STUDY AREA AND STUDY METHODS

The study area is situated in the Awash Valley in Ethiopian Rift Valley, about 150 km east of Addis Ababa. The Awash River flows through this region in a north-easterly direction, along the southeast boundary of the Awash National Park. The Awash Falls, located at the southernmost end of the park, separates the upstream plain habitat from the canyon habitat below the falls. Above the falls the riverine forest grows rather thick, whereas it is reduced to a scanty foreststrips and even disappears over some of the stretches below the falls. The dominant vegetation in this region is *Acasia* savanna.

The field study was carried out for about 160 days from October 5, 1975 to March 12, 1976. There was no rainfall, as the study period almost coincided with the dry season, but heavy rain fell only twice at night early March when the rainy season was about to begin. Mean minimum daily shade temperature during the study period was 22.2°C, and mean maximum was 30.6°C.

The author habituated the baboons to his close presence by means of artificial feeding at Site-I, 5.5 km east of the Awash Falls and at Site-II, some 11 km east of the falls near the edge of a cliff on the north bank of the Awash River (Fig. 1). The author discriminated individually all adult and subadult animals of one group composed of 61

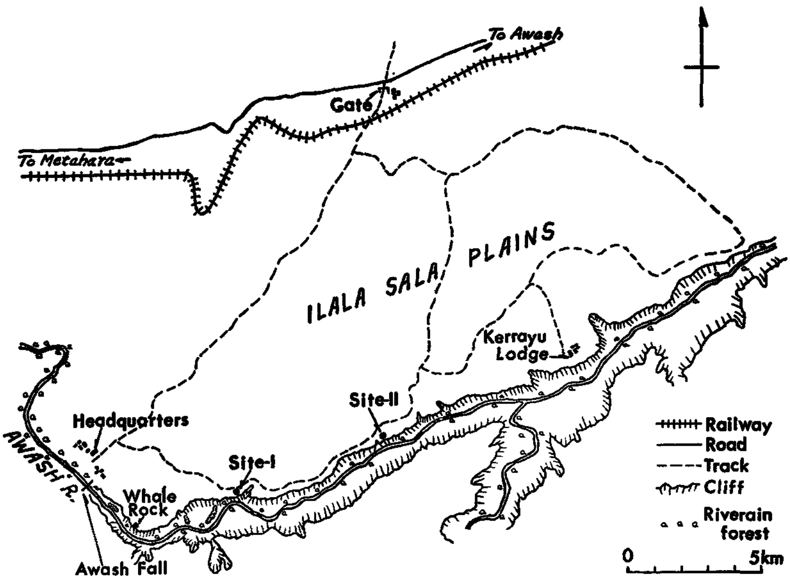


**Fig. 1.** The map of the study area, showing the main observation sites (black dots).

animals (the Gorge group) whose home range included both Site-I and Site-II. He also identified individually only adult males of the neighboring group downstream, composed of about 57 animals (the Kerrayu group), which sometimes visited only Site-II. The intensive study was focussed on the Gorge group, and quantitative and qualitative data were collected with regard to the social grouping, sexual relations, various kinds of social behavior, and inter-individual distances.

The observations were mainly carried out when the baboons were resting on and around the feeding site after they had finished eating. The traveling was traced as far as possible and the supplemental data were collected. The time duration of an observation ranged from 30 minutes to six hours. Throughout the study period about 400 hours were spent observing the baboons of the Gorge group from close range.

## The Degree of Hybridization from the Morphological View

Nagel (1973) classified the external appearance of adult males sampled from 11 groups living on the north bank of the Awash River by means of morphological hybrid index in order to measure the degree of hybridization in this region. The author applied the same method as Nagel's in measuring the degree of hybridization in the Gorge group, computing the morphological hybrid index for each of the adult males (Fig. 2). There is a wide morphological variation among 13 adult males. Of all males, *Rb* and *Hg* had a conspicuously hamadryas-like appearance, while *St* and *Wh* were intermediate. The rest of the males resembled anubis baboons in their appearance. 'Group hybrid index' (Nagel, ibid.) is computed at 11.1 by averaging the hybrid indices of all males; that is, the Gorge group is as a whole closer to the anubis type than to the hamadryas type.

In their population genetics study on the blood protein variations in baboons,

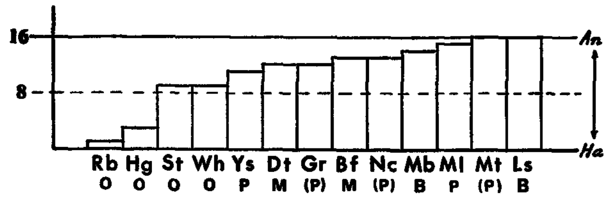


**Fig. 2.** Hybrid index of each adult male in the Gorge group. Hybrid index was calculated by the following procedure. Eight morphological characters with clearly different appearance in anubis and hamadryas males were selected. Each character was given score 0 for hamadryas appearance, score 1 for intermediate appearance and score 2 for anubis appearance. Hybrid index of each male is the sum of these eight scores. O: leaders of one-male groups; P: males of pair groups; (P): males of multi-male groups each of which has pair-link with a specific female; M: males of multi-male groups; B: bachelor males.

SHOTAKE et al. (1977) calculated the hybridization rate of the Gorge group from which blood samples had been collected and examined by electrophoresis. They concluded that 74.1% of the genes in the Gorge group originated from anubis. This result seems to coincide well with the author's conclusion stated above.

In the Kerrayu group neighboring the Gorge group downstream, the accurate hybrid indices could not be computed for all adult males. But eight of 13 adult males closely resembled hamadryas baboons in overall appearance. Three adult males had an intermediate appearance. Only two males had an anubis-like appearance, but even they had the fur with a much lighter color than that of typical anubis baboons. These facts suggest that the Kerrayu group is a hybrid group in which hamadryas features are more prevalent and that there is a clear difference in morphology between the Gorge group and the Kerrayu group.

NAGEL (1973) stated that the first group living in the canyon below the Awash Falls (the group C1) was composed of anubis baboons. In fact the Gorge group was the first group living in the canyon, and in 1975–1976 this was composed of hybrid baboons. It is highly probable that the Gorge group had originated from the group C1. The hybridization might have been in process in the group C1 for these seven years and it would have brought about a great change in the composition of this group.

## SOCIAL ORGANIZATION OF THE GORGE GROUP

### COMPOSITION OF THE GORGE GROUP

The Gorge group consists of eight subgroups each of which has a stable membership. The subgroups can be categorized into three types: the one-male group (OMG), the multi-male group (MMG), and the pair group (PG), according to the form of the relationship between male and female. The one-male group, like the one-male unit of hamadryas baboons, consists of one adult male, several adult females and their offspring. The multi-male group involves several males and females and their offspring. The pair group is the specific combination of one adult male and one adult or adolescent female. Other than these subgroups, several bachelor males without any permanent association with the females were found in the Gorge group.

All individuals of the Gorge group are listed in Table 1 according to their respective

**Table 1.** Age, sex, and individual composition of each subgroup in the Gorge group

| Types and names of subgroups | | Male | | | Female | | | Juveniles and Infants | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Adult | Adolescent | Puberty | Adult | Adolescent | Puberty | Juv. | Brown inf. | Black inf. | |
| One-male group | *Rb*-OMG | *Robes* (*Rb*) | | | *romi* (*rm*)↗? | | | | | F† | |
| | | | | | *roze* (*rz*) | | | | | M* | |
| | | | | | *rossa* (*rs*) | | | F | | | |
| | | | | | *rolita* (*rl*) | | | F | | | |
| | | | | | *armaz* (*az*)↙Bf-MMG | | | | M | | 9 |
| | *St*-OMG | *Saint* (*St*) | | | *suzanne* (*sz*) | | | F, M | | | |
| | | | | | *soutella* (*st*) | | | M | | | |
| | | | | | *sala* (*sl*)↙? | | | F | | | 8 |
| | *Hg*-OMG | *Hagos* (*Hg*) | | | *hana* (*hn*) | *haru* (*hr*) | *honey* (*ho*) | M | F | | |
| | | | | *Hans* (*Hs*) | | | | | | | 7 |
| | *Wh*-OMG | *White* (*Wh*) | | | *wfarem* (*wf*) | | | F | | | |
| | | | *Danielle* (*Dl*) | | *witch* (*wc*) | | | M | | | 6 |
| Pair group | *Ml*-PG | *Maler* (*Ml*) | | | *meskel* (*mk*) | | | | | | 2 |
| | *Ys*-PG | *Yosa* (*Ys*) | | | *yoko* (*yk*) | | | F | | | 3 |
| Multi-male group | *Bf*-MMG | *Baboof* (*Bf*) | | | *astere* (*ast*) | | | | | M | |
| | | | | | *bayech* (*bc*) | | | | F | | |
| | | *Necker* (*Nc*) | | | *genet* (*gt*) | | | M | | | |
| | | | *Paul* (*Pl*) | | *fox* (*fx*) | | | U | | F* | |
| | | *Danton* (*Dt*) | | | *scarlet* (*sc*) | | | F | | M* | 16 |
| | *Gr*-MMG | *Green* (*Gr*) | | | *kitsune* (*kt*) | | *nureme* (*nr*) | F | | F* | |
| | | *Matiou* (*Mt*) | | | | *marie* (*mr*) | | | | | 7 |
| Bachelor males | | *Louis* (*Ls*) | *Don* (*Dn*) | *Kire* (*Kr*) | | | | | | | |
| | | *Mirabeau* (*Mb*) | | *Jean* (*Jn*) | — | — | — | — | — | — | 5 |
| Total | | 13 | 3 | 3 | 18 | 2 | 2 | 14 | 3 | 5 | 63 |

The crosses and the stars indicate the death and the birth of animals, respectively. Up-directed and down-directed arrows indicate the emigration and the immigration of animals, respectively. The total numbers are represented by those confirmed at the end of the study period. Abbreviated names are shown in the parentheses. M: male; F: female; U: sex unknown.

subgroups. The Gorge group consisted of 61 animals (including two black infants) in November 1975. During the study period, one adult female disappeared, one black infant died, and four black infants were born. By March 1976, 63 animals (including five black infants) were present in the Gorge group.

The one-male group is very similar to the one-male unit of hamadryas baboons, whereas the multi-male group resembles a small troop of anubis baboons in its composition. Thus the basic social form of the Gorge group is a mixture of the troop of anubis baboons and the minimum social units of the hamadryas society. The characteristics of the male-female relationship in each subgroup will be analyzed in detail in the next chapter. It should be noticed that four males closer to hamadryas baboons in appearance than the others are the leaders of the four one-male groups, respectively. Moreover, there is a significant correlation between the rank order in which males are arranged according to their tendency to herd females[1] and their morphological rank order (hybrid indices) from hamadryas to anubis (Spearman rank correlation coefficient; $r_s = 0.7625$, $p<0.01$). Therefore it can be said that there is some parallelism between the form of male-female combinations and the morphological characteristics of the males.

In the Gorge group the appearance or disappearance of two females (*sl* and *rm*)[2] and the shifting of three females (*az*, *hr*, and *mr*) between the subgroups were recorded throughout the study period. These cases will be described and examined in detail later in this paper. Finally it was ascertained that 16 females (76.2%) of all adult and subadult females in the Gorge group had been the constant members of the respective subgroups for at least four months. NAGEL (1971, p. 55) stated, "most of the subunits of the hybrid group turned out to be unstable in composition." However, it is more adequate to state that each subgroup has basically a stable membership in the Gorge group, though the female shifting among subgroups sometimes occurs.

## GROUPING STRUCTURE OF THE GORGE GROUP

All members of the Gorge group were not always united into a single group during its group movements. They often splitted into several temporary parties which repeatedly joined and parted each other. In this paper, the term 'party' is applied to a group of baboons which appeared simultaneously at the same feeding site. It was often observed that a while after one group of baboons had arrived at the feeding site, another group came in the same direction to join the preceding one. In such cases two groups were regarded as independent parties only when the lapse of time between their respective arrivals exceeded one hour. Thus the size of 174 parties was recorded and the membership of all these parties was ascertained. There were 56 parties (32.2%) in which all the members of the Gorge group were present. These were distributed over 37 days (39.4%) of all the observation days, 94 days, on which a part or the whole of the Gorge group could be observed. During the first half of the study period (November 6–December 28) the gathering of all the members occurred on seven days (16.3%) of

1) Adult males are arranged as follows: i) the leaders of one-male groups; ii) the males of pair groups; iii) the males of multi-male groups each of which has the pair-link with one female; iv) the males of multi-male groups; v) bachelor males.

2) The abbreviated name of each female is represented by two or three small letters, and that of each male is by a combination of capital letter and a small letter.

43 days, while it occurred on 30 days (58.8 %) of 51 days during the latter half. It is possible that the regular artificial feeding attracted the baboons and prompted them

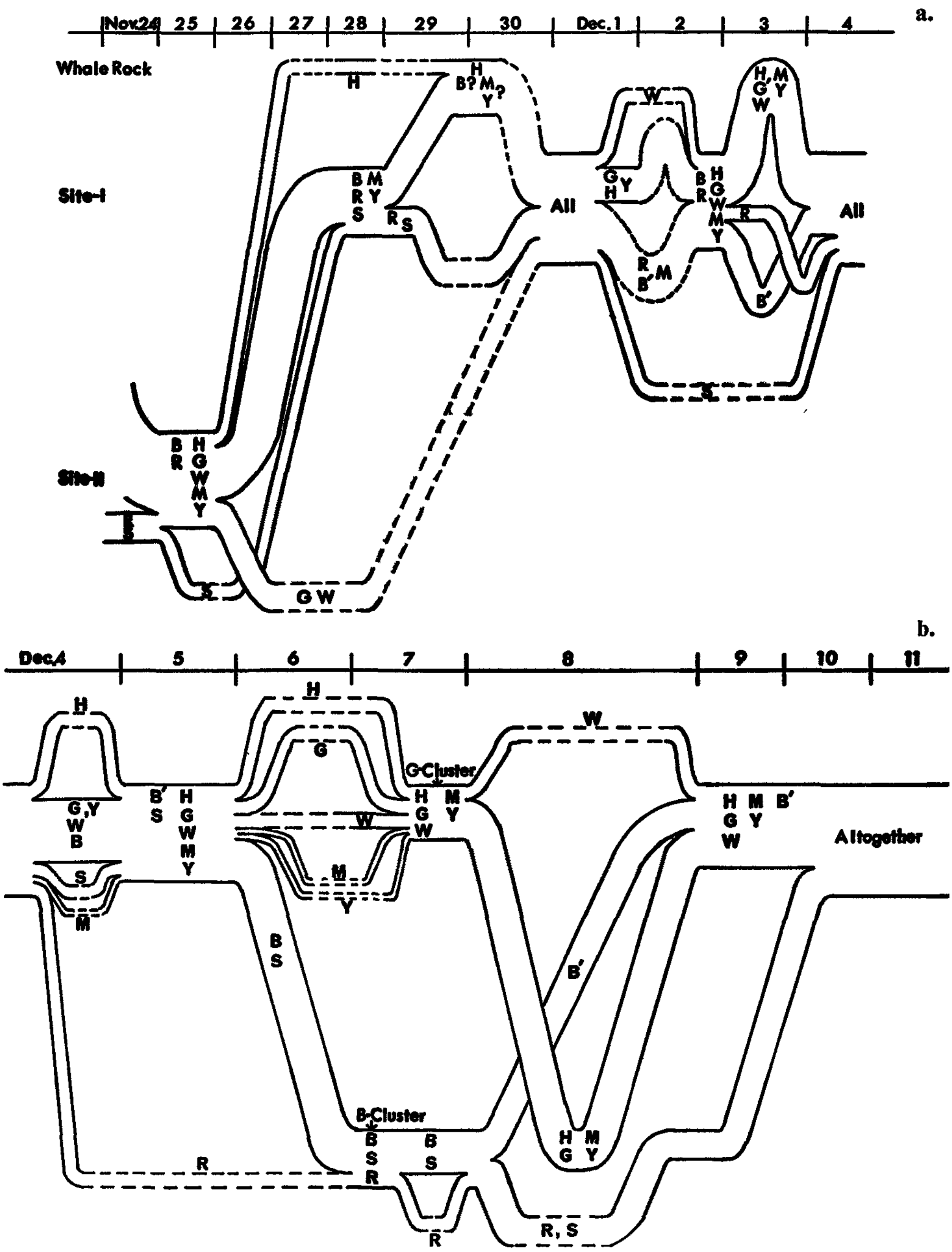


Fig. 3. The schema of the joining and parting of subgroups from November 24 to December 11. Capital letters with points indicate the subgroups in which one or more members were absent. R: *Rb*-OMG; S: *St*-OMG; H: *Hg*-OMG; W: *Wh*-OMG; M: *Ml*-PG; Y: *Ys*-PG; B: *Bf*-MMG; G: *Gr*-MMG.

to gather into a group, resulting in the remarkable increase of the rate of the joining of all the members in the latter half. It is therefore likely that under completely natural conditions all the members of the Gorge group only rarely form a single group in the daily nomadism.

A schema of the process of sequential changes of party formation ascertained at Site-I, Site-II, and the Whale Rock (see Fig. 1) from November 24 to December 11 is presented in Figure 3 in order to illustrate the dynamics of joining and parting of parties. Generally all the members of each subgroup were found together in a single party. But sometimes one or more members of the multi-male group were separated from the other members of the subgroup.

From December 26 to December 28 an adult female, *kt*, belonging to *Gr*-MMG was present in a party composed of *Bf*-MMG and *St*-OMG, separating from her own subgroup. During this period *fx* belonging to *Bf*-MMG was found in another party, separating from *Bf*-MMG.

On the contrary, it never arose that the females belonging to the one-male groups separated from their own leader males, excepting only one instance: On December 14 only two animals of *Wh*-OMG (*Wh* and *wc*) appeared at Site-I, whereas all other animals of the Gorge group, including *wf*, appeared at Site-II.

From Figure 3 it is readily apparent that there are sets of subgroups each of which is frequently found in the same party. In order to clarify this point quantitatively, the cluster-analysis method is applied (MORGAN et al., 1976).

The similarity ($S$) between any two individuals, i.e., the likelihood of the two being observed together, can be obtained by the following formula:

$$S = \frac{N(A, B)}{N(A)+N(B)} \times 1000$$

when $A$ or $B$ represents each individual, $N(A)$ indicates the number of parties in which $A$ was observed and $N(A, B)$ indicates the number of parties in which both $A$ and $B$ were present.

The similarities were calculated for all males of the Gorge group and Single Link Cluster-Analysis (SLCA) dendrogram was constructed from these similarities (Fig. 4). This dendrogram shows clearly that the Gorge group can be divided into three main clusters. One is the B-cluster which contains *Rb*-OMG, *St*-OMG, and *Bf*-MMG. Another is the G-cluster containing *Hg*-OMG, *Wh*-OMG, *Gr*-MMG, *Ml*-PG, and *Ys*-PG. The third is the cluster composed of four bachelor males, but these males are more frequently found together with the B-cluster than with the G-cluster. *Mb*, the most subordinate of all adult males, is included in none of these clusters.

Though these clusteres could not be distinguished until the degree of familiarity between any two subgroups was estimated during a certain span of time, they could be visible when each cluster itself sometimes formed an independent party (see Fig. 3b). Moreover, the subgroups belonging to the G-cluster appeared at Site-I more frequently than at Site-II, while the subgroups belonging to the B-cluster showed the opposite tendency. Therefore it is supposed that the G-cluster and the B-cluster might have their main nomadic ranges in the upstream area and downstream area, respectively.

Simply speaking, the basic mechanism of the joining and parting of parties among

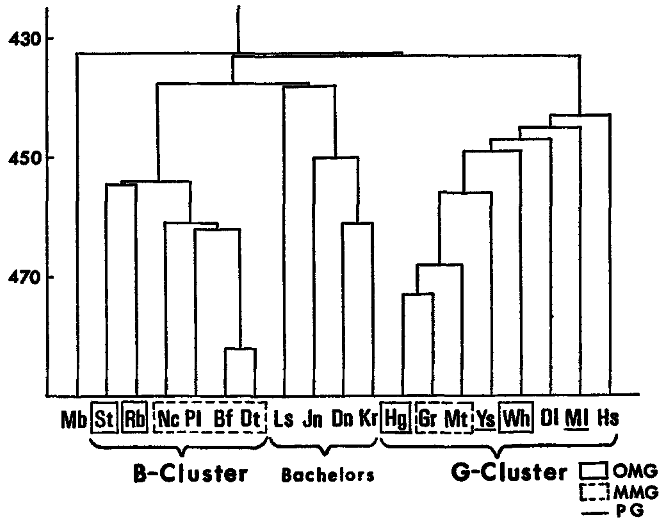


**Fig. 4.** Single Link Cluster-Analysis (SLCA) dendrogram representing the tendencies of any two males to be together in the same party.

the Gorge group consists in the alternation of fusion and separation between two main clusters, the B-cluster and the G-cluster. The following three occasions should be noticed for the factors which modified this basic mechanism:

1) The members belonging to the multi-male group tended to disperse and some of them occasionally participated in another party, separating from the major part of their own subgroup.

2) The one-male groups tended to move independently, forming a single party (see in Fig. 3, the movements of *Hg*-OMG from November 26 to November 28, of *Rb*-OMG from December 4 to December 7, and of *Wh*-OMG on December 8).

3) Pair groups sometimes formed a party together with the B-cluster, though they belonged to the G-cluster (see in Fig. 3a, the movement of *Ml*-PG and *Ys*-PG on November 28).

## The Gorge Group as a Social Unit

In the preceding section it was clarified that the Gorge group usually splitted into two or more parties and that two main clusters could be distinguished among it. What then are the grounds for considering the entire Gorge group as a single social unit?

We can find evidence for this in the relationship of the Gorge group to the neighboring group, the Kerrayu group. Not only could all the members of the Gorge group simultaneously feed at the same feeding site, but they could also use the same common cliff as their sleeping site. But no intermingling was ever observed between the Gorge group and the Kerrayu group. Further, antagonistic interactions arose between them when they happened to meet each other at the common border of their home ranges. The author observed on eight occasions the encounters between a part or all of the Gorge group and a part of the Kerrayu group at or around Site-II, which was situated in the common area of their home ranges. In five cases one party had no

**Table 2.** Observation of the contacts between the parties composed of the animals of the Gorge group and those of the Kerrayu group at Site-II

| Date | Party size G | Party size K | First occupying | Fight | Finally occupying | Contact duration |
|---|---|---|---|---|---|---|
| Nov. 19 | 8(2) | ca. 40(12) | G | − | K | — |
| Nov. 24 | 16(4) | ca. 12(3) | K | + | G | 17 mn. |
| Nov. 25 | 49(12) | 11(3) | K | − | G | — |
| Dec. 8 | 27(5) | 7(1) | K | − | G | a few mn. |
| Dec. 9 | 18(5) | 8(2) | G | + | G | 8 mn. |
| Dec. 12 | 60(13) | 40(9) | both | + | G | 62 mn. |
| Dec. 14 | 52(12) | ca. 40(9) | G | − | K | 21 mn. |
| Dec. 22 | 45(7) | ca. 43(13) | G | − | K | 27 mn. |

G and K indicate the part or the entire of the Gorge group and the Kerrayu group, respectively. Figures in the parentheses indicate the number of males which were present in each party.
'First occupying' indicates the party which was occupying the feeding site before the contact with another party. 'Finally occupying' indicates the party which occupied the feeding site after the contact.

sooner hurriedly left the feeding site than another approached there. But in three cases there arose confrontations or fights between them (Table 2). This suggests that the Gorge group and the Kerrayu group are independent groups and they usually avoid each other. It is to be noted from Table 2 that in almost every case the party containing the most adult males finally occupied the feeding site, but it is unknown whether there is a stable dominance-subordination relationship between the two groups as a whole.

Another fact suggesting the integrity of the Gorge group is that a party containing all the members sometimes traveled rapidly in a body over a long distance. Moreover all subgroups moved in the same direction whenever they departed from the feeding site to begin daily foraging. Therefore during the troop movements each subgroup pays particular attention to the preceding subgroup (CHANCE, 1967).

Further evidence can be found in the affinitive relationships between individuals among the group. There were occasional grooming interactions among females of different subgroups. Furthermore when the animals of a party were resting at evening just before descending the cliff to the sleeping ledges, many juveniles gathered and played around the bachelor males, such as *Ls*, at a long distance from their own subgroups. The above evidence suggests that all individuals of the Gorge group recognized each other very well and that there are friendly relations between the members of the different subgroups.

On the three grounds argued above, it can be concluded that the Gorge group is a single social unit, which lives within a definite home range, maintains an antagonistic relationship with the neighboring group, and is composed of individuals recognizing each other very well.

## AFFINITIES BETWEEN INDIVIDUALS AND THE INTEGRITY OF EACH SUBGROUP

### GROOMING RELATIONSHIP

#### Profile of Grooming Relationships among the Gorge Group

The author continuously observed the animals of each subgroup and recorded the time spent in every grooming interaction observed for each pair of adult and subadult members. As a result, a total of 5,980 min of grooming were recorded. The grooming relationships of the Gorge group underwent remarkable alterations after the sudden social change through which the new association between *Ml* and *hr* was formed on January 23, as will be described later. So the author divides the study period into two parts: from November 15 to January 22 (Period-I) and from January 23 to March 11 (Period-II). In the following descriptions, as a rule, Period-I and Period-II will be dealt with separately.

It was impossible to record the grooming interactions impartially for all individuals, because the observational facilities differed very much with individuals. Therefore it is appropriate to use as an index to represent the degree of affinity between any two individuals the ratio of the total minutes of grooming interactions observed between them to the total minutes of those in which each of them participated. In other words, a measure of similarities between *A* and *B*, which would reflect the closeness of their groomig bond, can be computed by the following formula:

$$S = \frac{T(A,B)}{T(A)+T(B)} \times 1000$$

when $T(A, B)$ indicates the total minutes of grooming between $A$ and $B$, while $T(A)$ indicates the total minutes of grooming in which $A$ participated.

The Maximum Spanning Tree (MST; MORGAN et al., 1976) of the grooming rela-

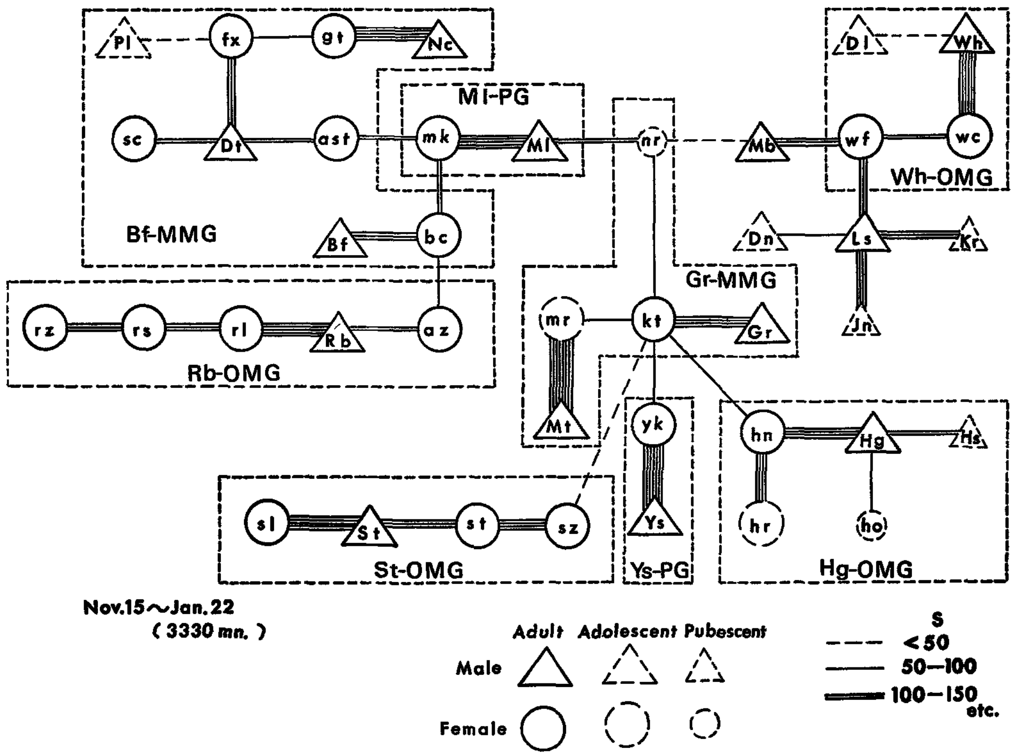


**Fig. 5.** Maximum Spanning Tree (MST) based on the time duration of grooming interactions observed among adult and subadult animals during Period-I. Connecting lines express the similarity coefficient.

tionship during Period-I was constructed from the similarities thus calculated (Fig. 5).

From Figure 5 it should be noted that each one-male group showed a definite concentration of grooming within itself, excepting *Wh*-OMG of which one adult female (*wf*) had frequent grooming interactions, as well as copulations, with such bachelor males as *Mb* and *Ls* only for several days (see the next chapter). The concentration of grooming within the subgroup was not so remarkable in pair groups and multi-male groups as in one-male groups. Namely it is difficult to distinguish *Ml*-PG from *Bf*-MMG as an independent cluster. On the other hand, it is clear that *Gr*-MMG is polarized into two pairs of specific bonds between a male and a female (*Gr—kt*, *Mt—mr*). Such a specific male-female bond is also found between *Nc* and *gt* in *Bf*-MMG. Hereafter such male-female bonds will be designated as pair-links. The mechanism maintaining the male-female bond is common between the pair group and the pair-link, as will be elucidated later, but the former can be distinguished from the latter on the ground that it moves as an independent minimum unit through the joining and parting of parties.

At last, the most remarkable feature of grooming relationships of the Gorge group was that grooming was observed most frequently between males and females, whereas it was never observed among adult males.

Grooming Relations in One-male Groups

Because there had not been conspicuous social changes in *Rb*-OMG and *St*-OMG

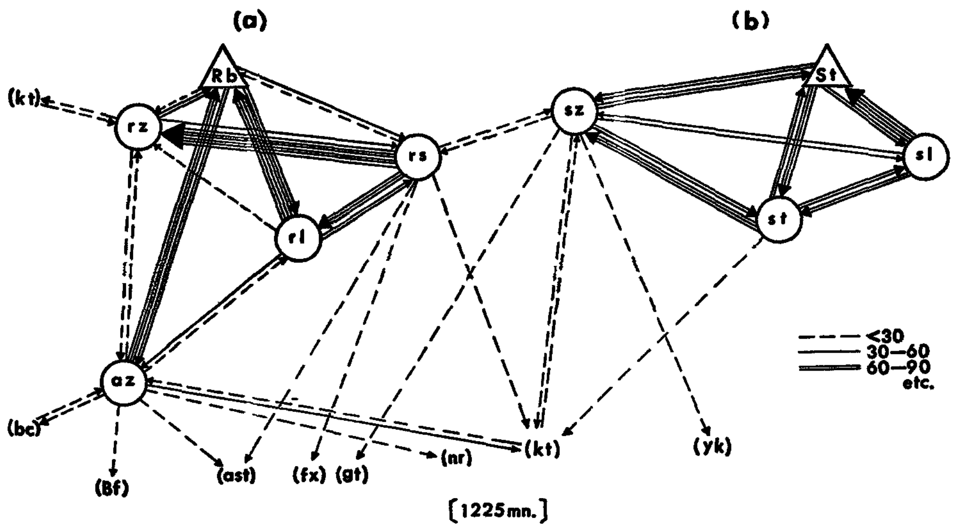


**Fig. 6.** Sociograms of two one-male groups based on the grooming interactions, excluding juveniles and infants, throughout the study period. (a) *Rb*-OMG (male-female distances are 1.3 m for *Rb—rz*, 3.1 m for *Rb—rs*, 2.9 m for *Rb—rl*, and 5.0 m for *Rb—az*.) (b) *St*-OMG (3.8 m for *St—sz*, 2.2 m for *St—st*, and 1.7 m for *St—sl*.) The graph distances between the leader and each female are proportional to the mean of recorded distances. Females of the same one-male group are arranged according to higher to lower dominance order. The numbers of arrows indicate the similarity coefficient. The arrows issue from the groomer to the groomee. Letters in the parentheses indicate the individuals outside these two subgroups.

during both Period-I and Period-II, the sociograms that were constructed for both one-male groups are based on the grooming relationships for the entire study period (Fig. 6). It is to be noted that there exist remarkable grooming relations, high grooming frequencies, between females in both one-male groups. Comparing these grooming bonds with those between females in *Bf*-MMG (Fig. 7), it should be noticed that some of the females of the one-male groups have by far the closer alliance between them than any of those of the multi-male group have. KUMMER (1968) stated that in hama-

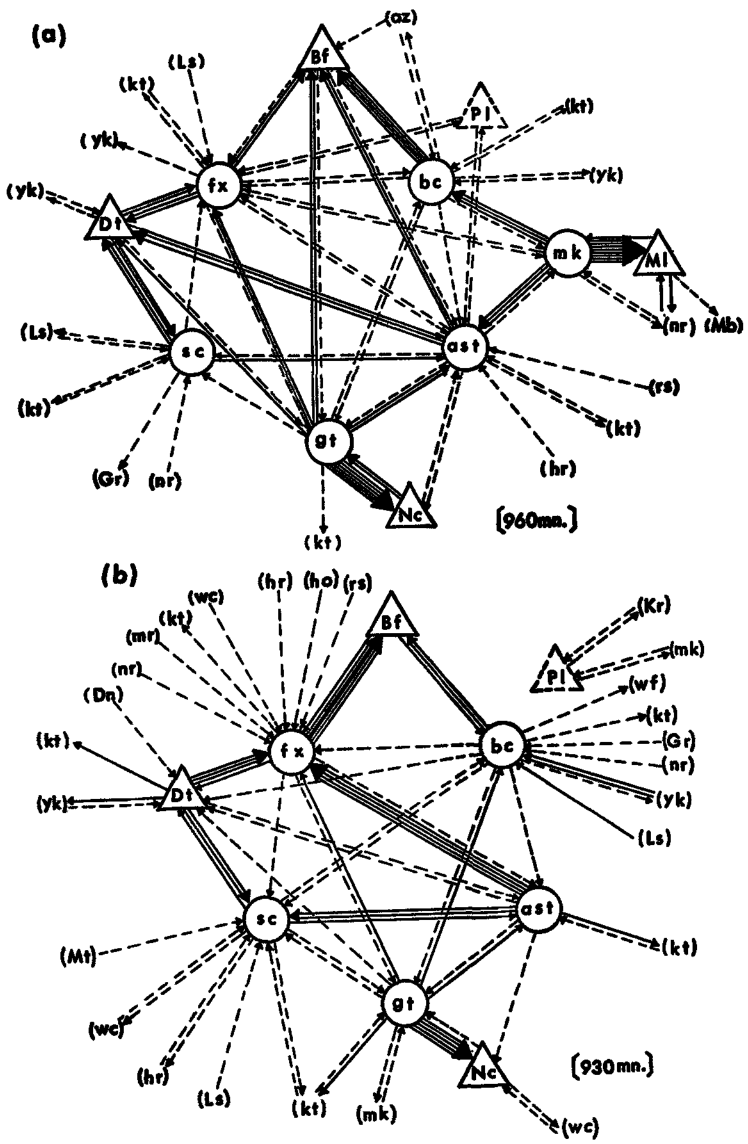


Fig. 7. Sociograms of *Bf*-MMG and *Ml*-PG for Period-I (a), and of only *Bf*-MMG for Period-II (b) based on the grooming interactions. Letters in the parentheses indicate the individuals outside *Bf*-MMG (a, b) or *Ml*-PG (a). See the notation of Fig. 6.

dryas one-male units grooming by females was concentrated on the unit leader and their own infants, very little being done among themselves. On the contrary, females of the one-male group often groomed one another, even in *Rb*-OMG, where the leader male showed the closest external appearance to that of hamadryas males. This point might suggest that the form of relationships among females in the Gorge group had been inherited from anubis society.

In *Rb*-OMG, 20.9% of the total grooming was spent in the interactions with females outside the subgroup, whereas grooming with non-members was only 3.0% in *St*-OMG. This high ratio of grooming with non-members in *Rb*-OMG is mainly caused by one female (*az*), which had been a member of *Bf*-MMG and was adopted by *Rb* into his OMG in middle December. She often groomed the females of *Bf*-MMG even after she became a new member of *Rb*-OMG (see the next chapter). It is considered that under ordinary circumstances grooming with non-members is very rare in one-male groups.

Grooming Relationships in Multi-male Groups or in Pair Groups

The grooming relations during Period-I in both *Bf*-MMG and *Ml*-PG are shown in Figure 7a, whereas those during Period-II in *Bf*-MMG only are shown in Figure 7b. Each adult male of *Bf*-MMG has a tendency to have peculiarly close grooming relations with particular females. For example, *Bf*, $\alpha$-male of this subgroup, frequently interacted with *bc* and *fx*, but never with *sc*. As for the grooming relations among females, two of the five females, *sc* and *bc*, seem to occupy rather isolated positions in the relationship among females.

It is interesting that no grooming was observed among males, especially between *Dt* and *Pl* which were frequently observed to sit in proximity to each other (cf. Fig. 9). It is supposed that the mature males have a strong tendency to avoid direct bodily contact such as grooming with each other even if they tolerate one another's spatial proximity. A comparison between the two periods makes it evident that *fx* was the focus of grooming interactions in Period-II. The baby to which she gave birth on February 3 might have become the center of attention not only of other members of her subgroup but also of many females outside the subgroup. As is clearly shown in Figure 8, *kt* (adult female of *Gr*-MMG) was also groomed by various females of other subgroups frequently. This is also considered to be because her black baby which was born on November 27 attracted many females.

Comparing the grooming relations in pair groups or pair-links to each other, the feature common to all of five pairs (*Ml—mk* and *Nc—gt* in Fig. 7a; *Gr—kt*, *Mt—mr*, and *Ys—yk* in Fig. 8) can be noticed. That is, in pair groups or pair-links the grooming partner of the male is almost restricted to only one female, while this female often interacts with several, if not many, other females in addition to the partner male. Thus, for the male of a pair group or a pair-link the friendly interactions with the partner female almost occupy the whole of his social life, but, on the other hand, for the female relations with the partner male are not the whole, though the major part, of her social life.

In contrast with the females of the one-male group, females of the multi-male group or the pair group often interacted with various females outside their own subgroup.

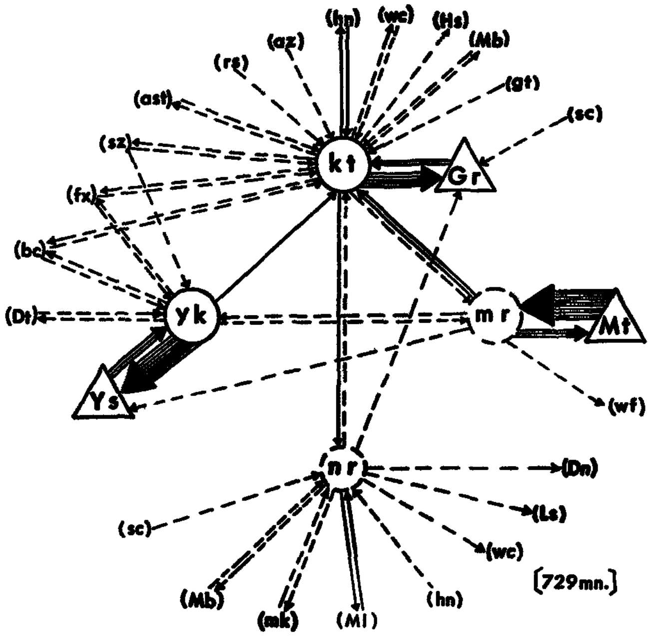


**Fig. 8.** Sociograms of *Gr*-MMG and *Ys*-PG based on the grooming interactions for Period-I. See the notations of Figs. 6 and 7.

Thus many females belonging to multi-male groups and pair groups were connected with each other by very variable grooming relations, even though their frequencies were rather low.

## Spacing Mechanism between Male and Female

In this section the spatial relations between males and females in each subgroup is examined and compared between each other in order to clarify the mechanism maintaining the integrity of each subgroup. Distances between all individuals, excluding juveniles and infants, which were present within a radius of 10 m from a certain male were recorded at every fifth minute when the baboons were resting in twos and threes under the shade of shrubs around the feeding site. In addition to this, all distances were recorded between centered male and the females which had obvious social bond with him, as far as they were found within the range of the observer's vision. By this method 12,171 inter-individual distances were obtained for 526 pairs throughout the study period.

### Profile of the Spatial Proximity between Individuals

The animals within 1 m were considered to be in proximity, and the similarities between any two individuals were calculated from the number of cases where they were in proximity. Thus an SLCA dendrogram on the data for Period-I was constructed in order that spatial relations within each subgroup, as well as between subgroups, might be visualized (Fig 9; cf. Figs. 4 & 5).

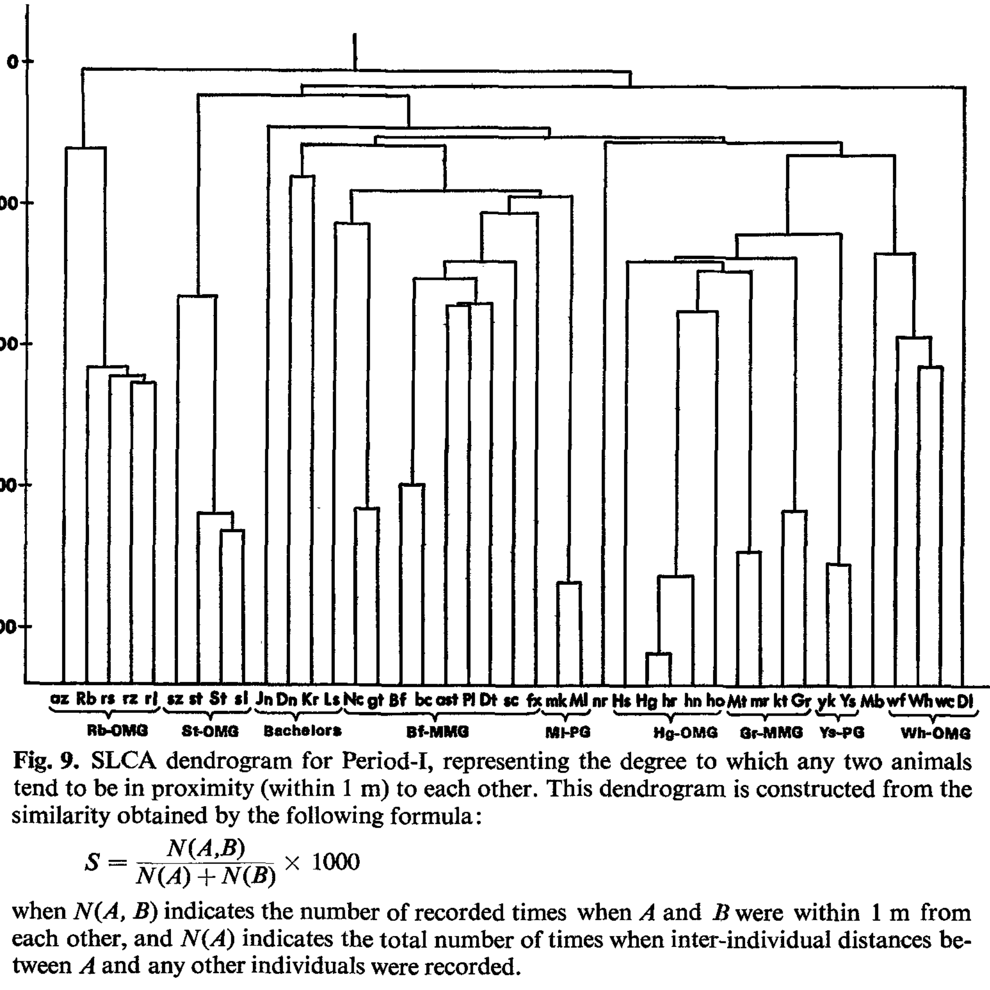


Fig. 9. SLCA dendrogram for Period-I, representing the degree to which any two animals tend to be in proximity (within 1 m) to each other. This dendrogram is constructed from the similarity obtained by the following formula:

$$S = \frac{N(A,B)}{N(A) + N(B)} \times 1000$$

when $N(A, B)$ indicates the number of recorded times when $A$ and $B$ were within 1 m from each other, and $N(A)$ indicates the total number of times when inter-individual distances between $A$ and any other individuals were recorded.

Each of three one-male groups (*Rb*, *St* and *Wh*-OMG) forms an independent cluster. Besides these three clusters, two large clusters can be distinguished, one of which includes *Bf*-MMG, *Ml*-PG, and one bachelor male (*Ls*) and the other includes *Hg*-OMG, *Gr*-MMG, and *Ys*-PG. Therefore spatial independence is a remarkable feature common to all one-male groups except *Hg*-OMG, which shows a strong tendency to be in proximity to the animals of *Gr*-MMG.

In *Bf*-MMG it should be noted that the pair-link of *Nc*—*gt* is isolated in this subgroup. *Ls*, a bachelor male, was frequently found in proximity to these two animals. As for the spatial positions of pair groups, *Ml*-PG is contained by the cluster formed by *Bf*-MMG while *Ys*-PG shows a tendency to be close to the cluster formed by *Hg*-OMG and *Gr*-MMG. This pattern of associations of pair groups with other subgroups is concordant with that found by the analysis of grooming relations.

The degree of spatial proximity showed by male-female pairs can be compared on the basis of similarity values. All pair groups and pair-links can be distinguished as the clusters obtained at a similarity greater than 310, at which level of all one-male groups only two clusters can be obtained, i.e., [*Hg, hn, hr*] and [*St, st, sl*]. Therefore it can be said that the spatial proximity between males and females in the pair group or the pair-link is more conspicuous than in the one-male group.

Behavioral Background

According to KUMMER (1968), in the one-male unit of hamadryas baboons the leader male makes threats, the most intense way of which being ritual neck-bite, toward the females when they get too far away from him. The female respond to such aggression by following the male closely. Thus such aggressive herding of females functions to maintain the one-male unit as a coherent spatial unit.

In the Gorge group typical neck-bites were observed in nine cases (12.5%) of 72 attacks addressed by males to females. Seven of these nine neck-bites were given by the leaders of one-male groups. However in *Rb*-OMG (containing the most females), *Rb* was never observed to give neck-bites to his females. Instead, he often stood and stared at one of his females, which was far away from him, with outstretched head. The usual reaction of the female was to run back to him with a grimace and a "staccato cough" (KUMMER, ibid.). It can not be determined whether or not the neck-bite is fixed genetically as the herding technique in the behavioral repertoire of the leaders of the one-male groups, but there is little doubt that aggressive herding in general is the important mechanism which maintains the spatial cohesion of one-male groups in the Gorge group.

Further evidence can be obtained from the progression order in the walking column which is formed when the one-male group descends the cliff or arrives at the watering place. The orders in 96 columns were completely recorded (Table 3). In both *Rb*-OMG and *St*-OMG it is very common for the leader male to walk at the head of the column ($p<0.001$). This demonstrates clearly that the spatial cohesion of the one-male group is primarily maintained by the response of females in following the leader male, and which is perhaps brought about by his aggression.

On the contrary, the mechanism maintaining the spatial cohesion of pair groups or pair-links differs very much from that in the case of one-male groups. The coordination of movements between a male and a female which had been sitting in proximity (within 1 m) to each other was recorded. In each of *Ml*-PG, *Ys*-PG, *Nc—gt*, and *Mt—mr* it was far more frequent that the female began to walk first and the male followed her (Table 4). It was evident from the general observations that the conspicuous spatial proximity between the male and the female of the pair groups or pair-links

**Table 3.** The position of the leader male observed in the progression order of each one-male group

| | 1st | 2nd | 3rd | 4th | 5th | Total |
|---|---|---|---|---|---|---|
| *Rb*-OMG | 30* | 17 | 2 | 0 | 0 | 49 |
| *St*-OMG | 14** | 4 | 0 | 2 | — | 20 |
| *Hg*-OMG | 4 | 10 | 5 | — | — | 19 |
| *Wh*-OMG | 1 | 7 | 0 | — | — | 8 |

1st: The head of the progression order; 2nd: The second position, etc. $*\chi^2 = 72.74$; $p<0.001$; $**\chi^2 = 23.20$; $p<0.001$.

**Table 4.** Coordination of movements between male and female in each subgroup

| Subgroup | Interaction | n | % | N |
|---|---|---|---|---|
| One-male group | *Rb*-OMG | | | |
| | *Rb*→F | 18 | 24.3 | 74 |
| | F→*Rb* | 56 | 75.7 | |
| | *St*-OMG | | | |
| | *St*→F | 11 | 28.2 | 39 |
| | F→*St* | 28 | 71.8 | |
| | *Hg*-OMG | | | |
| | *Hg*→F | 33 | 55.0 | 60 |
| | F→*Hg* | 27 | 45.0 | |
| | *Wh*-OMG | | | |
| | *Wh*→F | 23 | 53.5 | 43 |
| | F→*Wh* | 20 | 46.5 | |
| Pair group | *Ml*-PG | | | |
| | *Ml*→*mk* | 28 | 93.3 | 30 |
| | *mk*→*Ml* | 2 | 6.7 | |
| | *Ys*-PG | | | |
| | *Ys*→*yk* | 14 | 100.0 | 14 |
| | *yk*→*Ys* | 0 | 0 | |
| Pair-links | *Mt*—*mr* | | | |
| | *Mt*→*mr* | 69 | 94.5 | 73 |
| | *mr*→*Mt* | 4 | 5.5 | |
| | *Nc*—*gt* | | | |
| | *Nc*→*gt* | 28 | 92.9 | 28 |
| | *gt*→*Nc* | 2 | 7.1 | |
| | *Gr*—*kt* | | | |
| | *Gr*→*kt* | 12 | 52.2 | 23 |
| | *kt*→*Gr* | 11 | 47.8 | |

The symbol '*Rb*→F' indicates that *Rb* followed one of the females of his one-male group. The symbol '*Ml*→*mk*' indicates that *Ml* (male) followed *mk* (female), etc.

primarily resulted from the one-sided effort of the male to follow the female thoroughly and persistently.

Distribution of Inter-individual Distances between Male and Female

In Figure 10 distributions of inter-individual distances are shown between seven males and females for which they had a stable social relationship. The females in the closest proximity to each male were chosen. But in the one-male groups the distances between the male and the most centrifugal female are shown in the same graph. In *Bf*-MMG because *bc* was the closest female to *Bf* for Period-I and *fx* was the closest for Period-II, inter-individual distances for both pairs are shown.

In the one-male group the percentage of time spent by the centripetal female at any particular distance from the leader male decreases as the distance increases, so that the inter-individual distances between them only rarely exceed 5 m (1.8% for *Rb*—*rz* and 8.6% for *St*—*sl*). On the other hand the centrifugal female does not spend a similar amount of time at close distances, spending more time at longer distances from the male. But it is very rare that the distances between them exceed 20 m (0.9% for *Rb*—*az* and 2.6% for *St*—*sz*).

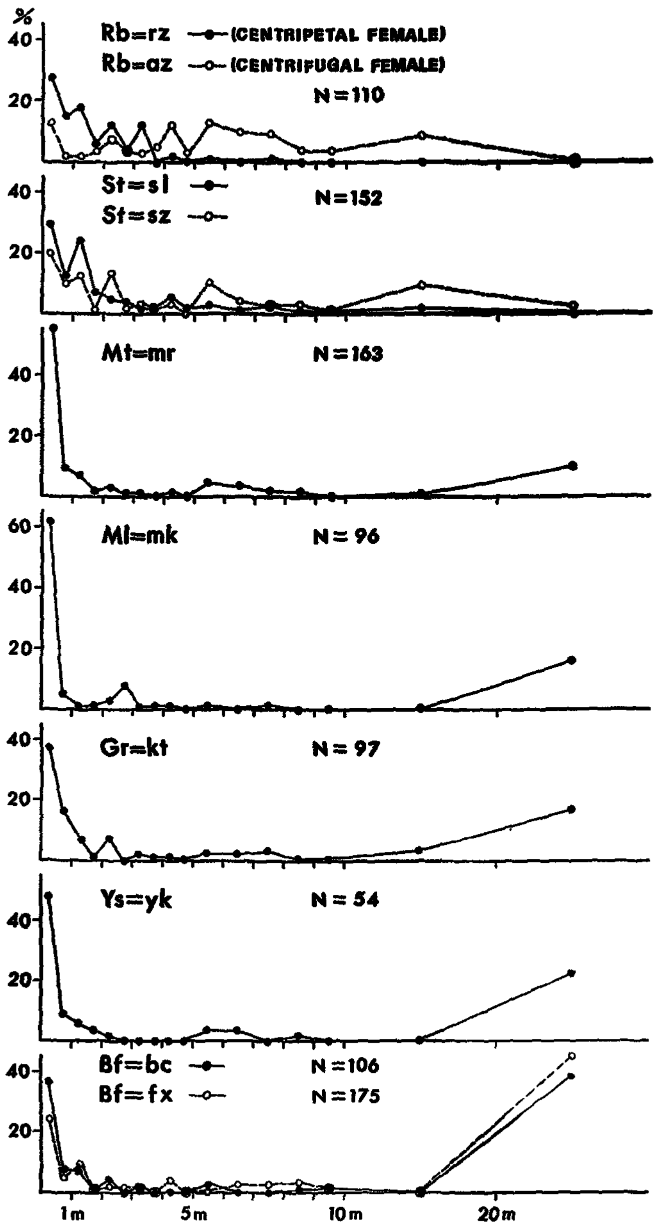


**Fig. 10.** Distribution of inter-individual distances between males and females that have stable social bond each other.

On the contrary, each of the distribution curves in the pair groups or pair-links shows a conspicuous upright pattern at the extremely short distances of less than 0.4 m. However, the long distances of more than 20 m at the tail of the curve are more frequent than in pairs in the one-male groups. Long distances between male and female are most frequent in pairs in the multi-male group. In the resting situation even the females in the closest proximity to *Bf* were present with the frequency of about 40% or more at such a great distance from *Bf* that they could not have direct social interactions with him.

Thus the inter-individual distances between male and female are very flexible in the one-male group, but only rarely do they exceed a certain degree. On the other hand, the male and the female of the pair group or the pair-link are either extremely proximal to each other or at a great distance from each other. This difference may be attributed to the fact that whereas the spatial proximity in the one-male group is supported by the mutuality between male and female, in the pair group it is maintained by the one-sided following by the male of the female. Under ordinary circumstances the male of the pair group or pair-link can maintain extreme spatial proximity to one female by following her persistently. But the female scarcely follows her male because he does not force her to be close to him by aggression. The female therefore has the potential to space out greatly from the male, which would come into effect whenever the following activity of the male is suspended or obstructed under other conditions. It is not until the female spontaneously follows the male that the truly stable association between male and female comes into existence. If this is true, the extremes of spatial proximity found in the pair group or the pair-link might be, in a sense, a manifestation of the fragility of these associations.

## SEXUAL RELATIONS AND SOCIAL CHANGES

### MALE-FEMALE MOUNTING

Four hundred and thirty-three cases of male-female mounting were observed in 38 different male-female pairs throughout the study period. Ejaculations were discerned to occur in 43 cases (9.9%) of these mountings (Table 5). The female partners showed perineal swellings in 336 cases (77.6%). As for the choice of the partner, 280 cases (64.7%) occurred in 22 pairs of male and female belonging to the same subgroup. One hundred and thirteen cases occurred in two pair-links (*Ml—hr* and *Ys—mr*) which were newly formed as the result of sudden social changes in Period-II. On the other hand 32 cases (in eight pairs) were observed in occasional copulations between males and females belonging to different subgroups from each other. From this brief sketch the following three points should be noticed: 1) Almost 80% of male-female mountings observed in the Gorge group can be regarded as sexual behavior; 2) Nearly 90% of all mountings, excluding those observed in newly formed pair-links, occurred 'within' the subgroups; and 3) If there were sudden changes in male-female associations, intensive sexual behavior would occur between the males and the females which formed new associations.

### SEXUAL RELATIONS AND SOCIAL CHANGES AMONG THE ONE-MALE GROUPS

#### Female Transfers

Figure 11 shows the estrous cycles, copulations with outsiders and transfers of all females over adolescence, excluding those of *Bf*-MMG, in the Gorge group. In *Rb*-OMG the black baby of *rm* died on November 24. After two weeks, on December 8,

**Table 5.** The number of episodes of male-female mounting

| Male addresser | Female addressee | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *rm* | *rz* | *rs* | *rl* | *az* | *sz* | *st* | *sl* | *hn* | *hr* | *ho* | *wf* | *wc* | *mk* | *yk* | *kt* | *mr* | *nr* | *ast* | *bc* | *fx* | *sc* | *gt* | Total |
| *Rb* | 1 | 7 | 5 | 19(2) | 3(1) | | 2 | | | | | | | | | | | | | | | | | 37(3) |
| *St* | | | | | | 10(2) | 10(1) | 6 | | | | | | | | | | | | | | | 1 | 27(3) |
| *Hg* | | | | | | | | | 13(1) | 3 | | | | | | | | | | | | | 1 | 17(1) |
| *Wh* | | | | | | | | | | | | 42(5) | 26(1) | | | | | | | | | | | 68(6) |
| *Ml* | | | | | | | | | | 96(3) | | | | 5 | | | | | | | 2 | | | 103(3) |
| *Ys* | | | | | | | | | | | | | | | 9 | | 17(3) | | | | | | | 26(3) |
| *Gr* | | | | | | | | | | 2(2) | | | | | | 1 | | | | | | | | 3(2) |
| *Mt* | | | | | | | | | | | | | | | | | 51(5) | | | | | 1 | | 52(5) |
| *Bf* | | | | | | | | | | | | | | | | | | | 2 | 32(3) | 4 | | 2(1) | 40(4) |
| *Dt* | | | | | | | | | | | | | | | 1 | | | | | | | 5 | | 6 |
| *Nc* | | | | | | | | | | | | | | | | | | | | | | | 24(5) | 24(5) |
| *Ls* | | | | | | | | | | 1 | | 7(1) | | | | | | | | | | | | 8(1) |
| *Mb* | | | | | | | | | | | | 15(6) | | | | | | | | | | | | 15(6) |
| *Pl* | | | | | | | | | | | | | | | | | 3(1) | | | | | | | 3(1) |
| *Dl* | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Dn* | | | | | | | | | | | 2 | | | | | | | | | | | | | 2 |
| *Hs* | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| *Kr* | | | | | | | | | | | | 1 | | | | | 1 | | | | | | | 2 |
| *Jn* | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| Total | 1 | 7 | 5 | 19 | 3 | 10 | 12 | 6 | 13 | 102 | 2 | 65 | 26 | 5 | 10 | 1 | 72 | 0 | 2 | 32 | 6 | 6 | 28 | 433(43) |

Figures in the parentheses indicate the cases where the ejaculations were observed.

*rm* also disappeared from the Gorge group. Because *rm* was a young and healthy female, it is unlikely that she had died. It is more probable that *Rb*-OMG encountered a party of the Kerrayu group when it alone was on the nomadic route downstream from Site-II (cf. Fig. 3b) and was probably deprived of *rm* through an ensuing fight. Just on that day when *rm* disappeared *Rb* began to approach or stare at *az*, which had belonged to *Bf*-MMG, and *az* responded to these displays from *Rb* by following him. Since then for ten days *az* had an unstable position, interacting frequently with members of both *Bf*-MMG and *Rb*-OMG. But after December 18 she was always in company with *Rb*-OMG, though she sometimes had grooming interactions with the females of other subgroups (Fig. 6).

The appearance of a new female was also observed in *St*-OMG. On December

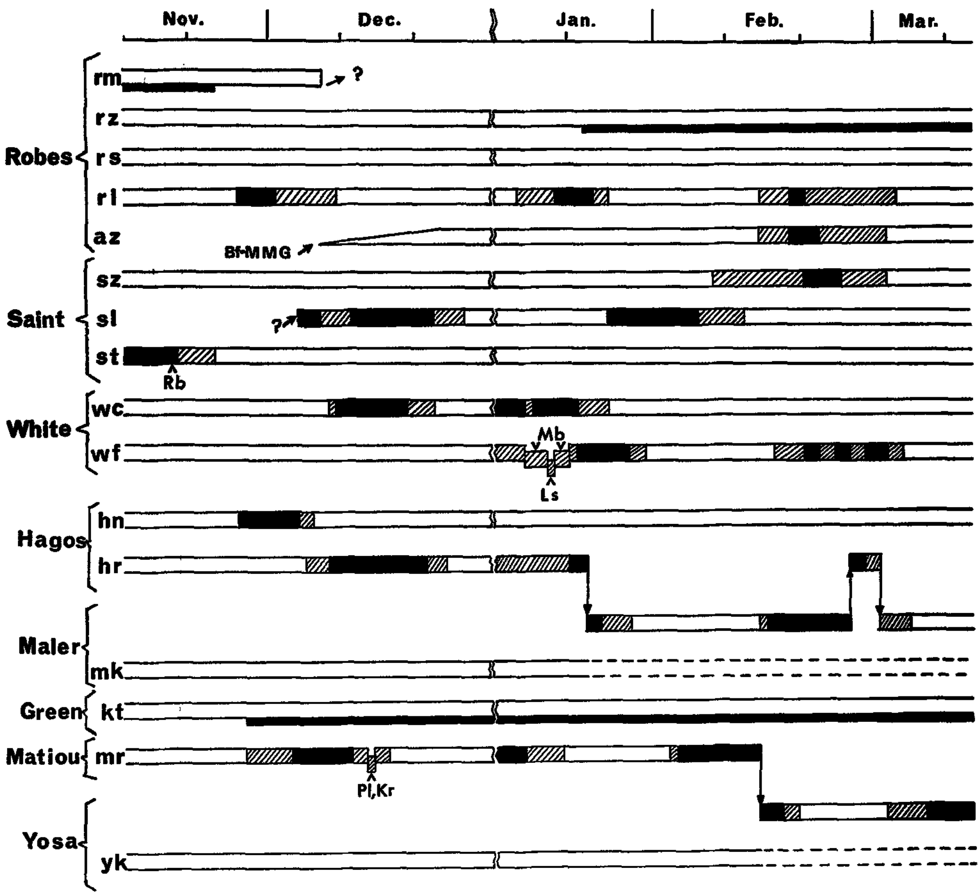


**Fig. 11.** Estrous cycles, transfers, and occasional copulations with outsider males in all adult and adolescent females, excluding those of *Bf*-MMG. Temporary consort relationships of the females with the outsiders are represented by small sections of the bar. Occasional mountings observed between each female and outsider males are represented by wedges (>). Female transfers between subgroups are represented by the shift of the bar. Black, dark, and white bars represent the stages of maximum swelling, half swelling, and the anoestrous states, respectively. Black thin bars represent black infants.

5 a new female, which had never been observed at that time, with maximum perineal swelling was found in the traveling column of *St*-OMG (Fig. 11). This female (*sl*) remained a member of *St*-OMG right up to the end of the study period. It is supposed that she had probably immigrated from another unit group into the Gorge group.

### Occasional Copulations of Females with Outsiders

Two cases of occasional copulations of the females of the one-male group with outsiders were observed: 1) November 18: *Rb* twice successively mounted an adult female of *St*-OMG (*st*) which was at the height of perineal swelling. 2) January 16–20: The old female of *Wh*-OMG (*wf*) showing a partial swelling frequently copulated with an adult bachelor male (*Mb*) which was the most submissive of all adult males. Another adult bachelor male (*Ls*) copulated with her intensively on only January 18. During this period *Wh* frequently copulated with another female (*wc*) of his one-male group which was at the peak of estrus, and he was usually at a distance of more than 30 m from *wf*. The intrusion by *Wh* upon copulations between *Mb* and *wf* was never observed, even when they copulated within sight of *Wh*.

Including the case of *Hg*-OMG which will be described in the following section, it can be said that in all four one-male groups either secessions of females from their original subgroups or occasional copulations of them with outsiders occurred. This fact suggests that in the Gorge group even the males with the closest appearance to the hamadryas male are lacking enough herding technique to persistently keep the females. On the other hand, it is clearly shown in Table 6 that all adult females, except *wf*, in one-male groups presented to only their own leader males. Thus adult females in the one-male groups usually bind their attention exclusively with the leader male (Chance, 1967). Moreover the leader male of the one-male group was able to 'herd' and absorb the females into his group from the multi-male group where the bonding between male and female was not so exclusive, as was shown in the case of *az*. Therefore the one-male groups in the Gorge group are always exposed to the possibility of destruction because of the incompleteness of the herding technique of the leader males, but, on the other hand, a vacancy of females can be filled up by rallying other females which have had no stable exclusive bonding with males.

## Sudden Change of Male-female Association in Pair-groups or Pair-links

In this section we will examine the alteration of sexual relations of six females belonging to *Hg*-OMG, *Ml*-PG, *Ys*-PG, and *Gr*-MMG (Fig. 11). The most remarkable social change occurred between *Hg*-OMG and *Ml*-PG.

On January 23, *Ml* abruptly began to follow the adolescent female of *Hg*-OMG (*hr*) which was at the peak of estrus, and frequently copulated with her. On January 24, *hr* was in proximity to *Hg*, a consort relation between *hr* and *Ml* being absent. From January 25 there arose again the close association between *Ml* and *hr*, which continued until February 27. On February 27 temporary copulations were observed to occur between *hr* and *Gr*. On the following evening severe fights were observed among males such as *Hg*, *Bf*, *Ls*, and *Mt*, resulting in the restoration of the close association between *Hg* and *hr* which continued only for three days. After that *Ml* followed *hr*, and the pair-link between them was formed for the third time and continued until the end of the study period.

**Table 6.** The number of episodes of the presenting behavior addressed by females to males

| Female | Male addressee | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| addresser | *Rb* | *St* | *Hg* | *Wh* | *Ml* | *Ys* | *Gr* | *Mt* | *Bf* | *Dt* | *Nc* | *Ls* | *Mb* | *Pl* | *Dl* | *Dn* | *Hs* | *Kr* | *Jn* | Total |
| *rm* | 3 | | | | | | | | | | | | | | | | | | | 3 |
| *rz* | 12 | | | | | | | | | | | | | | | | | | | 12 |
| *rs* | 8 | | | | | | | | | | | | | | | | | | | 8 |
| *rl* | 5 | | | | | | | | | | | | | | | | | | | 5 |
| *az* | 11 | | | | | | | | | | | | | | | | | | | 11 |
| *sz* | | 11 | | | | | | | | | | | | | | | | | | 11 |
| *st* | | 14 | | | | | | | | | | | | | | | | | | 14 |
| *sl* | | 7 | | | | | | | | | | | | | | | | | | 7 |
| *hn* | | | 7 | | | | | | | | | | | | | | | | | 7 |
| *hr* | | | 4 | 5 | 10 | 6 | 4 | | 6 | 12 | 2 | 11 | 2 | 3 | | 1 | | | | 66 |
| *ho* | | | | 2 | 2 | 3 | | | | | | | | | | 1 | | | | 8 |
| *wf* | | | | 2 | | | | | | | | 1 | | | | | | | | 3 |
| *wc* | | | | 6 | | | | | | | | | | | | | | | | 6 |
| *mk* | | | | 2 | 3 | | | | | | | | | | | | | | | 5 |
| *yk* | | | | | | 5 | 1 | | 1 | | | | | | | | | | | 7 |
| *kt* | | | | | | 1 | | | | | | | | | | | | | | 1 |
| *mr* | | | | | 3 | 19 | 15 | 15 | 1 | 9 | | 21 | 1 | | | | 3 | | | 87 |
| *nr* | | | | 2 | | 3 | | 1 | | | | 2 | | | | | | | | 8 |
| *ast* | | | | | | | | | 2 | 2 | 1 | | | | | | | | | 5 |
| *bc* | | | | | | | 1 | | 21 | 4 | | | 1 | | | | | | | 27 |
| *fx* | | | | | 1 | | | | 1 | 1 | | 1 | 1 | | | | | | | 5 |
| *sc* | | | | 1 | | | 2 | 1 | 4 | 7 | 2 | 2 | 2 | | | | | | | 21 |
| *gt* | | 1 | | | | | | | 5 | 1 | 4 | | | | | | | | | 11 |
| Total | 39 | 33 | 11 | 20 | 19 | 37 | 23 | 17 | 41 | 36 | 9 | 38 | 7 | 3 | 0 | 2 | 3 | 0 | 0 | 338 |

The females are arranged in the column, and the males in the row.

Another instance of a sudden change of a male-female association occurred between *Ys*-PG and *Mt—mr*.

On February 15, *Ys* suddenly began to follow *mr* which was at the peak of the estrus and copulated with her intensively. This new association between *Ys* and *mr* continued until the end of the study period. After the pair-link between *Ys* and *mr* was formed, *Mt* avoided *mr* and moved away from her whenever she approached him, so that affinitive social interactions between them completely vanished.

First point to be noticed is that such sudden changes in male-female associations occurred when the female was at the peak of estrus. Second point is that both *hr* and *mr* were adolescent females which were just reaching sexual maturity. As these two females showed sexual swellings repeatedly in a short cycle, their sexual activity was supposed to be greatly heightened. This supposition is supported by the fact that both of them presented very frequently to various males (Table 6). In sum young females which have not yet had a first pregnancy are in estrus repeatedly during a short period, tending to be highly receptive to every male during this period of turgescence. Such high sexual receptiveness of young females would prompt the new males to follow them.

On the contrary, the bond between a male and a fully mature female is believed to be stable even during a rather long anoestrous period of females, i.e., gestation plus lactation, supposed to be about 16 months in anubis baboons (PACKER, 1977). For instance, the pair-link of *Gr—kt* continued throughout the study period. The female, *kt*, was supposed to have been sexually inactive not only during the study period but since about half a year before, because she gave birth to a baby on November 27. Indeed, throughout the study period the author observed only one case where *kt* was mounted by the male and in this case the mounter was the partner male, *Gr*.

Comparing the grooming network of *mk* during Period-I with that of Period-II, an interesting point will be noticed (Fig. 12; cf. Fig. 7a). During Period-I, *mk* had fre-

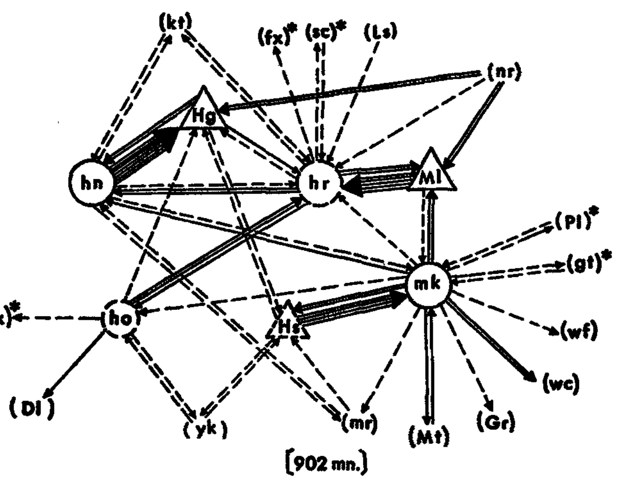


**Fig. 12.** Sociograms of *Ml*-PG and *Hg*-OMG based on the grooming interactions for Period-II. Letters in the starred parentheses indicate the members of the B-cluster. See the notations of Figs. 6 and 7.

quent grooming interactions with the females of *Bf*-MMG in the B-cluster, whereas during Period-II such interactions were rarely observed and, instead, grooming interactions with the individuals of the G-cluster were frequently observed. In other words, as *Ml* began to follow *hr* and shifted his social position from the B-culster to the G-cluster, the partners in affinitive relations of *mk* were transferred to the members of the G-cluster. From this comparison a hypothesis can be drawn that the persistent following by a male of a female can arouse a tendency to remain close to the male on the female's side.

## SOCIAL RELATIONSHIPS AMONG MALES

### DOMINANCE-SUBORDINATION RELATIONSHIPS AMONG MALES

In order to investigate the dominance-subordination relationships among males, the author intensively recorded antagonistic interactions where one male attacked another in a one-sided manner or where one displaced another concerning food or a preferable location. Four hundred and fifteen cases of one-sided attack or displacement were obtained. As it was rare for the young males and one adult male (*Mb*) to participate in one-sided attack or displacement, the dominance relationships among 12 adult males, excluding *Mb*, are examined.

Were there no dominance relationship between two animals, A and B, and were it decided at random in every interaction which of them became the addresser of attack or displacement, the probability that A became the addresser more than $r$ times out of $n$ interactions can be obtained by the following formula:

$$p = \sum_{i=r}^{n} {}_nC_i \left(\frac{1}{2}\right)^n$$

when $p$ is small enough it can be judged that A is dominant to B. Accordingly this $p$

| | Rb | Wh | St | Hg | Bf | Ml | Ys | Nc | Ls | Dt | Gr | Mt |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rb | ＼ | △ | △ | ? | ? | ◉ | ◉ | ◉ | △ | △ | △ | ◎ |
| Wh | | ＼ | △ | x | ? | x | ○ | ○ | △ | ○ | △ | ◎ |
| St | | | ＼ | ◎ | ◎ | ◉ | ◎ | ◉ | △ | ◉ | △ | ◉ |
| Hg | | | | ＼ | △ | ○ | ○ | △ | △ | = | △ | ○ |
| Bf | | | | | ＼ | ◎ | △ | △ | ○ | ◉ | △ | ◎ |
| Ml | | | | | | ＼ | ◎ | ○ | x | ◎ | ○ | △ |
| Ys | | | | | | | ＼ | ◉ | ◉ | ◉ | ◉ | ◉ |
| Nc | | | | | | | | ＼ | △ | △ | ? | = |
| Ls | | | | | | | | | ＼ | ◎ | △ | △ |
| Dt | | | | | | | | | | ＼ | = | ◎ |
| Gr | | | | | | | | | | | ＼ | = |
| Mt | | | | | | | | | | | | ＼ |

Column>Row
◉ p≤0.01
◎ 0.01—0.10
○ 0.10—0.20
△ 0.20—0.50
= p>0.50
Row>Column
x 0.20—0.50

**Fig. 13.** Supposed dominance relationships for all combinations among 12 adult males. "Column>Row" indicates that the males arranged in the columns are supposed to be dominant to those arranged in the rows at respective significant levels.

was calculated for each of all combinations among 12 adult males and it was supposed that there might be a clear dominance relationship in the combinations for which $p$ is equal to or smaller than 0.20 (Fig. 13).

It was also clear that all of these 12 males were dominant to *Mb* and the two adolescent males (*Pl* and *Dl*), while the latter three animals were clearly dominant to four pubescent males. Consequently it can be concluded that the dominance relationships in the Gorge group are organized into a hierarchy (Fig. 14). As a rule all animals belonging to the upper level are dominant to each of those belonging to the lower one.

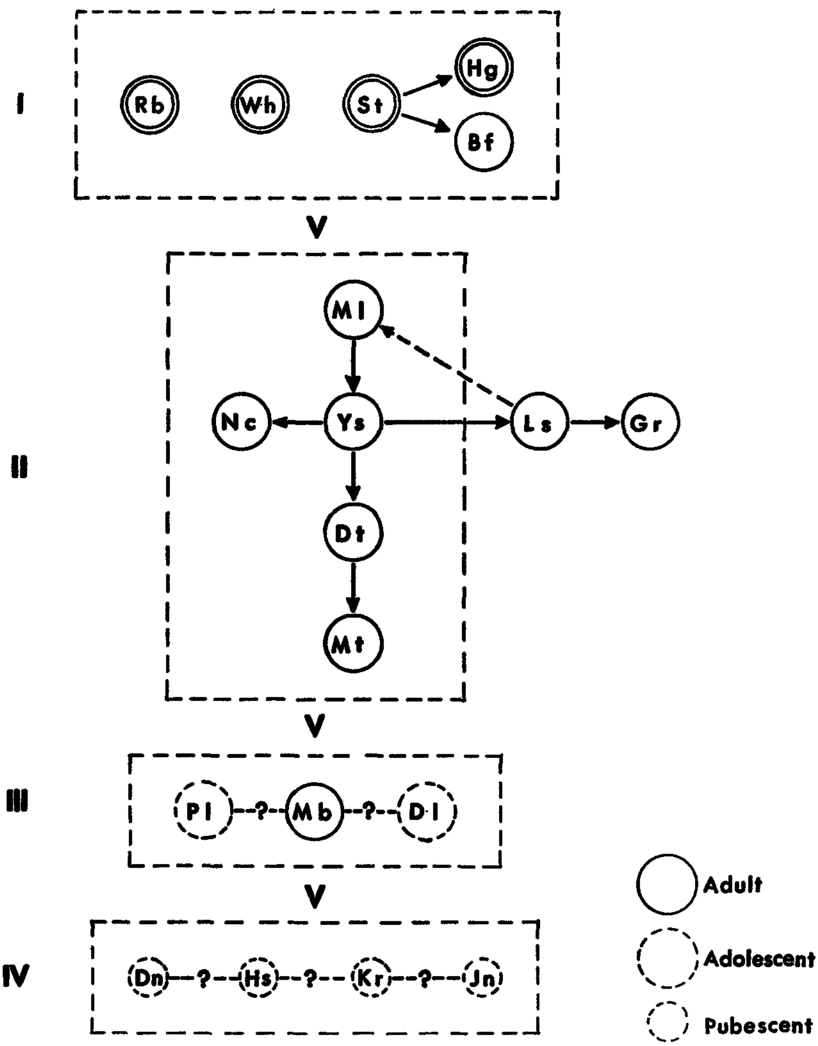


**Fig. 14.** Hypothetical dominance hierarchy among adult and subadult males in the Gorge group. "A→B→C" indicates that A is dominant to B and C, and B is dominant to C. The dominance relationship between A and C is ambiguous when a broken arrow issues from C to A. The broken rectangles represent dominance levels in this hierarchy. Doubled circles indicate the leader males of one-male groups.

However, an exception is the ambiguous dominance relationship between the animals of Level-I and *Ls* or *Gr* (Level-II). Similarly the relationship is ambiguous between *Wh* (Level-I) and *Ml* (Level-II).

It deserves attention that the uppermost level is occupied by the four leader males of the one-male groups, among which the dominance relationship is indistinct. Such indistinctness of dominance relations is assumed to be originally peculiar to the relationship among leader males of different one-male units in a hamadryas band. On the other hand, in the Level-II males can be arranged, though incompletely, into an almost linear dominance order. Thus an affinity can be recognized between the dominance relationship among these males and that of males in the anubis baboon society, where all males in the same troop can generally be arranged into a linear dominance order (PACKER, 1977).

### APPEASEMENT-DOMINANCE BEHAVIOR AMONG MALES

The social behavior among males, excluding obvious aggression, can be categorized into the following five types: 1) Turning behavior (TU): A approaches B, which has been sitting at a rather long distance (5–20 m) away, with a rapid step. As soon as A has come very close (0.5–1.0 m) to B, A turns abruptly and immediately begins to walk away more rapidly from B in the same direction as he came; 2) Presenting (PR); 3) Touching genitals (TG): A approaches B and grips B's penis or scrotum or touches his anal region; 4) Touching genitals mutually (TM): This interaction is initiated by the same behavior of A as was just mentioned under 3) above. As soon as A touches the genitals of B, B in turn touches the genital-anal region of A; and 5) Mounting (MT).

The behavior described under 1) can be considered to be the same kind of behavior as was observed among the unit-leaders of hamadryas baboons and was named "notifying behavior" by KUMMER (1968). In the Gorge group 84% of all cases (69 cases) observed were performed by the three leaders of the one-male groups. Moreover, this behavior was performed most frequently by *Rb* which had the closest appearance to a hamadryas male. Therefore, it can safely be considered that this behavior might be species-specific to hamadryas males.

In order to examine the correlation between the occurrence of these five types of behavior and the dominance relationship among males, the author categorized all cases of each behavior into the following three categories and calculated the percentage in each category for each respective behavior: (a) the cases where dominant males were the addresser; (b) the cases where subordinate males were the addresser; and (c) the cases where the dominance relationship between the participants was ambiguous. The expected percentage of each category can be obtained from the number of combinations among males on the basis of dominance relationships shown in Figure 14 (Table 7).

As there is no significant difference between observed and expected frequency in TM, it is highly probable that this behavior might occur independently of the dominance relationship among males. However, the occurrence of the other four types of behavior is probably influenced by dominance relations. That is, there is a strong tendency for MT and TU to be addressed by the dominant toward the subordinate,

**Table 7.** Dominance relationship between the addresser and the addressee of each social behavior observed among males

| Dominance | Expectation | MT | TU | TG | TM | PR |
|---|---|---|---|---|---|---|
| D → S | 40.35 | 73.3 | 59.4 | 39.3 | 32.5 | 24.3 |
| S → D | 40.35 | 11.1 | 10.1 | 30.3 | 43.6 | 50.5 |
| Ambiguous | 19.30 | 15.6 | 30.4 | 30.3 | 23.9 | 25.2 |
| Number of episodes | — | 45 | 69 | 145 | 117 | 107 |
| Significant level | — | 0.001 | 0.001 | 0.01 | ns | 0.01 |

'D → S' indicates the episodes in which each behavior was addressed by the dominant male toward the subordinate; 'S → D' indicates the reverse cases; 'Ambiguous' indicates that the dominance relationship between the addresser and the addressee could not be ascertained; Figures indicate the percentage of episodes corresponding to each of above categories; MT: mounting; TU: turning behavior; TG: touching genitals; TM: touching genitals mutually; PR: presenting.

while PR is most frequently addressed in the opposite direction. TG tends to occur among those males between which the dominance relationship is ambiguous.

Comparing the five types of behavior with each other, the percentages of the dominant addresser are arranged as follows: MT>TU>TG>TM>PR. On the contrary the percentages of the subordinate addresser are arranged as follows: PR>TM>TG>MT≑TU. It is likely that these types of behavior might be functioning as the appeasement or the dominance bahavior among males. The primary function of TU and MT especially can be considered to be a display of dominance, while that of PR is in appeasing the animals which are dominant to the addresser. TG and TM are characterized as behavior with ambivalent motivation.

In the group of chimpanzees NISHIDA (1970) recognized about eight types of one-sided greeting behavior including genital touching and mounting. He also pointed out that there was almost no apparent difference between appeasement and one-sided greeting behavior except the behavioral situation. If the term 'greeting' is used restrictively to describe the social behavior which occurs between two animals when they meet again after a certain period of separation, the appeasement-dominance behavior in the Gorge group can scarcely be labeled as the greeting behavior because the 'behavioral situation' in which each episode occurred was not so distinct. But in a society usually splitting up into several parties the appeasement-dominance behavior might have the function of easing the tension which would rise inevitably between powerful males when they happen to be together in the same party. If this is true, this behavior could be regarded as a kind of non-verbal communication which is rooted in a common base with the greeting behavior found in the chimpanzee society.

## DISCUSSION

Now let us compare the characteristics of the social organization of the Gorge group with those of anubis and hamadryas societies, and discuss how those characteristics have arisen through the hybridization between them.

According to ALDRICH-BLAKE et al. (1971), the troop of anubis baboons living on the riverside some 12 km upstream of the Awash Falls dispersed into small parties which are spatially and temporally independent for several hours during daily foraging, but in the evening these parties gather again into a group at the sleeping site every day. In the Gorge group, however, several parties often ranged on different nomadic routes from one another for many days. Therefore, the party formation of the former can be regarded as a temporary segmentation which arises accidentally through daily nomadism, whereas that of the latter is made possible by the stability and independence of each subgroup. Such stability and independence of each subgroup in the Gorge group can be regarded as being based on the character of hamadryas society.

But it is difficult to make a clear comparison between the grouping structure of the Gorge group and that of hamadryas band, because the actual organization of hamadryas band remains very vague. KUMMER (1968) found that several of foraging parties during the day were of stable size, and he called such parties band and concluded that they were stable components of the troop. But, as he states, there is no evidence for the assumption that "the bands appearing on route, during battle and during the break of camp are identical and remain constant over longer periods of time" (p. 106). If, as KUMMER's work suggests, the hamadryas band maintains its integration all day long and if there never occurs the joining and parting of one-male units in the same band, it can be said that the joining and parting of subgroups is a peculiar character to the Gorge group.

When we turn our attention to the inter-individual relationships within the Gorge group, we can notice again the mixture of anubis and hamadryas characters. In the Gorge group affinitive bonds were recognized among females within each subgroup. Moreover females often groomed one another even if they belonged to different subgroups. These features of the relationship among females of the Gorge group make a sharp contrast with those of the hamadryas society where no evidence of bonds among adult females was found within or between one-male units (KUMMER, ibid.). On the contrary, the absence of grooming interactions among adult males is common character to the relationship among males in the hamadryas society, where grooming is never observed among leaders of mature one-male units (KUMMER, ibid.). But it is pointed out that there is usually very little grooming between adult males also in savanna baboon societies (HANBY, 1975; PACKER, 1977).

In a troop of yellow baboons or of anubis baboons all males can be arranged in a single linear dominance order (HAUSFATER, 1975; PACKER, ibid.). The linear dominance order both among males and among females has been also recognized in the rhesus monkey and Japanese macaque (SADE, 1967; KAWAI, 1958). It can be supposed to be a general character of dominance relationships among males or females in multi-male troop of macaques and baboons. But this general character could not be found among males in the Gorge group. Rather, a hierarchy was recognized in the dominance relationship among males in the Gorge group. This phenomenon is closely connected with the grouping pattern of the Gorge group. Namely, in the society segmented into cohesive subgroups, like the Gorge group, such a stable relationship among males as was adequately called 'male cohort' (CHANCE, 1967) can hardly be formed, and it would be difficult for the linear dominance order to be fixed and recognized by all members. Concerning the dominance relationship among unit leaders of hamadryas troop, KUMMER (1968) wrote, "Dominance in the usual restricted meaning...can be assumed to exist among hamadryas males, but its manifestations in troop life are minimal..." (p. 153). In the Gorge group also the dominance relationship was particularly ambiguous among the leader males of one-male groups. Therefore it is supposed that the more stability or cohesiveness the subgroups or subunits in a group gain, the more ambiguous the dominance order among its members becomes.

NAGEL (1973) supposed that anubis baboons are generally dominant to hamadryas baboons because the former are heavier than the latter. However, it was shown in the Gorge group the leaders of the one-male groups, which had the closest appearance to hamadryas males, occupied the most dominant level in the hierarchy. What was the factor that permitted them to be dominant to other males? The herding technique of the hamadryas male is a specific way of manifesting aggression. It can be supposed that males closer to hamadryas could manifest aggression more effectively than anubis-like males also in the male-male interactions. Therefore, in contrast with NAGEL's supposition, it would be more well-grounded to suppose that hamadryas males can dominate anubis males by means of aggressive display.

We should elucidate the origin of the Gorge group, in order to interrelate intricate social characteristics of this group and comprehend them as a whole. It is very probable that the original form of the Gorge group might have been the anubis troop because anubis features were found to be prevalent both morphologically and genetically in this group. Hamadryas males or hybrid males which had the ability of herding females by aggression would have intruded into an original anubis troop to form one-male groups by herding anubis females and copulating with them. Thus hybridization began to occur and it produced hybrid offspring, some of which might have the same ability of herding females as their fathers had. NAGEL (1973) stated that the mating of hamadryas males with anubis females was never observed in anubis groups. But KAWAI and SUGAWARA (1976) observed that a male with hamadryas appearance frequently copulated with at least six estrous anubis females in the anubis troop, named Ittu troop, living 5 km upstream from the Awash Falls. This troop was proven to be composed of pure anubis baboons by genetical examination (SHOTAKE et al., 1977). The intrusion of hamadryas (or hybrid) males and their copulations with anubis females must have also occurred as the main cause of the hybridization of the Gorge group.

NAGEL also reported that the anubis troop (C1) which lived in the canyon separated at night into sleeping units of variable size and composition. He attributed this subgrouping pattern to the fact that this group used three well-separated sleeping cliffs in its home range. But it is difficult to think that the integrity of an anubis troop can be broken down to such a degree that the separation between subgroups continues day after day by only such an ecological condition as the number of sleeping sites. Therefore it is within the range of possibility that hybridization was already in process, slight as it was, in the anubis troop which was living in the canyon even when NAGEL observed it.

KUMMER et al. (1970) stated that the female's keeping close to an aggressor needs no particular genetic basis and that such a response can easily be learned by anubis females which know no herding behavior. In other words the difference between the basic social structure of hamadryas baboons and that of anubis baboons originates primarily in the difference of male's behavior between these two species. In the Gorge group, likewise, it would be the behavioral difference between males that gave rise to the structural difference between the subgroups. SHOTAKE et al. (ibid.) collected blood samples from 18 animals of the Gorge group and examined these by electrophoresis. These 18 animals consist of eight adult males (*Hg*, *Ml*, *Gr*, *Nc*, *Mt*, *Bf*, *Mb*, and *Ls*), two subadult males (*Dl* and *Kr*), one adult female (*ast*) and seven juveniles and infants. It was found that Tf (*Plasma transferin*) locus was the best genetic marker for discriminating between anubis and hamadryas. For this locus, only *Hg* and *Ml* were proven to have alleles originating from hamadryas baboons (SHOTAKE, pers. comm.). It is supposed that the leaders of one-male groups inherit the genetic basis of herding females by aggression from hamadryas baboons from the fact that one leader male (*Hg*) had alleles specific to hamadryas baboons. This supposition is further supported by the point that the four males having one-male groups are closer to hamadryas baboons in morphology than are other males.

It was elucidated that the male-female bond in the pair group or pair-link found in the Gorge group is based on the persistent effort of the male to follow the female continuously and to keep in proximity to her. The exclusive access of a male to his sexual consort is generally found in the society of savanna baboons and Japanese macaques (HALL et al., 1965; PACKER, 1977; TOKUDA, 1961). The peculiarity of the pair group or the pair-link of the Gorge proup consists in the fact that the interest of the male is not restricted to the sexual attractiveness of any female but is fixed on a specific female even in anoestrous state. We can assume that in the first step of the formation of stable subgroups among the one-level society the interest of males, having been oriented toward the sexual attractiveness of any female, becomes fixed on a specific female. Moreover it is probable that the persistent following behavior of a female by a male might be the simplest form of behavior which manifests the interest fixation on a specific individual.

KUMMER et al. (1970) assumed that the hamadryas pair-bond is not primarily based on the sexual motivation of males but on a hypothetical motivation which can be labeled "social possessiveness." By an examination of blood proteins *Ml*, an adult male of a pair group, was shown to have alleles originating from hamadryas baboons (SHOTAKE, pers. comm.). But it is not proven that the other four males (*Ys*, *Mt*, *Gr*, and *Nc*), each of which has a pair bond with a specific female, have alleles originating from hamadryas. So there is no certain evidence that these males genetically inherit the motivation of "social possessiveness" from hamadryas baboons. But there remains the possibility that in any one-level society of primates an appropriate social environment might prompt some individuals to fix their interest persistently on other individuals. Furthermore such an attitude of 'interest-fixation-on-a-specific-other' could be learned and acquired by individuals of the succeeding generation. Discussing the precultural variation of possessive behavior among primate societies, KUMMER (1973, p. 230) wrote that, "seeing adults interact intensely with a class of objests could orient the interest and possessive motivation toward such objects in the onlooking juveniles...." Likewise, the possessiveness toward females shown by hamadryas or hybrid males which had intruded into an original anubis troop must have influenced the juvenile males of this troop and have prompted them to orient their possessive motivation toward females. It would be difficult for the juveniles which had no genetic basis to imitate the herding behavior, but it would be possible for them to introduce into their personality an attitude of interest-fixation-on-a-specific-female which forms the basis of the herding behavior of hamadryas males.

One of the most important characteristics of the Gorge group is that the transfer of females into another unit group might be occurring. The possible phenomenon of females transfer suggests that close consanguineous ties among females may have been loosed by subgroup formation in this group. Moreover in the Gorge group the control of males over females is not complete enough to prevent them from scattering. If these social characters are common to all hybrid groups in the Awash Valley, it is very probable that female transfers might widely occur among hybrid groups. In order to corroborate this argument, further investigation is required, including individual identification of the neighboring groups.

Female transfers were ascertained to occur among subgroups in the Gorge group. We can presume that there are three directions of the transfer of females: from MMG to OMG, from MMG to PG, and from OMG to PG. No female transfer was observed from PG to OMG but it can probably occur in this direction. As the social bond between male and female is not so exclusive in the multi-male group, its males are liable to be deprived of females by males which have stronger tendencies to possess them. KUMMER et al. (1974) assumed that the hamadryas pair bond between male and female is protected by a pair gestalt inhibiting the competitor's interactions when the two are together. The effective gestalt consists of spatial proximity and tactile interaction between subject and object. In the Gorge group 'proximity' and 'interaction' were also clearly found between a male and a female of pair groups or pair-links. But no evidence of an inhibitory mechanism of pair gestalt could be found in the author's study. In order to understand the life cycle of the one-male units of hamadryas, it would be more proper to suppose that the transfer of adult females sometimes occurs among hamadryas one-male units rather than to consider that each one-male unit is strictly protected by the pair gestalt inhibition.

The last and the most important problem is whether the idiosyncratic structure of the Gorge group will be maintained for a long time or not. If hybridization between two species has produced hybrid groups which have a different social structure from either of the parental species, the following three conditions are indispensable for the maintenance of such a unique structure: 1) The reproductive success of hybrid animals is not inferior to that of the animals of the original species; 2) The organization of hybrid groups is stable for a long time and has a high adaptive value; and 3) The hybridization rate in these groups undergoes little change.

In early November when the intensive observation of the Gorge group was begun, there were two black infants both of which were estimated under one-month-old. Assuming that no other baby was born and dead during October, six infants were born in the Gorge group during a total of 3,097 female-days from beginning of October to March 11. This gives a reproductive rate of $1.937 \times 10^{-3}$ births per female per day. This rate is much higher than the value ($1.513 \times 10^{-3}$) estimated by ALTMANN and ALTMANN (1970) for the yellow baboons of Amboseli. Therefore it cannot be thought that hybridization has had an unfavorable effect on the reproductive success in the Gorge group population. That is, in the Gorge group the condition under 1) is thought to be satisfied. It remains to be elucidated by a further longer field study whether the conditions under 2) or 3) are satisfied in this group. For the present, the following point should be noted. The social organization of the Gorge group contains several factors which might cause instability in this group, but they are not necessarily maladaptive. For example, the grouping pattern of the Gorge group, i.e., joining and parting of subgroups, is the most distinct sign of the disintegration of this group, but at the same time, this grouping pattern might be the most effective way not only to moderate the social conflicts among males which have various behavioral tendencies and different types of bonds with females, but also to enable the animals of this group to scatter and exploit a wide range in their habitat.

## SUMMARY

A group of hybrid baboons between *Papio anubis* and *P. hamadryas* was studied for about 400 hours in the Awash Valley, Ethiopia. Morphologically, anubis features were prevalent in this group, but four males with closer appearances to hamadryas had respectively one-male groups. Other than these, two pair groups and two multi-male groups could be distinguished as the subgroups with the stable membership. This group often splitted into several parties, without stable membership, which repeatedly joined and parted each other. There were affinitive bonds among females within or between subgroups, while no grooming was observed among adult males. The spatial cohesion of the one-male group was maintained by the response of females in following the leader male, which was brought about by aggressive threats by the leader toward them. Whereas that of the pair group or pair-link in the multi-male group was maintained by one-sided following by the male of the female. Linear dominance order could not be recognized among males. Rather, dominance relationship among them was organized into a hierarchy, where leaders of one-male groups occupied the uppermost level. It was concluded that this group had originated from an anubis troop. The hybridization of this original anubis troop was probably caused by the intrusion of hamadryas or hybrid males and their copulations with anubis females in it.

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Author's Address: KAZUYOSHI SUGAWARA, *Primate Research Institute, Kyoto University, Kanrin, Inuyama, Aichi, 484 Japan.*