

## Characteristics of the Social Life of Bonnet Macaques (*Macaca radiata*)

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**ABSTRACT.** The social behavior of wild bonnet macaques impresses upon us a peculiarity and uniqueness which is different from other macaques. Although there is a clear-cut ranking relationship among adult males and they carry out their proper social roles according to each situation, many social behaviors are carried out independently of or ignoring the ranking order. The animals are organized in a flexible and tolerant social unit, but they don't abandon the advantages of group life.

The uniqueness of bonnet behavior and society is recognized to be related to the highly developed individuality of this species.

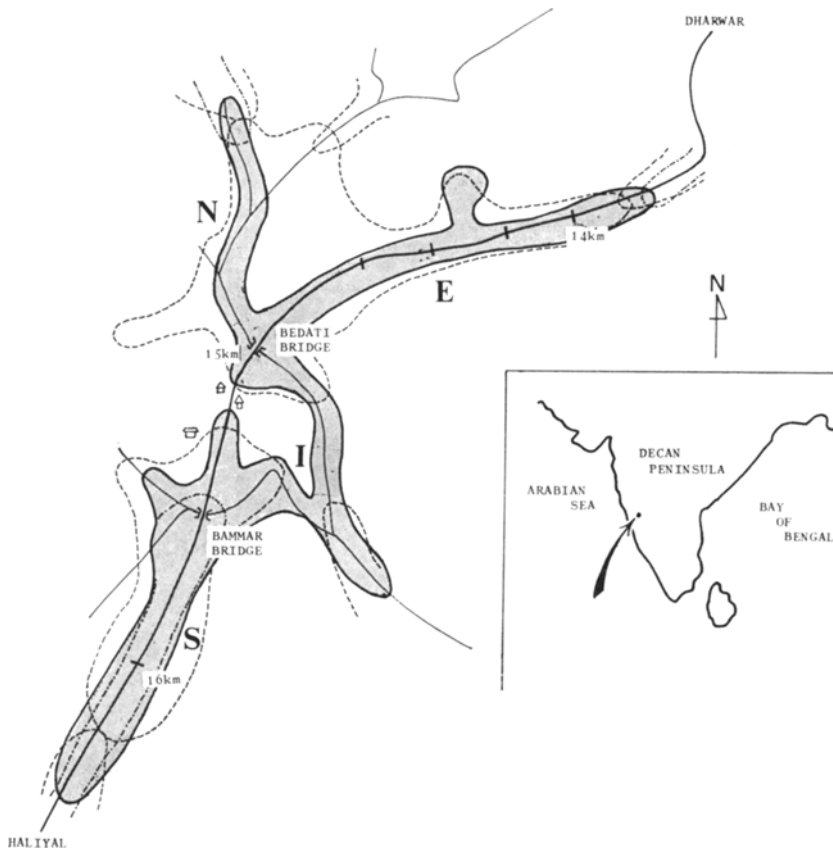
### INTRODUCTION

The bonnet macaque (*Macaca radiata*) is a small macaque weighing about 8 kg in the adult male and about 5 kg in the adult female. Its geographical distribution covers the southern half of the Indian Peninsula, from the evergreen forest of the Western Ghat Mts. to the dry area of the Decan Plateau. It is a highly adaptive species, coexisting with the lion-tailed macaque (*M. silenus*) in the evergreen high forest of the South-Indian high range and with the hanuman langur (*Presbytis entellus*) in the dry deciduous forest of the Western Ghat Mts. (SUGIYAMA, 1964, 1968).

Study of the ecology and sociology of this species was begun by NOLTE (1955) and was intensified by SIMONDS (1965) and RAHMAN and PARTHASARATHY (1967, 1968, 1969ab). My first impression of the behavior and social organization of a wild bonnet troop was that they were peculiar and unique among macaques, but it seems that the characteristics of the social life of this species have not yet been clarified. The present paper is an attempt to clarify them.

The field work on which this paper is based was a part of the Japan-India Joint Project in Primate Investigation, which was carried out at Dharwar, South India, between April, 1961 and April, 1963. As the main purpose of this Project was the ecological and sociological study of the hanuman langur, which lives in the same area as the bonnet, the data on the latter species is not sufficient and the main work for this paper was gathered only between March and September, 1962.

The main study area (Fig. 1) lies about 15 km west of Dharwar (15.5N°, 75E°), on the Dharwar-Haliyal road; Dharwar is about 500 km north of other scientists' study fields. The common vegetation of this area is dry deciduous forest, with a rainfall of less than 1000 mm a year. The main troop for the study, named 'D,' had, as its base



**Fig. 1.** Study area. The chain shows the home-ranges of bonnet macaque troops, the shaded area showing the home-range of troop D while N, E, I, and S indicate its parts; the broken line shows the home-ranges of the hanuman langur troop. Figures on the map show the distances from Dharwar.

of daily life, the evergreen roadside trees and gallery forest which were surrounded by cultivated fields. The rainy season is from May to October, and 80% of the rain falls in May, July, August, and October. Between December and March there is no rain.

The main roadside trees were such evergreens as figs (*Ficus bengalensis* and other spp.), nihm (*Azadirachta indica*), and pongam (*Pongamia glabra*). There were also many acacias (*Acacia catechu*, *A. farneciana*), teak (*Tectona grandis*), Jawa-pulm (*Syzygium cumini*), mango (*Mangifera indica*), tamarind (*Tamarindus indica*), and other kinds of trees. The main trees of the gallery forest were flame-of-the-forest (*Butea monosperma*) and karwanda (*Carissa conjeet*), in addition to the roadside tree species. The cultivated field was covered by paddies between June and November, but it was grassland during the other seasons. Lantana (*Lantana aculeata*), the dominant shrub, grew densely throughout the area, except in the cultivated fields.

The Bedati-halla River, with a width of about 3–5 m, became a muddy stream during the rainy season, but was a little streamlet during the other seasons. For

additional environmental description of the study area, please refer to my previous paper (1965).

Bonnet troops which moved along or near the roadside trees immediately became accustomed to my presence, and I was able to approach to within 10 m of them without disturbing their movements and/or behavior. Only when confirmation of rank among monkeys or the settlement of an experimental situation concerning social organization was needed, was a small amount of wheat and juar (small maize) distributed; otherwise, the setting of regular artificial feeding places was rigorously avoided.

## ECOLOGY

### a) Home Range and Land Utilization

The pattern of the troop's home-range utilization between March and September, 1962, during which troop movement and daily activity were traced, could be divided into five stages. In the first stage the troop concentrically used the (E) part of the home range; in the second stage it used the southern part (S) the intermediate part (I), and the vicinity of the Bedati-bridge; in the third stage it roamed throughout the entire home range, moving quickly; in the fourth stage it again used (E), and in the fifth stage it utilized the northern part (N), together with (I) and (S). Dependent on the fruit-bearing season of each tree species, the troop persisted in the same pattern of daily movement for several days and changed the pattern as it searched for new kinds of foods in different parts of home range as the food of the area it occupied decreased and because, perhaps, it became tired of the same diet for several days.

The duration in which it persisted in the same pattern of movement was about two weeks to a month. For example, during the second stage karwanda and pongam bore fruit. Karwanda grew densely near Bammar-bridge but was rarely found in the other parts of the home-range. Pongam abundantly grew along the roadside in (S), so during this period the troop exclusively used, for about a month, the parts where there was much of these two foods. The troop thoroughly roamed all over the home-range during the year, however.

Mean daily movement distance was about 790 m (Table 1), which agrees roughly with the data of NOLTE (1955), i.e., 820–1100 m. Although on some days it did not move, on other days it moved more than 2 km; the variation in distance of daily

**Table 1.** Seasonal change of the utilization of the home-range and daily movement.

Period	Part of home-range				Daily movement (m/day)			Observation days
	E	N	I	S	Max.	Min.	Mean	
1. Mar. 22–Apr. 8	7*(days)	4			2000 (m)	400	850	10 (days)
2. Apr. 15–May 11		2	7	8	1400	0	680	12
3. May 24–Jun. 26	5	4	2	5	1700	0	790	14
4. Jul. 30–Aug. 10	6	1			1500	400	730	6
5. Sept. 4–Sept. 23	1	9	4	5	1700	300	880	15
Total	19	20	13	18			c. 790	57

\*Number of days the part was utilized in the period. When the troop uses more than one part in a day, each part is considered as having been used for a day and is so counted.

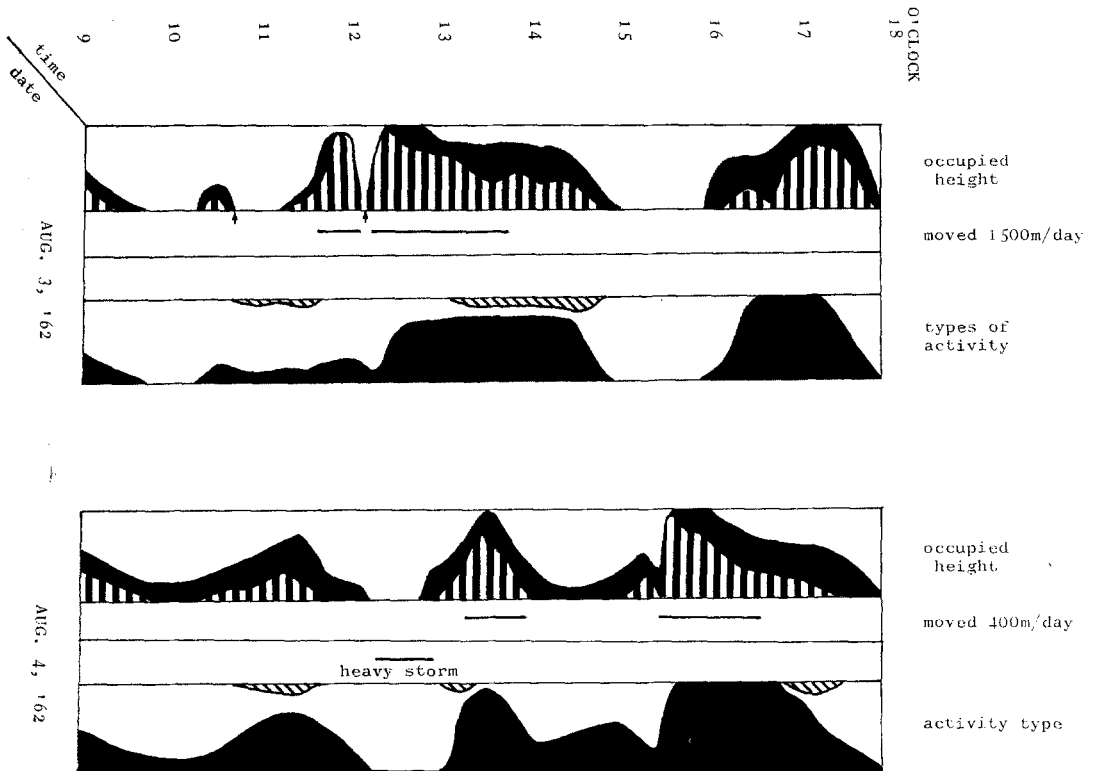
movement depended on the distribution and volume of food. When the troop used (I) or the eastern part of (E) it usually moved more than 1 km in a day, as there were few trees in (I) and it was mainly used as a passage from (S) to (N) and (E). The troop only once spent the night in (I). (E) was frequently used for feeding but never for sleeping; even when the troop fed there until late evening it moved away and slept in a different part. On the other hand, when it used the vicinity of the Bammar-bridge in hot May, where big pongam and nihm trees formed cool resting places over a pool of the river with a dense thicket of karwanda nearby, the troop didn't move during the day; this area had favorable conditions for resting, feeding, and sleeping, as well as shelter from predators. Therefore, it can be said that the troop's pattern of movement was decided not only by food distribution but also by the safety and comfort of the places it occupied according to the distribution of trees and other environmental conditions. It can also be said that each part of the home range had its own value for the troop, either as a source of food or as shelter from predators.

Bonnets are more terrestrial than arboreal and, though they seemed more accustomed to people than the langurs of the same area, they moved less far from the trees on the open ground than the latter. When they advanced to the grassland they frequently stood up bipedally, nervously looking around (Fig. 2). The grassland and the cultivated field restricted troop D to an area near the trees and the forest and, in consequence, the troop's home-range shows a peculiar striped form.

The home-range of troop D was about 40 ha, which figure coincides with that of RAHMAN and PARTHASARATHY of about 100 ha occupied by their two troops; NOLTE however, has a figure of about 260 ha and SIMONDS has one of about 520 ha, which are quite different from mine and that obtained by RAHMAN and PARTHASARATHY. The egg-shaped area which comprises the entire range of troop D is about 200 ha, so it can



**Fig. 2.** Bonnet macaques often stand bipedally and look around at the open ground.



**Fig. 3.** Daily activity of a bonnet troop shown by the number of animals. Occupied height is divided into white (more than 2 m), black (less than 2 m), and striped patterns (ground); activity types are divided into striped (play), white (rest), and black (feeding) patterns. The arrows indicate attacks by villagers or dogs and the vertical line indicates movement of the troop.

be assumed that, in certain cases, areas such as passages, which are little used, might be included in the home range; on the other hand, for troop D, at least, the home range consists only of the core area, which is frequently used due to the particular fact that the district is an open, sparsely wooded area.

**b) Daily Activity and Feeding Habits**

Bonnets rest on trees, clustering in a group and huddling together, for one or two hours during the daytime (Fig. 3). This resting period and clustering is seen extremely often during the dry seasons.

They usually feed while moving slowly on the ground, though they sometimes eat in trees. Bonnets spend about 30% of the daytime in terrestrial activity, a figure which agrees that of SIMONDS and is approximately the same as that of the langur, which is about 25%. According to my observations, however, in the high forest on the borders of Kerara and Madras States, South India, most bonnet activities, such as resting, feeding, and traveling, were performed in trees. A rough calculation of their terrestrial daytime activities did not reach 10% of their total activities. This difference suggests that the terrestrial-arboreal ratio of a species changes depending on the situation.

Troop D mainly fed on the berries, flowers, and young leaves of the lantana, which was dominant in the study area and had flowers and berries throughout the year. Other main food items were the fruit and young leaves of pongam, fig, karwanda, acasia, tamarind, and nihm, plus grasses and herbs. Bonnets greatly favored grasshoppers as food; during the dry season they frequently scattered on the grassland and went grass-hopper hunting. Once a bonnet was observed to catch and eat a small lizard (YOSHIBA, Pers. comm.).

### c) Sexual Seasonality

Sexual behavior of bonnets was seen between late April and September and peaked in early September, although detailed observations were carried out only between March and October (Table 2). Sexual behavior was also observed in October and November in general observations. There might be sexual activity throughout or nearly throughout a year, although there was very little during the dry season between January and March. (SIMONDS observed sexual activity throughout the year [LANCASTER & LEE, 1965].) The period of peak activity must, however, be short.

**Table 2.** Sexual activity observations.

Date	No. of ob. days	Number of copulated days						Total
		M1	M3	M4	M5	M6	M7	
Mar. 16-31	2 (days)							
Apr. 1-15	4							
Apr. 16-30	5	3					1	4 (days)
May 1-15	3						1	1
May 16-31	6	2						2
Jun. 1-15	4	1						1
Jun. 16-30	2					1		1
Jul. 1-15	1						1	1
Jul. 16-31	1	1						1
Aug. 1-15	3	2						2
Aug. 16-31	0							
Sept. 1-15	8	1(+7)*	5(+2)	3(+2)	5	5		19(+11)
Sept. 16-30	3		1	1				2
Oct. 1-15	0							
Total	42	10(+7)	6(+2)	4(+2)	5	6	3	34(+11)

\*Figures in parentheses show the instances in which copulation itself could not be confirmed but in which the male consorted with a female and displayed sexually associated behavior.

As the birth season of troop D was seen in late February and late May (Table 3), if we assume the gestation period to be between 5 and 5.5 months, in accordance with NAPIER and NAPIER (1967), copulation which lead to fertilization must have taken place mainly between early September and late December.

Langurs which lived in the same area as bonnets reached their sexual peak between June and August, although sexual behavior could be observed throughout the year (SUGIYAMA et al., 1965). On the other hand, macaques in the Japanese islands, where the climate and environmental conditions change remarkably from season to season, have a strictly restricted sexual season (KAWAI et al., 1967). That is, the pattern of sexual seasonality in bonnet macaques does not resemble that of a species of the same genus which lives in a quite different environment but resembles that of a distantly related species which lives in the same habitat.

**Table 3.** Blood relations among troop D members.

Mother	Age (estimated birth year)						Birth date of 1962-baby
	Full grown	58	59	60	61	62	
FA							♀ Apr. 10-13
FB							♀ Apr. 19
FC							
FD							
FE							♂ May 10-15
FG							Mar. 29 (Apr. 1-6 missed)
FH							late Feb.-early Mar.
FI							♀ Apr. 23-28
?							
?							
?							
?							
?							
?							
♂/♀	5/8	2/1	3/0	1/3	3/0	2/4	Total 16/16

d) Relationship with Langurs

A great portion of the home ranges of langur troops overlap those of bonnet troops (Fig. 1)<sup>1</sup>. Although langurs use the openfield more extensively than bonnets, they depend on the roadside trees and gallery forest as the base of their daily life as much as do the bonnets. Consequently, the bonnet troop frequently came near and made contact with the langur troop during its daily movement. Sometimes two troops of both species mingled and/or traveled together several hours and only rarely did either of the two troops avoid or reject the other.

The adult male langur weighs about 15 kg and the adult female 12 kg, weights of which are double those of the bonnet, but if monkeys of the two species came too near each other, the langur usually avoided the bonnet, without, however, any expression of fear, although it occasionally exhibited a slight defensive expression.

Adults of both species had almost no interest in each other, but subadult or juvenile bonnets sometimes made mock charges against langurs. However, neither

1) I have already commented (SUGIYAMA, 1965) on the social organization and its change in langur troop No.30, which has its home range in (N) and (E).

true antagonism nor fights among monkeys of the two species could be observed. Moreover, the daily movement of each troop was never disturbed by the troop of the other species.

KAWAMURA (Pers. comm.) succeeded in baiting troops of bonnets and langurs simultaneously about 16–17 km from Dharwar along the Dharwar-Haliyal road and observed clashes of one troop against the other at his artificial feeding ground, but such open antagonism must have occurred as the result of competition for occupation of the feeding place where there was a particularly valuable food for both species in a restricted spot. He also observed infants of both species play-wrestling, something which never occurred in a natural situation.

I note in passing that at the border of Kerala and Madras States, South India, the lion-tailed macaque had a status similar to that of the langur in Dharwar in the relations with the bonnet (SUGIYAMA, 1968).

Any troop of monkeys segregates its home-range from neighboring troops of the same species, either territorially or nonterritorially or, at the very least, it exclusively occupies its own core-area within the home-range. How can Indian monkey troops coexist in the same area with near-relative species which have similar life forms while taking little interest in each other? Both the bonnet and langur prefer fruit to leaves as food; however, in comparing the two species, the langur eats many more leaves than the bonnet. Bonnets and langurs often consume certain kinds of fruit in the same area, while the food habits of bonnets and lion-tails of South-India are almost identical.

HADDOW (1952) suggested that slight differences of food habits permitted the coexistence of two or more than two kinds of *Cercopithecus* species in the same forest, as at Budongo, Semiliki, and some other forests of East Africa. I have also studied non-human primates at the Budongo Forest and confirmed that two near-related species, in this instance the blue monkey (*Cercopithecus mitis*) and the red-tailed monkey (*C. ascanius*), frequently mixed in fruit-bearing trees and ate together, showing no antagonism toward each other, although each troop was antagonistic toward neighboring troops of the same species; we can only conclude the difference in food habits of the two species must not be the problem. Although the problem is not yet resolved, I suggest that a slight difference in behavior repertoire and the innate releasing mechanism in the ethology of the two species must be the reason for each species' permitting the other's simultaneous coexistence in a given area and the refusal to conform to the general ecological principle of "one species in one niche."

## TROOP ORGANIZATION

### a) Troop Size and Its Composition

The mean troop size of the twelve troops which had their home-ranges near or along the Dharwar-Haliyal road and which I easily and frequently observed was 30 (Table 4). The troop size of the Dharwar bonnets differed but little from that recorded by NOLTE, SIMONDS, and RAHMAN and PARTHASARATHY. Although SIMONDS (1965) suggested that the troop size of bonnets living in the open-land was larger than that of those living in the forest, I could not find any difference in troop size between open-



**Table 4.** Social composition of bonnet macaque troops (DWR-HYL roadside, June–Sept., 1961).

Range observed (km from DWR)	Ad		SAd & J			I & B			Total	Remarks
	♂	♀	♂	?	♀	♂	?	♀		
Grassland & cultivated field										
4.4	7	9			8			8	32	
6.0–6.2	7	8	1	4	1			3	24	
7.4	5	7			6			5	23	
10.0–10.2	8	9	1		6			4	28	
10.6–10.8	5	5	3		1			2	16	
11.0	9	9	1		4			4	27	
15.6	8	11			8			6	33	
15.0–16.5	7	9	7		3	2		4	32	Troop D
16.2–17.5	11	13			13			7	44	Troop F
Forest										
18.4–19.2	10	10			6			4	30	
27.1	8	13	2		6	1		4	34	
28.2–29.5	11	13			8			4	37	
Mean	8.0	9.7			7.5			4.8	30	

\* Ad: Adult. SAd: Subadult. J: Juvenile. I: Infant. B: Baby.

land and forest-dwelling bonnets, in spite of recognizing a remarkable difference in troop size among the open-land and forest-dwelling langurs in Dharwar (SUGIYAMA, 1964).

The important point concerning troop composition of bonnets must be the adult sex-ratio, that is, the adult male/adult female ratio was about 0.828 ( $\sigma=0.117$ ). SIMONDS' sex-ratio figure was, however, much higher than that obtained in Dharwar. In contrast, the adult male/female sex-ratio of the Japanese macaque (*Macaca fuscata*) and the rhesus macaque (*M. rhesus*) is about 0.5 (ITANI et al., 1963; SOUTHWICK et al., 1965), excluding data of Japanese macaques of artificially baited troops, the population of which increased extremely, and of troops isolated on small islands where the occurrence of solitarization is difficult. That is, half of the males may have been lost from the troop by solitarization or accidents which may affect the number of females less. As it is difficult to believe that the probability of accidents among bonnets is far less than in other macaques, the difference in sex-ratio may depend on the difference in the ratio of male solitarization. This point is to be discussed again in relation to troop D (see p.263).

b) Agonistic and Associative Relations among Troop Members

i) Rank and Spatial Distribution

When wheat or juār was thrown to bonnets who appeared in the open ground, the animals ate it under fixed spatial distributions, as shown in Table 5. On the other hand,

**Table 5.** Spatial distribution of Troop members.

Center		Periphery		
<i>M1</i>		<i>M5</i>	<i>M3</i>	<i>M4</i>
<i>M2</i>		<i>M6</i>		
		<i>M7</i>		
<i>FA</i>	<i>FB</i>	<i>FD</i>	<i>FE</i>	<i>FG</i>
	<i>FC</i>			<i>FH</i>
	<i>FF</i>			<i>FI</i>
----- J -----*				

\*Juvenile often distribute about here.

ranking relationships among adult males observed from dominant and subordinate behavior was strictly linear (*M1-M2-M3* . . .), but occasionally the peripheral males *M3* and *M4* were dominated by *M5*, *M6*, and *M7*, who were reinforced by *M1* or *M2*. Linear ranking relationship was also observed among adult females (*FA-FB-FC-FD-FE* . . .) when they appeared at the artificial feeding ground, but it was observed only in an artificial situation.

ii) Dominance Manifestation<sup>2)</sup>

Clarification of dominance manifestation among the bonnets of troop D was obtained by scattering wheat and juār on the open ground and recording the reaction (Table 6). In this troop of 32 individuals, about 20 to 30 dominance manifestations occurred in periods of twenty minutes, and so the troop was often dragged into noisy confusion. Nearly half of the dominance manifestations were carried out by the leaders, *M1* and *M2*. Nearly 70% of the dominance manifestations were made by adult males, but the peripheral males *M3* and *M4* did not contribute to this kind of trouble.

More than 70% of the individuals who were attacked or intimidated were juveniles and infants. Most of the dominance manifestations were carried out by feeding adult males who casually stopped eating, looked around, and suddenly attacked or intimidated young animals feeding nearby. The young animal who was intimidated ran away screaming, but the direct reason for the anger of the male was rarely recognized. Some of the dominance manifestations were directed by a dominant male against a juvenile who was feeding near a subordinate male, and this kind of the dominance manifestation must be considered an indirect threat by the dominant male to the subordinate male.

These dominance manifestations of the leading male may have a role in main-

**Table 6.** Dominance manifestation which was seen at feeding time in open ground; each observation had a duration of 20 minutes.

Date	Attacked	Attacker					J	Total
		<i>M1</i>	<i>M2*</i>	<i>M3&amp;M4</i>	<i>M5,M6,&amp;M7</i>	AdF**		
May 28, '62 14:28-14:48	<i>M5,M6, &amp; M7</i>	1	1	0	1	0	0	3
	AdF	1	0	0	0	0	1	2
	J	4	3	0	3	3	5	18
	Total	6	4	0	4	3	6	23
May 31, '62 13:02-13:22	<i>M5,M6, &amp; M7</i>	2		1	0	1	0	4
	AdF	1		0	0	0	0	1
	J	7		0	6	3	0	16
	Total	10		1	6	4	0	21
Jul. 30, '62 16:32-16:52	<i>M5,M6, &amp; M7</i>	2		0	0	1	0	3
	AdF	3		0	4	1	0	8
	J	6		0	6	4	3	19
	Total	11		0	10	6	3	30
Sum total		27	4	1	20	13	9	74
Ratio (%)		42		1	27	18	12	100

\**M2* deserted the troop after the first observation. \*\*AF: Adult female.

2) Terminology of behavior patterns follows KAUFMAN and ROSENBLUM (1966) as closely as possible.

taining the tension and social order of the troop in open ground, and for this role *M3* and *M4* might not have an important status in the troop.

iii) Associative Relation

*Grooming*: Social grooming between adults was observed 439 times (Table 7). Although the ranking order among adult males was linear, the social grooming of bonnet males was not one-way social behavior from a dominant to a subordinate. In some cases a dominant male groomed a subordinate male more frequently than the latter did the former. A similar grooming relationship could be found among adult females, although a mother with a young baby was more frequently groomed than a female without a baby. Adult males as well as adult females were active in social grooming.

The above-mentioned characteristics on the grooming activity of bonnets were also observed by SIMONDS in a natural troop and by KAUFMAN and ROSEMBLUM (1966) in a laboratory colony.

*Clasping*: Clasping during rest is characteristic associative behavior of bonnets. From five to ten individuals huddle together in a group and rest or sleep in the daytime (Fig. 4); a bonnet rarely rests alone. Males usually gathered by themselves as did females. In a female group, mothers gathered to huddle with each other and single and immature females drew close to babies. On the other hand, juvenile males drew close to a big male and the other males drew close to the juveniles.

When bonnets was actively moving, adult males maintained a certain distance between each other, but many times they had a chance to touch bodies, especially at resting time. Bonnet males had the habit of touching and embracing the troop leader and other big males and of being cared for by them since childhood. This characteristic clasping behavior of bonnets during their resting time was also noted by ROSEMBLUM and KAUFMAN (1967) in their study of a laboratory colony.

*Play*: In monkeys group play among juveniles and infants of nearly the same age and who have similar physical strength is common but is rarely seen in adult males.

**Table 7.** Grooming relations among adults (April 19–September 23, 1962).

Groomer	Groomee															Total		
	<i>M1</i>	<i>M2*</i>	<i>M3</i>	<i>M4</i>	<i>M5</i>	<i>M6</i>	<i>M7</i>	<i>FA</i>	<i>FB</i>	<i>FC</i>	<i>FD</i>	<i>FE</i>	<i>FF</i>	<i>FG</i>	<i>FH</i>		<i>FI</i>	
<i>M1</i>			3	2		1	2	1		9	1		5				2	26
<i>M2*</i>	4			2		4					1		1					12
<i>M3</i>	4					1				4	1			10				20
<i>M4</i>	7		1		3	3					1			1				16
<i>M5</i>	6			3		4	3	3		1	1	4	1			1	1	28
<i>M6</i>	10	3	1	3	4		2	4		1	1	3			3	3	2	40
<i>M7</i>	9	3	1	1	2	1		3		1		1			1	1		24
<i>FA</i>					1	2	3		8	1	1	2	4			3	1	26
<i>FB</i>								12		2			5	1	1	7		28
<i>FC</i>	1		2		1		1	3	2			3	12	1	3	2		31
<i>FD</i>	8	2			2			12	4	3		6		1	8	10		56
<i>FE</i>		1		1	2	2	1	3	1	1	4		1			2	5	24
<i>FF</i>	2							8	10	2	1	2		1	2	2		30
<i>FG</i>			11			1	1	1	5		1	1			1	2		24
<i>FH</i>	1		1		1	3		1	4		6	4	2	1		6		30
<i>FI</i>	1				1	1		1	4	2	4	2	1		7			24
Total	53	9	20	12	17	23	13	52	38	27	23	28	32	20	32	40		439

\**M2* deserted the troop on May 29 or 30.



**Fig. 4.** Bonnet macaques gather in a lump and embrace each other for resting.

Bonnet juveniles and infants, however, frequently wrestle with big males; they boldly and repeatedly leap at, kick, cling to, and bite big males. The big male reacting to the juveniles' false challenge makes a counter attack with an exaggerated gesture. The mock fight may be initiated not only by the juveniles but also by the adult male. Sometimes more than one adult male joins the wrestling party. SIMONDS also observed that adult males of all ages regularly and often jointed in the play.

Sometimes an adult male pulls a juvenile male close to him and holds him in his arms, and at other times juvenile males come to an adult male and cling to and embraced him. Consequently, the male resting group and the wrestling party are easily interchanged.

#### iv) Sexual Relations

A dominant or elder male has the tendency to consort and mate with the same female for many days, while younger males consort and mate with many females in a short time (Table 8). Females do not have the tendency to change mating partners from subordinate to dominant males with the onset of their period of estrus. The peripheral males *M3* and *M4* sometimes went far from their home-range with estrous females, often more than 500 m from the troop, and mated in the core-area of a neighboring troop. The leader male, *M1*, rarely attacked a consorting couple mating in front of him.

The repertoire of sexual and related behavior patterns is basically similar to that of the Japanese macaque (MIZUHARA, 1957), but anogenital exploration is characteristic of bonnets (Fig. 5). Anogenital exploration among bonnets was observed quite often. Sometimes a male who was consorting with a female inspected other females who passed in front of him and at other times a male patrolled the entire troop, inspecting the genitals of all adult and subadult females. If coagulated sperm was attached to the vagina of a female, the explorer took it off and ate it. Sometimes a subordinate male

**Table 8.** Number of days sexual relation was observed (March–September, 1962).

Female	Male							Total
	<i>M1</i> 10–13*	<i>M2</i> ** 14–17	<i>M3</i> 12–17	<i>M4</i> 16–20	<i>M5</i> 6–7	<i>M6</i> 4–5	<i>M7</i> 4–5	
<i>FA</i> 16 +*			1 (day)	1	1	2		5
<i>FB</i> 5–8					1	1		2
<i>FC</i> 9–15	15		1				1	17
<i>FD</i> 16 +			1			1	1	3
<i>FE</i> 9–15							1	1
<i>FF</i> 4	1			2	3	2	1	9
<i>FG</i> 5–8	1		5	3				9
<i>FH</i> 5–8								
<i>FI</i> 5–8								
Total	17	0	8	6	5	6	4	46

\*Estimated age. \*\**M2* deserted the troop on May 29 or 31.

came to inspect and removed the coagulated sperm of a female who was mating with a dominant male, and at other times a dominant male did the same to a female who was mating with a subordinate male. Ranking order had no relation to anogenital exploration.

v) Some Other Social Relations among Adult Males

*Mounting*: About two-thirds of 32 observed mounting between adult males were carried out from a dominant to a subordinate male, but the rest were from a subordinate to a dominant male (Table 9). *M1* frequently presented himself to a subordinate male who was hesitating to mount the leader male and forced him to do so. During the time he was being mounted, he peeped back through his legs, grinning and clicking his tongue. Although this response was not popular with all adult males, the mounting relation between adult males was not always decided by ranking order. SIMONDS also recognized this characteristic of male bonnets.



**Fig. 5.** Anogenital exploration of an estrous female by *M5*.

**Table 9.** Mounting relations among adult males.

Mounted	Mounter							S/D*
	M1	M2	M3	M4	M5	M6	M7	
M1		4	3		2			9
M2	1							
M3	1							
M4	2		2		1		1	2
M5	4	2	1					
M6			2					
M7	2		2			2		
D/S**	10	2	7			2	21	11

\*Subordinate male mounts dominant male. \*\*Dominant male mounts subordinate male.

*Grinning and Clicking:* Although grinning is a defensive expression among many monkeys, the grinning with tongue-clicking behavior of bonnets is not always a defensive or pardon-begging expression. It was observed in dominant as well as subordinate males as an appeasement or affectionate expression for relieving tension between animals or as a greeting, as shown in the above section.

*Embracing:* When two big adult males met at a place unexpectedly, they sometimes embraced each other, furiously grinning and clicking their tongues. Occasionally one male gripped and shook the scrotum of the other or bit him on the shoulder with an exaggerated gesture while embracing (Fig. 6). Between dominant males such behavior was especially exaggerated, but no wound could be found as a result of this kind of biting. The social tension between them might be relieved by this behavior, which might also have the meaning of 'greeting.'

*Gripping of genitals:* A male would approach another and grip the latter's scrotum; the latter would be surprised and run away, grinning and clicking his tongue. This kind of behavior was often observed. While embracing, males sometimes grip the scrotum



**Fig. 6.** M1 (left) and M2 (right) embrace each other grinning and clicking the tongue. M1 is gripping the scrotum of M2 by his right hand.

of the other, as mentioned above. This was not always performed by the dominant male, for occasionally a subordinate male gripped the scrotum of the dominant one. For example, *M5* once did this to *M1* and the dominant male, *M1*, leaped and ran away at full speed.

*Hand-stretching and gentle touching*: Once *M3* stretched his hand to *M2*, who had come near him. Although *M2* paid no attention and ignored him, *M3*'s behavior looked as if he was appeasing the aggression of *M2*. This behavior appeared similar to the hand-shaking invitation of chimpanzees and the circumstances were also the same (SUGIYAMA, 1969). Sometimes a male stretched his hand and touched the back of the bonnet who was sitting beside him, but without any change of facial expression. The former may have been showing affection toward the latter. VAN LAWICK-GOODALL (1968) observed a similar behavior pattern in chimpanzees, which she called the 'appeasement' gesture.

Although bonnet males show a clear-cut linear ranking order in an artificial baited situation, associative behavior which may reduce social tension or which occurs independent of ranking relationship in their daily life in natural situations was observed extremely often.

### c) Organizing Behavior

#### i) Protection

When a monkey observed a tiger, leopard, wild cat, dog (domestic), or kite, it immediately uttered the high-pitched alarm call <kern, kern>. The alarm caused a chain reaction among the other monkeys and most of them rushed into the bush or climbed a tree. Adult males often continued to utter the alarm for long time, exposing themselves in the tree tops. *M1*, especially, frequently and nervously watched the movements of the predator. After the predator went away, *M1* displayed tree shaking, and then sat on a branch, young males coming to groom him or juvenile males to cling to him. Such behavior of those young and juvenile males must be a type of calming behavior.

When the troop crossed the road or open land, one or several babies were sometimes left behind, as they were absorbed in play. Usually, on hearing the high-pitched screams of the babies, a mother or mothers went back to pick them up, but on a few occasions even mothers hesitated to go back from fear of passing close to the observer. On such occasions, young adult males, such as *M5*, *M6*, or *M7*, by themselves or leading the mothers, went back to the other side and returned to the troop carrying the babies on their backs or running with them. The troop members waited, watching them without proceeding.

#### ii) Procession order

The typical procession after a long term rest can be divided into the following two patterns: (1) the leader male starts first, and the other members follow in twos and threes; (2) young adult males, females and juveniles gradually start to move but, after having moved about 50 m, wait until the leader and the central part start.

When the troop was moving slowly, divided into three parts separated from each other, one or a few adult males could be found in the first part, as well as in the central and last parts, of the traveling troop, and even when all the adult males had

been in the first part only at the start of the movement, they scattered into the first, central, and last parts during the movement. *M1* was usually in the first or the central part of the progressing troop.

Troop members did not always follow the leader's move. In spite of the central part of the troop's having begun to move, several females and juveniles sometimes persisted in resting in trees. On such occasions, one or two males returned, rounded up those females and juveniles, and, accompanying them, rejoined the troop's main body. Although the major part of the troop was waiting for them at a distance of about 50 m or so, it began to move quickly once the strays were returned. It is clear that the major part did not proceed because they were waiting for the tardy females and juveniles. *M3* was the regular guide of the members who dropped behind.

#### d) Desertion

*M2's desertion*: Until May 28, 1962, troop D was organized with *M1* and *M2* as leaders, judging from their dominance manifestation and organizing behavior. However, *M2* deserted the troop on May 29 (or 30), but I could not find a direct reason for his desertion. After the incident, a change in the behavior of the troop members was seen in dominance manifestation at the feeding place; that is, about the same amount of dominance manifestation that had been performed jointly by *M1* and *M2* was now exhibited solely by *M1* (Table 6), i.e., *M1* became busier controlling the troop members.

*M5's temporary desertion*: In the first week of June, 1962, *M5* and the baby of *FG* deserted the troop, *M5* returning to the troop alone on September 4th at about 11:00. He went directly to the center of the troop and without any hesitation actively walked and fed. Within an hour after returning, he groomed *FE*, *FG*, and *FH*, and was in turn groomed by *FH*; he also inspected the vaginas of six of nine adult females, that is *FA*, *FB*, *FD*, *FG*, *FH*, and *FI*. While he was busy with the grooming and anogenital exploration, *M1* was eagerly following *FC*, who was in estrus, and paid little attention to the 'ill-mannered' behavior of *M5*. Even after one hour had passed, *M5* continued to inspect females. At 15:15, *M5* mounted *M1*, *M1* neither avoiding *M5* nor attacking him and readily submitting to being mounted. Even after *M5* had dismounted both males behaved calmly. *M5* assumed the same status and rank as before.

I was unable to determine where *M5* had been and what he had done during the time he was away from the troop. The baby of *FG*, who disappeared with him, did not reappear. Because the time when they disappeared coincided with the time when the adjacent troop, troop F, invaded the home-range of troop D, it might be possible that they followed troop F during the time it stayed in troop D's home-range.

*Solitarization*: After the above-mentioned occurrence there was no change in the membership of troop D until April, 1963, except for the natural increase due to newborn babies. No solitary male was found either in or near the home-range of troop D or in the Dharwar forest throughout the study period. SIMONDS did not find a solitary male, either, so solitary bonnets must be rare.

The fact, however, that two adult males out of seven disappeared from troop D within half a year must have had a great effect on the small-sized troop. The fact is that a high percentage of adult troop males disappeared from the troop; however,



because the adult sex-ratio (male/female) in a troop of bonnets is higher than in other kinds of macaques, most males who deserted the troop must have joined another troop soon after desertion, without the intervening process of solitary life.

#### e) Intertroop Relationship

Bonnet troops adjacent to troop D in the north and east rarely came to the range of troop D and interaction among them could not be observed. (S) was also within the range of troop F and was frequently utilized for feeding, resting, and sleeping by troop D as well as by troop F. Neither troop used (S) at the same time, but one of them might have avoided the other before direct contact. The approach of those two troops could not be observed until June 6, 1962, when troop F passed (S) and (I) and entered (E). Troop F fed at a point about 14.6 km from Dharwar (See Fig. 1) and spent the night there. The next day, after spending nearly one day in the center of the home-range of troop D, troop F left the Bedati-bridge area at about 15:00, passed through (I), and returned to the southern part of (S). During this time troop D was in the southernmost part of (I), which it rarely used, and came back to the Bedati-bridge area after troop F returned to its own range.

Troop D must have taken refuge from troop F in the peripheral part of its home-range. Such being the case, although direct contact between the two troops could not be observed, the dominancy of troop F was surmised. On the other hand troop D, in its turn, sometimes invaded the central part of the home-range of troop F when the latter was traveling in another part of its home-range. In spite of this fact, the dominance relation between the two adjacent troops could be presumed; it can also be said that bonnets have no exclusive territory in the strict definition. YOSHIBA (Pers. comm.) observed a troop invaded the home-range of another troop and fierce fighting occurred between them. KAWAMURA (Pers. comm.) observed a troop move for a few kilometers, leaving its own home-range and passing through the home-range of other several troops. It looked as if it was a migration.

## DISCUSSION AND CONCLUSION

It is a well known principle of macaque society that a troop consists of many members, including both sexes and all ages, that a troop has a strict ranking order among adults, especially among adult males, and that members of a troop compactly move as a unit. Social relationships among individuals depend on the above-mentioned social principle and it can be said that most individual behavior has some relation with ranking order.

The bonnet troop consists of both sexes and all ages, the ranking order of adults is clearly linear, and the troop size is standard, as in other macaques; however, I was embarrassed by the difficulty of determining rules, which are easily found in Japanese macaque society, for the relation among the concerned animals' status in the troop, their behavior pattern, and their situation. The following characteristic behavior and social relations among individuals suggest that the bonnet troop has no strict social order, as have most Japanese macaque troops.

Frequency of grooming of the adult male bonnet is much higher than that among Japanese macaque (SUGIYAMA, unpublished). In comparison with Japanese macaque society, in which a subordinate animal grooms a dominant one more often than vice versa, the groomer-groomee relationship among bonnets is not always parallel to rank relation. Although adult male bonnets often play with juveniles and infants, sometimes even with adult males, adult Japanese macaques rarely do. Bonnets gather in tightly packed groups and clasp each other while resting. Adult male bonnets are extremely tolerant of juveniles and infants, as is seen in play and rest. Mounting relations between adult male bonnets do not always parallel rank relations; on the other hand, in Japanese macaques, a dominant male always mounts a subordinate. Adult male bonnets embrace each other when resting as well as when greeting. The grinning and tongue-clicking of bonnets are not always defensive expressions and sometimes a dominant male exhibits them to a subordinate male to relieve tension. Anogenital exploration by young male bonnets can be seen even if a dominant male is nearby, and many other phenomena which are never observed in Japanese macaque society, being strictly organized under order of rank, are to be seen among bonnets. I got the impression, from the following facts, that inter-troop relationships also have a characteristic similar to that of the inter-individual relationships mentioned above and which may be called 'disorder.'

The home-ranges of adjacent troops overlap and an inter-troop relationship is loosely maintained in a given area. For example, one area is usually occupied by only one troop, but territory is not established and troops sometimes traverse their home-range without much anxiety; occasionally a troop migrates out of its original range.

On the other hand, other observations suggest that the bonnet troop has a highly organized society. We note that the leader males maintain tension and control the troop members at the center when the troop is feeding in open ground; the leader and some adult males place themselves in front of a predator emit alarm calls while the other members of the troop rush and hide in the jungle, and they move under the adult males' control; young adult males protect and care for the babies which are left behind; adult males scatter in each part of the traveling troop and they care for and control the straggling females and juveniles. The leading actors in each situation is different, sometimes being the leader, sometimes the peripheral adult males, and of other times the young adult males. This type of control behavior of leaders and followers is popular in macaques and baboons and is believed to be related to the strict social hierarchy centered in ranking order. But the behavior of bonnets, especially that of adult males, in calm situations is characterized by associativeness and complications in relation to the circumstances as if there were neither social hierarchy nor social organization. The characteristic associativeness of bonnet society and behavior may ease the situations by which adventurous males emigrate from and/or immigrate to the troop. This may make possible habitual as well as genetic exchange among troops, although solitary males could rarely be found.

Although a highly organized troop of macaques is generally maintained by a strict social order which brings the daily life of members under severe restrictions, that of bonnets is shaded behind a highly flexible behavioral capacity in their daily life. In other words, it can be said that social adaptability among bonnets is of such a high

order that they can utilize the advantages of group life without maintaining a strict social order. In such a kind of group life, individuals may be able to maintain and develop the high individuality which distinguishes bonnets from other macaques.

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