

**SOCIAL BEHAVIOUR AND COMMUNICATION AMONG
WILD LION-TAILED MACAQUE (*Macaca silenus*) IN THE
INDIRA GANDHI WILDLIFE SANCTUARY, TAMIL NADU**

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**By
ROOPALI RAGHAVAN**

***Under the Supervision of*
DR. ATUL.K.GUPTA**



**भारतीय वन्यजीव संस्थान
Wildlife Institute of India**

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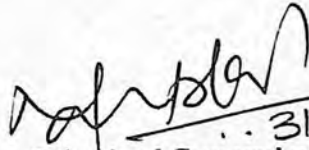


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Wildlife Institute of India

CERTIFICATE

This is to certify that **MS. ROOPALI RAGHAVAN** of the Wildlife Institute of India has carried out an original piece of work titled "**SOCIAL BEHAVIOUR AND COMMUNICATION AMONG WILD LION TAILED MACAQUE *Macaca silenus* IN THE INDIRA GANDHI WILDLIFE SANCTUARY, TAMIL NADU**" in partial fulfillment of the M.Sc. (Wildlife Science) degree of Saurashtra University. These investigations were carried under my supervision at the Wildlife Institute of India from November 2000 to June 2001. I also certify that this work has not been submitted for any other degree of any university.

Date : Dehradun
Place : 31st July 2001.


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Principal Supervisor
Dr. A.K. Gupta
Department of Population
Management, Capture and
Rehabilitation
Wildlife Institute of India

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SUMMARY

This study on the social behaviour and communication among wild lion-tailed macaque was carried out between November 2000 and April 2001, on a group of lion-tailed macaques that inhabit the wet evergreen Puthutotam forest fragment, located within the Indira Gandhi Wildlife Sanctuary in the Anaimalai hills, Tamil Nadu.

The troop consisted of 16 to 19 animals. For the purpose of this study, social interactions within and between adults and subadults of both sexes were considered. Focal animal sampling and instantaneous scan sampling was thus conducted on only ten identified individuals (four males and six females) in the troop.

A complete ethogram describing all behaviour observed during the period of the study was prepared. The time-activity budget was calculated for the troop. The predominant behavioural states among all the individuals were Active Forage (mean $\pm$ SD of $22.4 \pm 0.08\%$), Active Feed ($17.0 \pm 0.05\%$), Sit ($16.6 \pm 0.04\%$), Move ($13 \pm 0.03\%$), Passive Forage ($6.8 \pm 0.02\%$) and Passive Feed ($6.5 \pm 0.02\%$). The adult males and females of the study troop differed in the proportion of time spent by them in the different behavioural states. Autogroom and Allogroom accounted for the principal difference between the sexes. Adult males spent relatively greater time Autogrooming than females, while females Allogroomed relatively more.

Dominance ranks were calculated independently for males and females in the study troop. Among both males and females, rank position in the dominance hierarchy appeared to be influenced strongly by body size. This is an unusual finding for the females of a cercopithecine primate species, implying the existence of an unique individual-based dominance hierarchy among the study females.

There was a remarkable similarity in the frequency with which dominant and subordinate females displayed virtually all behaviours towards each other in dyadic

interactions. This provides support to the prevailing view that lion-tailed macaques indeed display an egalitarian nature.

Classification of the gestures and vocalisations were observed to be largely dependent on the dominance rank of the individuals, with certain gestures being characteristic of submission. Males and females showed differential use of the gestures and expressions.

CHAPTER 1: INTRODUCTION

1.1 GENERAL INTRODUCTION

From an evolutionary point of view, the order Primates include some of the most complex and highly evolved taxa in terms of their social organisation and inter-individual relationships (Smuts *et al.* 1987). Primates live in groups of varying sizes that exhibit different degrees of social complexity, ranging from solitary individuals that associate occasionally, to large troops comprising several males and females (Smuts *et al.* 1987). The successful functioning of any primate society emerges partly from the interactions between the individuals of the group and their environment, and partly from the social relationships between the different individuals that comprise the society (Dunbar 1988). Inter-individual interactions constitute the most important factor in maintaining the structure and cohesiveness of a primate society; interestingly, they also seem to influence the patterns of exploitation of the local environment by the group (Hinde 1983). Studies of primate social organisation, therefore, provide better insight, not only into the motivations of the individuals in that society, but also into that of the species as a whole and into the ways in which it has adapted to its environment.

Another important component regulating the dynamics of social relationships is communication. Communication between individuals in a social group is achieved by a variety of means including vocalisations, facial expression and gestures, movements, and even postures, the purpose in all cases being to communicate a message by signals. These diverse behavioural signals have an important role to play in determining aggression, competition, affiliation and the sexual behaviour of the members of a primate troop

(Cheney and Seyfarth 1990; Tomasello and Call 1997). Relatively little is known, however, about the meaning or context of different behaviours used in communication: such studies have only been conducted on socially housed captive primates (van Hooff 1967; Redican 1975; Cheney and Seyfarth 1990; Maestriperi 1996a, b; Maestriperi and Wallen 1997). Since captive primate troops usually live under extremely artificial, and often stressful, conditions, the description of the different modes of social communication and an evaluation of their importance for the cohesion and functioning of the troop can only emerge from a study of natural, free-ranging groups.

One of the most neglected areas of animal behaviour research concerns its applications in the field of animal conservation. Knowledge of the social behaviour of certain disturbed populations, for example, can influence our understanding of how these populations function in fragmented habitats, their response to exploitation and disturbance, effective population size, captive breeding and reintroduction efforts, and population monitoring and modelling (reviewed in Caro 1999). While detailed behavioural studies of any of the endangered or threatened Indian primates are rare, almost no efforts have been made to devise or evaluate conservation strategies for these species from the perspective of the species behavioural profiles or individual behavioural decisions.

The macaques (genus *Macaca*), with 19 species distributed mainly across a range of ecological habitats in Asia, represent the most socially diverse of all the cercopithecine primates (Fa and Lindburg 1996). Comparative studies on the evolution of primate social organisation, communication and cognition would, therefore, most benefit from an understanding of this genus. Long-term field studies of macaques in their natural habitats are, however, rare, and only captive groups of about 6 - 8 species have been studied to any

great detail. Given that many of the macaques are also threatened or endangered, particularly, in India, such knowledge is also essential if we are to understand the social dynamics of these troops, particularly in relation to their ecology. This can also be used to devise appropriate conservation strategies for their management.

1.2 REVIEW OF LITERATURE:

The lion-tailed macaque (*Macaca silenus*, Linnaeus; Family Cercopithecidae) is one of India's most endangered primates (IUCN 1996) and is listed in Schedule I of the Indian Wildlife (Protection) Act of 1972 (Anon 1992). It is endemic to the tropical wet evergreen forests of the Western Ghats in southwestern India, and typically occurs in forest patches with a mean elevation range of 150 to 1,500 m above mean sea level (Green and Minkowski 1977; Kurup 1978; Ali 1985; Kumar 1985). Till recently, the lion-tailed macaque was contiguously distributed from the southern-most hills of the Western Ghats in Kerala to the State of Maharashtra in the north. The severe loss and fragmentation of wet evergreen forests in the last four decades have, however, resulted in local extinction of macaque populations in the States of Goa and Maharashtra. The lowland wet evergreen forests in Kerala have also been wiped out, confining the remaining populations to the higher elevations alone (Kumar 1995). At present, the species is restricted to three states, of which Kerala has about 2,000 animals and Tamil Nadu and Karnataka about 1,000 animals each (Kumar 1995). The Working Group on Census and Distribution during the 4th International Symposium on the Lion-tailed Macaque (Kumar et al. 1995) identified at least 490 isolated populations of which 26 had less than two groups each, nine had between 3 and 10 groups, and only five had more than 10 groups. Numerous surveys have been conducted all along the Western Ghats in order to gain information on their distribution range as well as status of the species in the different habitats (Kurup 1978; Ali

1985; Karanth 1985; Kurup 1988; Hohmann and Sunderraj 1990; Bhat 1994; Ramachandran 1994; Easa *et al.* 1997; Singh *et al.* 1997a, b; Singh *et al.* 2000). The current population estimates of the number for wild groups is expected to be between 160 – 170, with 2,975 to 3,252 individuals (Lacy *et al.* 1996)

Several studies have been done on the ecology, demography and general behaviour of several free-ranging groups of this species (Sugiyama 1968; Green and Minkowski 1977; Johnson 1980; Kumar and Kurup 1981; Kumar 1987; Hohmann 1988; Karanth 1992; Kumar and Kurup 1993; Kumar 1995; Singh *et al.* 1998; Umapathy 1998; Menon and Poirier 1996; Kumar *et al.* 1998; Kumara *et al.* 2000; Singh *et al.* 2000 Umapathy and Kumar 2000).

Lion-tailed macaques usually live in groups of 8 – 40 animals, consisting of one to four adult males, five to eighteen adult females, one to five subadults, the remaining being juveniles and infants (Kumar 1995; Singh *et al.* 1998). The mean group size, reported for this species, is slightly less than that for other macaques (Fa and Lindburg 1996) and lies in the range of 20-30 individuals.

Like most other macaques, this species is omnivorous and is known to feed on items that are rich in simple carbohydrates or lipids (seeds, ripe fruits, flowers, gums, resins and nectar) and proteins (chiefly invertebrates, and rarely on smaller vertebrates such as lizards, the young of giant squirrels and flying squirrels, birds and bird eggs) (Kumar 1987; Kumara *et al.* 2000).

Births occur throughout the year with a peak between December and February (Kumar 1987; Kumar and Kurup 1993). The species is known to have a low birth rate of 0.28/female/year, with females usually giving birth first at an age of 6.5 years and exhibiting an inter-birth interval of about 2.5 years (Kumar 1987, 1995b).

Preliminary behavioural studies indicate that the principal group activities of ranging, foraging, feeding and resting differ across troops and are strongly influenced by group size, habitat quality and seasonal variation in food availability (Menon and Poirier 1996; Singh *et al.* 1998). Low levels of social interactions have been reported, with the adult males remaining at the periphery of the troop and rarely interacting with the other group members (Menon and Poirier 1996; Singh *et al.* 1998, A. Kumar *pers. comm.*). Detailed behavioural studies on the social behaviour, and long-term social strategies of identified individuals conducted in the wild are very few (Kumar 2000; Ananda Kumar 2001; Kumar 2001).

There is however, almost no information about dominance hierarchies, patterns and rates of inter-individual aggression and affiliation, or on patterns of social communication within free-ranging lion-tailed macaque groups.

On the other hand, there have been several behavioural studies on the social organisation and communication patterns exhibited by this species, but they have invariably been conducted on socially housed captive troops in western Europe and North America (Hohmann and Herzog 1984, 1985; Prosser 1988; Lindburg 1990; Birky 1993; Preuschoft 1995; Abegg *et al.* 1996).

The Anamalai Hills in the State of Tamil Nadu harbours a fairly large population of lion-tailed macaques (Singh *et al.* 1997). But in this region, due to a history of forest felling for commercial plantations such as tea, the rainforest habitats have become highly fragmented. Further, these fragmented patches of forest are subjected to varying degrees of human interference making these habitats very disturbed.

This project proposed to investigate the social organisation of an endangered, but ecologically well-studied, group of lion-tailed macaques in the Indira Gandhi Wildlife Sanctuary, located in the Anamalai hills, Tamil Nadu. Particular emphasis was laid on the social relationships, communication patterns and behavioural strategies of individually identified group members belonging to representative age- and sex-classes. It was projected that such a study would not only facilitate an understanding of the social behaviour of an extremely endangered, endemic, south Indian primate species, but would in the long run enable the design of species- and group-specific conservation and management strategies.

1.3 OBJECTIVES

This study proposed to investigate the social organisation of an ecologically threatened group of lion-tailed macaques in the Indira Gandhi Wildlife Sanctuary, Tamil Nadu. The specific issues addressed include:

- Construction of an ethogram for the species
- Estimation of a time activity budget for the group, to look at proportion of time allocated for various behaviours, by the individuals.

- Documentation of the social behaviour of identified individuals (adults and subadults) with special emphasis on the establishment and maintenance of dominance hierarchies, agonistic and affiliative relationships between adult females and males, the existence of cliques within hierarchies, levels of aggression and cohesion within and between such cliques.
- Description of the patterns of gestural and vocal communication between individuals.

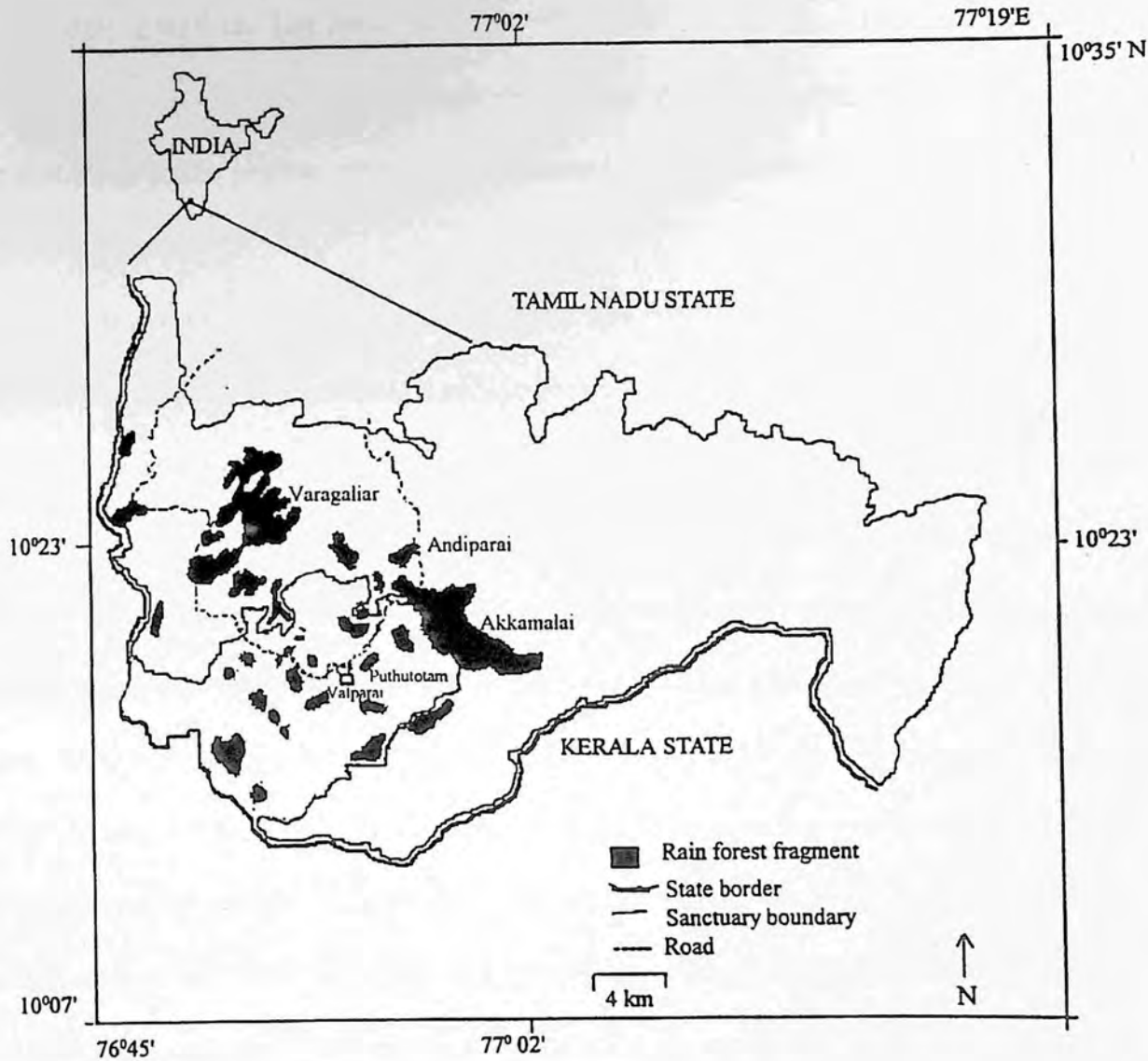
CHAPTER 2: STUDY AREA

The Indira Gandhi Wildlife Sanctuary ($10^{\circ}12' \text{ N}$ to $10^{\circ}54' \text{ N}$ and $76^{\circ} 44' \text{ to } 77^{\circ} 48' \text{ E}$) in the Anamalai hills of Tamil Nadu is one of the largest sanctuaries in south India, covering an area of about 987 km^2 . Almost at the centre of the sanctuary are nearly 180 km^2 of tea and coffee plantations, with Valparai town at their centre. The sanctuary is criss-crossed by a large network of roads, including three major public roads and a number of smaller roads connecting Valparai town to various estate settlements. The Anamalai hills once had extensive wet evergreen forests. In the early part of the history of deforestation there was extensive clear felling for cultivation of tea, coffee and chincona. In the recent years deforestation has occurred due to submergence caused by the construction of reservoirs, plantation of eucalyptus and development of roads and human habitations. Most of the landscape now exists as fragments amongst the matrix of plantations and settlements.

The altitude of the sanctuary ranges from 220 m in the foothills to 2513 m above mean sea level. The rainfall varies considerably, ranging from 500 mm in the eastern slopes to about 5,000 mm on its western slopes. The sanctuary receives both the southwest and the northeast monsoons, but with the former contributing to about 80% of the annual rainfall (Kumar *et al.* 1998). The temperature ranges between 4° C to 32° C during the year.

The study area (Fig.2.1) was one of the fragments within the sanctuary, the Puthutotam Estate fragment. The privately owned Puthutotam Estate ($10^{\circ} 20.468' \text{ N}$, 76

Fig. 2.1 : The map of Indira Gandhi Wildlife Sanctuary showing some of the rainforest fragments including the study area Puthutotam. (Source : Umapathy and Kumar 2000)



58.025'E), about 1.5 km from Valparai town on the Pollachi-Valparai Road, comprises approximately 65 hectares of wet evergreen forest (Pascal 1988), and is surrounded by tea estates on three sides and coffee plantation on the fourth. The fragment was isolated in 1906 and has absolutely no contiguity with any other forest patches. It has been selectively logged many times, the last time being in 1991 (Umapathy 1998). About half the area is under-planted with cardamom, although these areas are not presently being maintained. The adjoining coffee plantations have been planted with *Maesopsos eminii* as a shade tree.

Although heavily exploited for firewood and small timber by the local people, this fragment is known to be a permanent refuge for two troops of lion-tailed macaques, which have overlapping home ranges. It does not harbour any other species of primates except for a lone Nilgiri langur (*Trachypithecus johnii*) that occasionally entered the fragment during the study period. Other fauna that are present in the fragment include the Three striped Palm Squirrel (*Funambulus palmarum*) the Malabar giant squirrel (*Ratufa indica*), Large Brown Flying squirrel (*Petaurista petaurista philippensis*), Porcupine (*Hystrix indica*), Brown Palm Civet (*Paradoxurus jerdoni*), Brown mongoose (*Herpestes fuscus*), Stripednecked Mongoose (*Herpestes vitticollis*), Mouse deer (*Tragulus meminna*), Barking deer (*Muntiacus muntjak*), Sambar (*Cervus unicolor*), Gaur (*Bos gaurus*), and occasionally, Leopards (*Panthera pardus*) and Elephants (*Elephas maximus*) that pass through the fragment.

CHAPTER 3: METHODS

3.1 STUDY TROOP:

This study was conducted on a free-ranging group of lion-tailed macaques that inhabit the wet evergreen Puthutotam forest fragment, located within the Indira Gandhi Wildlife Sanctuary in the Anaimalai hills. The troop, under virtually continuous observation since 1993, is habituated to human observers.

The Puthutotam troop originally consisted of about 41 to 43 individuals (Menon 1993; Menon and Poirier 1996), which regularly split up into several foraging sub-groups (Sakthivelou and Kumar 1998). The area now supports two distinct troops of lion-tailed macaques having overlapping home ranges. Troop 1 is the larger of the two troops and comprises approximately 54 individuals, while Troop 2 consists of 19 individuals (*pers. obs.*).

Troop 2 was selected as the intensive troop for the study and all observations were made on individuals of this troop (Table 3.1). The troop consisted of 16 to 19 animals during the study period (from November, 2000 to April, 2001), the increase in number being due to the birth of three infants in January, February and April 2001, respectively.

For the purpose of this study, social interactions within and between adults and subadults alone have been considered. Focal animal sampling was thus conducted on only 10 individuals in the troop (Table 3.2).

Table 3.1: Age and sex composition of the study troop

INDIVIDUAL	AGE CLASS	SEX	PRESENT DURING	RELATED TO
NC	Adult	Male	Entire Study	
RM	Adult	Male	Entire Study	
SA	Adult	Male	Entire Study	
JI	Subadult	Male	Entire Study	BR
FC	Adult	Female	Entire Study	
NP	Adult	Female	Entire Study	
BR	Adult	Female	Entire Study	
LI	Adult	Female	Entire Study	
JN	Adult	Female	Entire Study	
BG	Adult	Female	Entire Study	
JK	Juvenile	Male	Entire Study	BR
NA	Juvenile	Male	Entire Study	NP
BA	Juvenile	Female	Entire Study	BR
BY	Juvenile	Female	Entire Study	BG
NM	Infant	Male	Entire Study	NP
BJ	Infant	Male	Born in January 2001	BR
BE	Infant	Female	Born in February 2001	BG
LX	Infant	Unknown	Born in April 2001	LI

Table 3.2: Dominance rank and body size rank of the study individuals and hours observed

Note that males and females have dominance ranks independent of each other but body size ranks have been assigned on a common scale.

INDIVIDUAL	SEX	DOMINANCE RANK	BODY SIZE RANK	HOURS OBSERVED
NC	MALE	4	5	20.00
RM	MALE	3	5	22.00
SA	MALE	2	4	20.25
JI	MALE	1	3	20.25
FC	FEMALE	4	3	20.25
NP	FEMALE	4	3	20.50
BR	FEMALE	3	3	20.75
LI	FEMALE	2	2	20.50
JN	FEMALE	1	1	20.25
BG	FEMALE	1	1	19.75

3.2 OBSERVED BEHAVIOUR

All the observed behaviour could be classified into *behavioural states* and *behavioural events*. Behavioural states refer to those behaviours that occur over a well-defined period of time, e.g. Sit, Sleep, Move, Stand, or Rest. Behavioural events, on the other hand, are instantaneous behaviours or those that occur with a certain frequency, but do not occupy any significant span of time. The behavioural events have been further categorised into *individual events* and *social events*. Individual events include self-directed behaviour such as Scratch or Autogroom and behaviours that an individual performs but are not directed towards any other individual or even itself in particular, e.g. Yawn, Urinate, Defecate. Social behavioural events have been further classified into Affiliation, Aggression, Dominance, Play, Sexual Behaviours, Infant-related Behaviours and Neutral Behaviours. The list of behaviours that were observed and used for analysis is given in Chapter 4, Section 4.1, while a complete ethogram has been included in Appendix 1.

3.3 FIELD METHODS

Behavioural data were collected from the study troop during a continuous period of five months from November 2000 to April 2001. Since the study troop had already been observed prior to this study, prior habituation of the troop to the presence of an observer was not necessary. Initial qualitative observations *ad libitum* for one month (November – December 2000) led to the identification and naming of all the adult individuals in the troop on the basis of their physiognomy as well as other facial and body marks. The study troop was found to be active approximately between 0600 H in the morning and 1800 H in the evening. Observations were thus conducted during this period of activity, the day being divided into two sessions: Morning (0600 – 1200 H) and afternoon (1200 – 1800 H).

The study troop, being accustomed to the presence of humans, allowed detailed observations at close range; binoculars were used to observe interactions as well as individual behaviour whenever the individuals were higher up on trees or were not clearly visible. No attempt was made to artificially feed or interfere otherwise with the normal activities of the study animals.

Behavioural data, used for this analysis, are based on approximately 204.5 hours of focal animal sampling (Altmann 1974) on the six adult females in the group, with a mean ($\pm$ SD) of 20.33 ($\pm$ 0.34) hours of sampling time per female, and four males (three adults and one subadult), with a mean ($\pm$ SD) of 20.63 ($\pm$ 0.92) sampling hours per male (Table 3.2). Each focal sample of an individual, chosen randomly without replacement, had a duration of 15 min. Observations were made on all individual behavioural events as well as all social interactions of the focal animal with every other adult and subadult individual in the group. The number of focal animal samples per individual was distributed equally over the two time sessions of the day.

Each focal animal sample was initiated with an instantaneous scan (Altmann 1974) on the focal animal. Scans were conducted to sample behavioural states in order to calculate time-activity budgets for the different individuals. The forest was broadly divided into four strata – ground, undergrowth, intermediate trees or branches, and canopy – and the position of the individual on these strata also recorded during the instantaneous scan. Finally, proximity measures of the focal individual, relative to all the other troop members, were also estimated during these scans. The three proximity measures that have been considered in this analysis include: sitting in contact, sitting close (within $\frac{1}{2}$ metre of each other), and sitting between $\frac{1}{2}$ m to 3 m of each other.

3.4 ANALYTICAL METHODS

A comprehensive detailed ethogram defining and describing the various behaviours observed during the study period has been prepared and included as Appendix 1.

The data on behavioural states, collected by instantaneous scans on the different individuals, have been analysed in terms of the proportion of time spent in various behavioural states. The proportion of time spent in a behavioural state j by an individual i was calculated as:

$$\frac{S_{ij}}{T_i}$$

where S_{ij} is the number of scans in which individual i displayed behaviour j and T_i the total number of scans conducted on individual i .

Data on both individual events as well as social interactions, recorded during focal animal sampling, have been analysed in terms of the frequency of events initiated per hour. The frequency of a particular behavioural event j displayed by an individual i was thus calculated as:

$$\frac{n_j}{N_i},$$

where n_j is the number of times individual i displayed behaviour j and N_i the total duration of time (in h) that individual i was observed. For dyadic social interactions, such frequencies were obtained from the focal animal samples of both the individuals involved in the interactions.

For certain behaviours of particular interest, e.g. Autogroom and Allogroom, in addition to their initiated frequencies, the proportion of time spent in these particular

behavioural states were also noted. Accordingly, the proportion of time in which an individual i directed allogrooming towards an individual j was calculated as:

$$\frac{t_{ij}}{T_{ij}},$$

where t_{ij} is the total time spent by individual i in grooming individual j , and T_{ij} the total time that dyad i - j was observed.

Apart from the frequencies for the different behaviours, a cumulative frequency for certain interactions such as Affiliation, Total Aggression, Non-contact Aggression, Contact Aggression, Dominance, and Submission were also calculated.

Affiliation is a composite behaviour of 17 affiliative behaviours including Affiliative Bared-teeth Face, Affiliative Grunt, Allogroom, Allogroom with Lip-smacking, Follow, Friendly Approach, Hold, Hug, Mouth-touch, Pat, Raise Brow, Seek Allogrooming, Seek Support, Sit Close, Sit in Contact, Sleep Together, and Touch.

Total Aggression is also a composite behaviour, constituted by agonistic interactions of two kinds: Contact aggression and Non-contact Aggression. *Contact Aggression*, involving actual physical contact between the adversaries, includes the acts of Aggressive Bite, Pull Roughly, Push Away, and Strike with Contact. *Non-contact Aggression*, in contrast, consists of agonistic interactions at a distance that do not involve any physical contact; these include Aggressive Bark, Bared-teeth Display, Branch Shake, Chase, Display Bounce, Eye-flash, Lunge, Open-mouth Threat, Strike without Contact and Warning Growl.

Dominance is a composite behaviour comprising of Aggressive Approach and Approach Retreated From.

Submission is a composite behaviour that is constituted by submissive responses including Crouch, Fear Grimace, Flee and Retreat.

Dominance hierarchies were independently assigned, within the six females and the four males, respectively, on the basis of the direction and frequency of both Aggressive Approach and Approach Retreated From between each pair of females and each pair of males. Decreasing ranks (corresponding to relatively lower positions in the hierarchy) were given lower numerical values, as indicated in Table 3.2.

A measure of social affiliation, Hinde's Index (Hinde and Atkinson 1970, Hinde 1983), was also enumerated separately for individuals A and B within each dyad. This index was calculated as:

$$CM_{AB} - MA_{AB} ,$$

where CM_{AB} is the frequency with which individual A displayed Friendly Approach towards individual B and MA_{AB} the frequency with which it Moved Away from B. Friendly Approach refers to any approach made by an individual towards another followed by either the two individuals sitting in contact or displaying any affiliative behaviour towards each other. Correspondingly, Moving Away refers to the moving away of an individual from another, terminating thereby either an act of sitting together in contact or the display of any affiliative behaviour towards each other. Positive values of the Hinde's Index, a measure of the interest shown by an individual towards maintaining an affiliative social relationship with another, indicate a positive interest in the relationship while negative values signify a lack of such interest.

A Body Size Rank scale was established in order to assign all the individual males and females into a single linear scale of different relative size classes (Table 3.2). Relatively larger individuals were given larger numerical values, as indicated in Table 3.2.

During the analysis of vocal communication patterns, the Contact Call and the Long Call have both been divided into three categories each: Calls with positive response. Calls with negative response and Reply call. Analysis was carried out independently on the frequency of occurrence of all these categories.

The analysis of the data has primarily employed non-parametric statistical tests (Siegel 1956; Sokal and Rohlf 1995, Rohlf and Sokal 1995). The principal tests that have been performed include Kendall's rank correlation, G test of independence, Mann-Whitney U test, Kruskal-Wallis test and simple linear regression. In cases where multiple parameters correlated with each other, non-parametric partial correlations were carried out. All tests, unless otherwise specified, are one-tailed. The statistical software – Statistica (Version 4.5) (Statistica 1994) and SPSS (Version 8.0) (SPSS Inc. 1999) were used for analysis. For the analysis of communication patterns, multi-dimensional scaling was used to obtain a graphical representation of differences in the display of gestures and vocalisations across the study individuals.

CHAPTER 4: RESULTS

4.1 ETHOGRAM

A detailed list of all the behavioural states and events that were observed in the study troop and used for analysis is given in Table 4.1. A complete ethogram has also been included in Appendix 1.

4.2 TIME-ACTIVITY BUDGETS

The time apportioned to different behavioural states, as well as the spatial and temporal correlates of these states, were analysed from the data on instantaneous scans in order to characterise the time-activity budgets for the different individuals in the study troop.

Behavioural states:

The relative proportion of time dedicated to different behaviours by the study individuals is shown in Table 4.2. On an average, the predominant behavioural states among all the individuals were Active Forage (mean $\pm$ SD of $22.4 \pm 0.08\%$), Active Feed ($17.0 \pm 0.05\%$), Sit ($16.6 \pm 0.04\%$), Move ($13 \pm 0.03\%$), Passive Forage ($6.8 \pm 0.02\%$) and Passive Feed ($6.5 \pm 0.02\%$).

The adult males and females of the study troop differed in the proportion of time spent by them in the different behavioural states (G-test of independence, $G = 49.200$, $p < 0.001$). Autogroom and Allogroom accounted for the principal difference between the sexes; adult males spent relatively greater time Autogrooming than did the females (Kruskal-Wallis test, $KW = 6.936$, $p < 0.01$), while females Allogroomed relatively more

Table 4.1. List of behavioural states and events observed

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Table 4.2: Relative proportion of time spent in different behavioural states by the study individuals.

INDIVIDUAL	Sit	Sit Alert	Sleep	Move	Active Forage	Passive Forage	Active Feed	Passive Feed	Drink
Males:									
NC	0.138	0.000	0.013	0.138	0.100	0.075	0.225	0.063	0.000
RM	0.193	0.023	0.011	0.193	0.091	0.102	0.182	0.057	0.000
SA	0.173	0.012	0.012	0.123	0.210	0.025	0.198	0.086	0.000
JI	0.160	0.025	0.000	0.086	0.284	0.062	0.198	0.111	0.012
Females:									
FC	0.207	0.012	0.012	0.159	0.244	0.073	0.073	0.073	0.012
NP	0.268	0.037	0.000	0.110	0.183	0.098	0.122	0.061	0.000
BR	0.133	0.012	0.000	0.108	0.253	0.036	0.265	0.036	0.000
LI	0.134	0.000	0.037	0.146	0.256	0.073	0.159	0.061	0.000
JN	0.111	0.000	0.000	0.123	0.395	0.049	0.111	0.037	0.000
BG	0.139	0.000	0.000	0.114	0.228	0.089	0.165	0.063	0.000

INDIVIDUAL	Survey	Stand	Stand Alert	Receive Grooming	Scratch	Allogroom	Play	Rest	Autogroom
Males:									
NC	0.050	0.000	0.000	0.075	0.025	0.000	0.000	0.038	0.063
RM	0.011	0.034	0.000	0.000	0.000	0.011	0.000	0.045	0.034
SA	0.025	0.012	0.000	0.012	0.025	0.000	0.012	0.037	0.037
JI	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.012	0.025
Females:									
FC	0.024	0.024	0.000	0.024	0.024	0.024	0.000	0.012	0.000
NP	0.000	0.012	0.000	0.073	0.000	0.024	0.000	0.000	0.000
BR	0.000	0.024	0.000	0.036	0.000	0.072	0.000	0.024	0.000
LI	0.000	0.037	0.012	0.012	0.012	0.024	0.000	0.012	0.024
JN	0.000	0.025	0.000	0.025	0.025	0.037	0.000	0.025	0.000
BG	0.000	0.025	0.000	0.025	0.051	0.076	0.000	0.025	0.000

(KW = 6.923, $p < 0.01$). Interestingly, males also tended to Active Feed (KW = 3.366, $p = 0.07$), Survey (KW = 2.849, $p = 0.09$) and Rest (KW = 3.077, $p = 0.08$) more than females, while females exhibited a tendency to dedicate a relatively greater proportion of time to Active Forage (KW = 3.36, $p = 0.10$); note, however, that none of these results are statistically significant at a probability level of 0.05, perhaps due to small sample sizes (Figure 4.1).

Temporal and spatial correlates of behavioural states

The distribution of behavioural activities, displayed by the troop, varied over the course of the day, and significant differences emerged between the performance of behaviours by individuals across both morning ($G = 29.502$, $p < 0.005$) and afternoon ($G = 25.712$, $p < 0.005$). Within each of the sexes, however, there were no differences in the activity patterns between the two different times of the day (males: $G = 16.214$, $p > 0.05$; females: $G = 11.88276$, $p > 0.05$).

The two sexes displayed significant differences in the utilisation of the four habitat strata ($G = 32.907$, $p < 0.001$). Males spent more time on the ground, while females were more frequently observed on intermediate trees and branches, as well as in the canopy (Table 4.3). Moreover, the group, as a whole, exhibited differential use of strata during the morning ($G=25.864$ $p < 0.001$) and the evening ($G = 11.113$, $p < 0.025$). This appeared to be due primarily to the females, who spent more time in the canopy and intermediate trees in the morning and increased their use of the ground in the afternoon ($G = 11.296$, $p < 0.01$). Males, in contrast, did not differ in the utilisation of habitat strata across the day ($G = 3.881$ $p < 0.5$).

Figure 4.1: Relative proportion of time spent by males and females in different behavioural states.

The asterisks represent statistically significant differences between the two sexes (see text for details). Act.Frg. = Active Forage; Pass.Frg. = Passive Forage; Act.Feed = Active Feed; Pass.Feed = Passive Feed

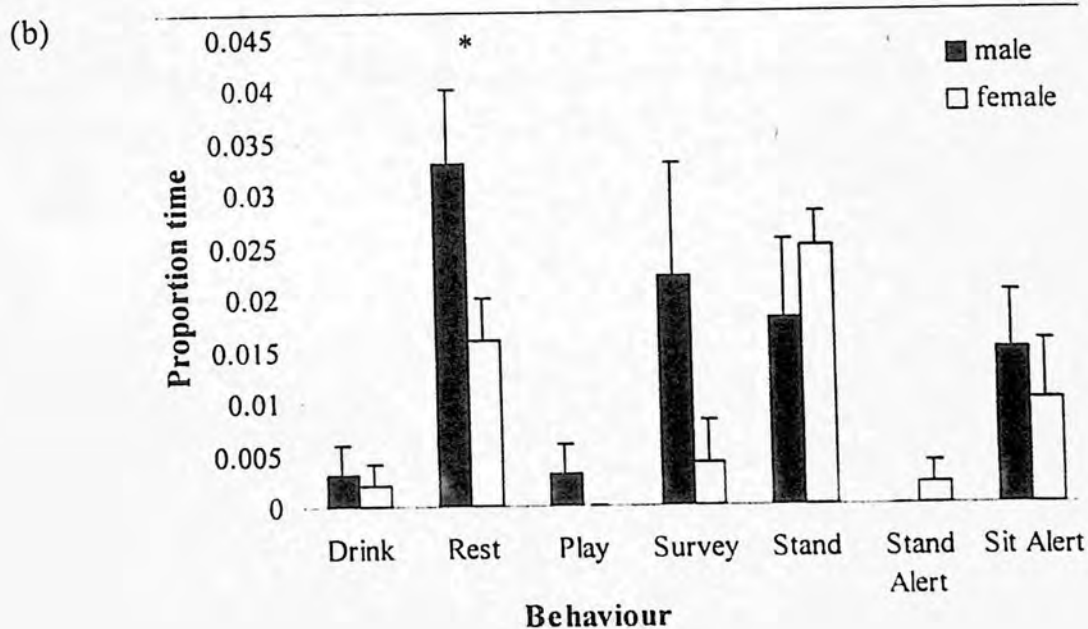
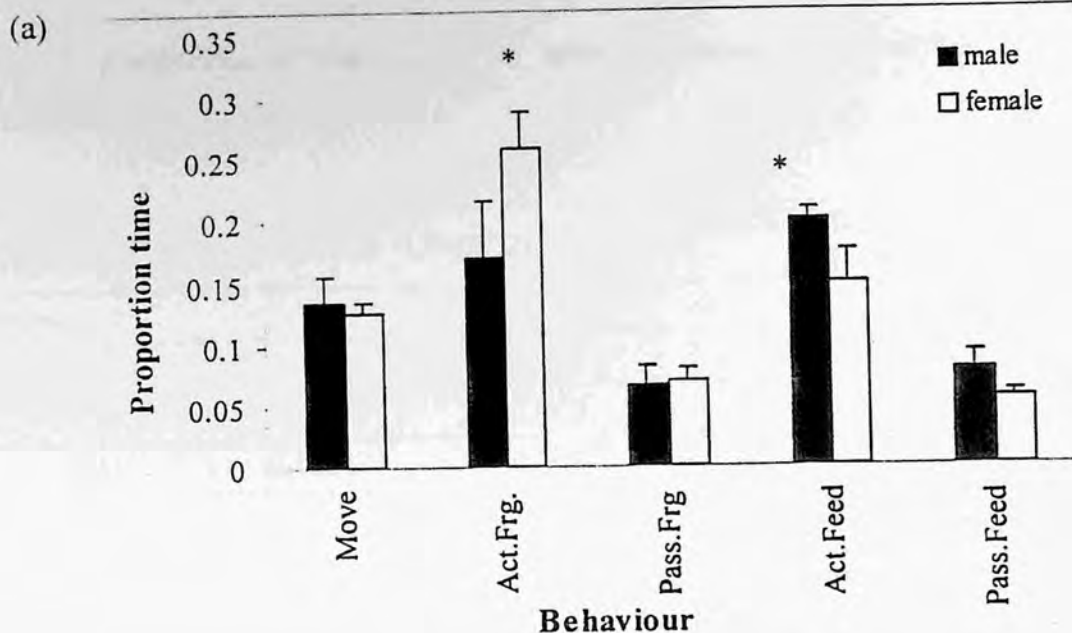


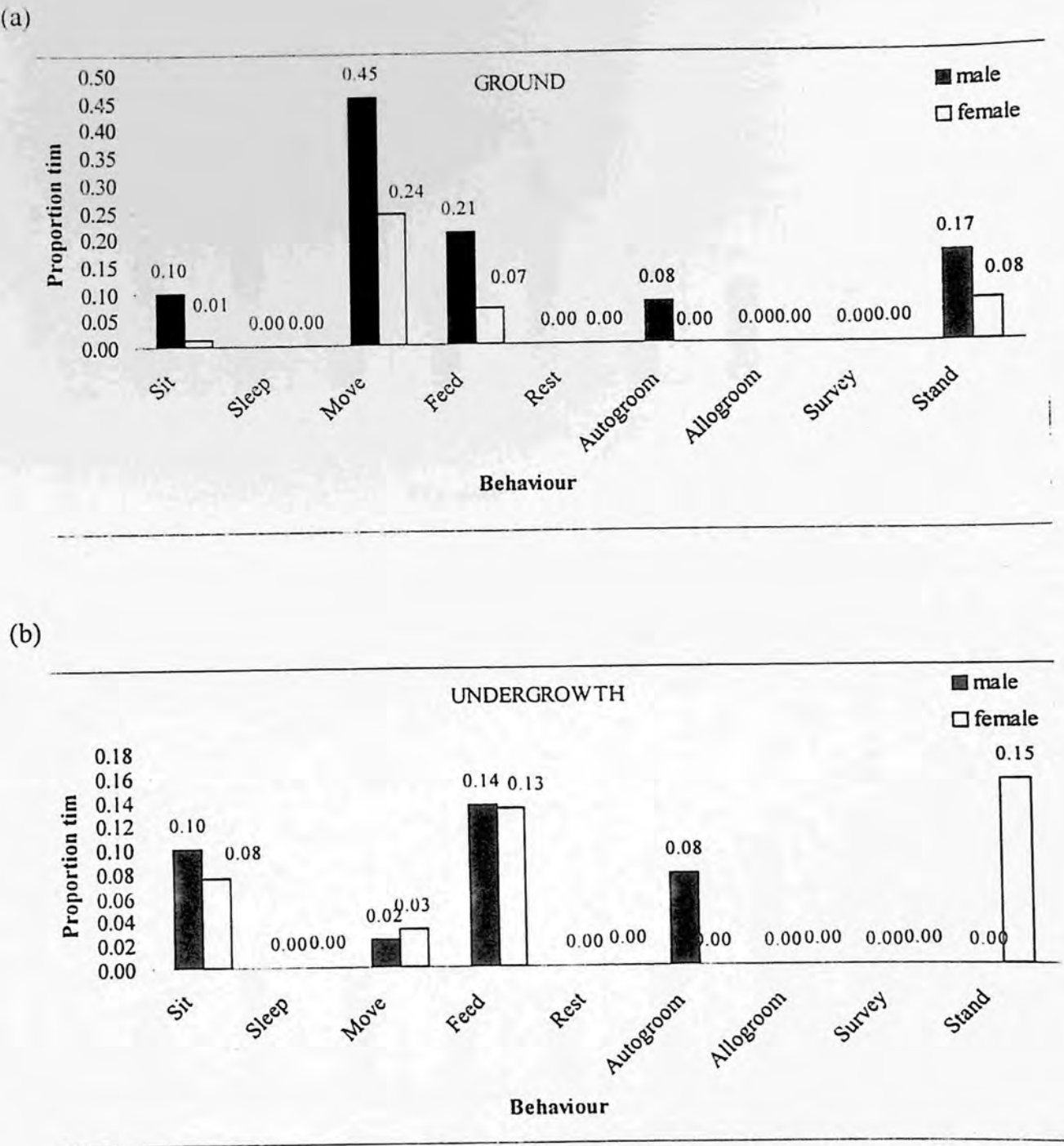
Table 4.3: Proportion of time spent by each individual in the different strata of the habitat

INDIVIDUAL	GROUND	UNDERGROWTH	INTERMEDIATE TREES	CANOPY
Males:				
NC	0.225	0.088	0.375	0.313
RM	0.250	0.080	0.398	0.273
SA	0.185	0.099	0.469	0.247
JI	0.123	0.123	0.519	0.235
Females:				
FC	0.061	0.061	0.585	0.293
NP	0.049	0.098	0.646	0.207
BR	0.133	0.108	0.554	0.205
LI	0.085	0.134	0.622	0.159
JN	0.025	0.062	0.667	0.247
BG	0.101	0.127	0.494	0.278

There was a clear differential use of habitat strata for the display of certain behaviours by the study troop (Figure 4.2). Sit, for example, was observed more on higher strata, namely the canopy and intermediate trees, for the group as a whole ($G = 54.005$, $p < 0.001$), as well as for females ($G = 44.428$, $p < 0.001$) and males ($G = 14.888$, $p < 0.005$), considered independently. The troop also exhibited a differential pattern for Move ($G = 27.289$, $p < 0.001$), with females preferentially moving on intermediate trees ($G = 19.683$, $p < 0.001$) and males on the ground ($G = 12.727$, $p < 0.025$). Intermediate trees and branches were preferred as sites for Foraging and Feeding (taken together) by all individuals in the group (group: $G = 77.566$, $p < 0.001$; females: $G = 75.272$, $p < 0.001$; males: $G = 14.384$, $p < 0.005$). The group, as a whole, and males preferentially used this stratum for Rest as well (group: $G = 17.945$, $p < 0.001$; males: $G = 11.246$, $p < 0.025$), although females did not seem to show any particular habitat preference for this behaviour ($G = 7.075$, $p > 0.1$). The members of the study troop were observed to Survey the surrounding area primarily from the canopy ($G = 8.451$, $p < 0.05$), although no significant difference could be detected when males and females were considered separately (males: $G = 6.750$, $p > 0.1$; females: $G = 1.726$, $p > 0.9$). No such differential habitat use was evident for certain other behaviours like Sleep or Stand (Figure 4.2).

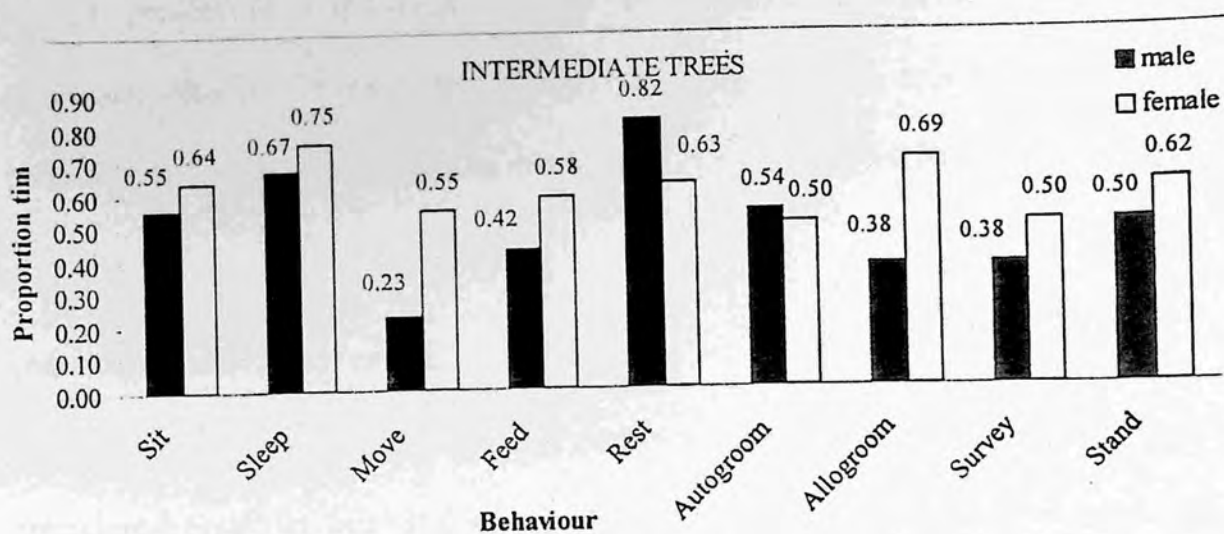
The study individuals did not appear to discriminate between different habitat strata while Autogrooming (group: $G = 5.143$, $p > 0.5$; females: $G = 1.726$, $p > 0.9$; males: $G = 3.990$, $p > 0.5$), although they did appear to do so when Allogrooming. The group and the females, thus, preferred intermediate trees and the canopy to Allogroom (group: $G = 39.395$, $p < 0.001$; females: $G = 33.307$, $p < 0.001$), but the males did not show any such preference ($G = 3.990$, $p > 0.5$).

Figure 4.2: Proportion of time spent by males and females in different behavioural states in the different habitat strata

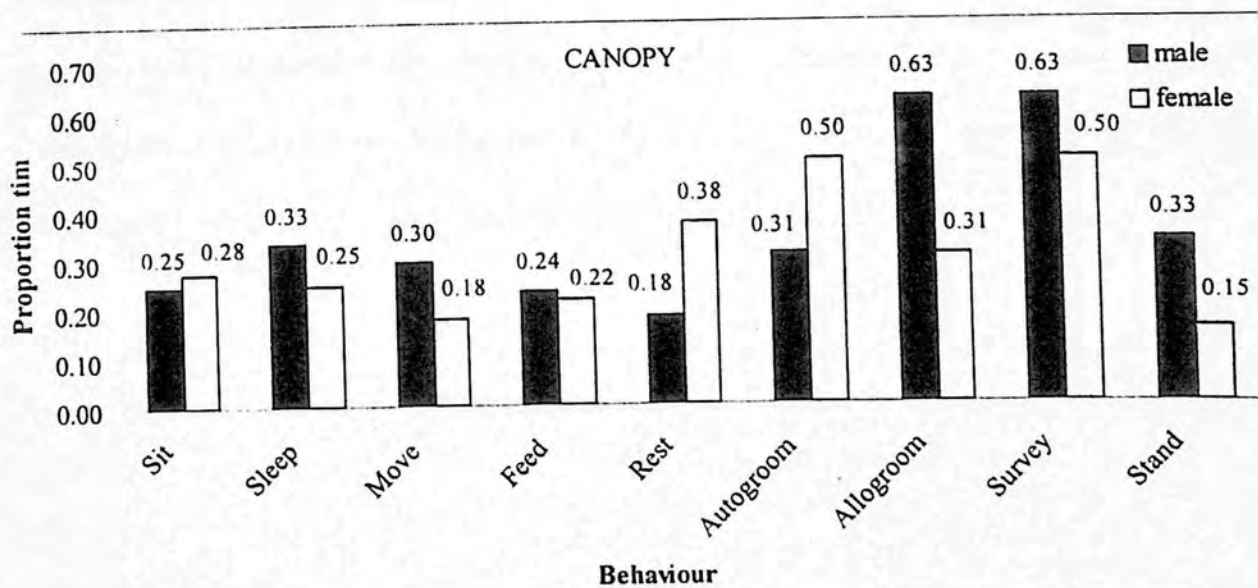


Continued ...

(c)



(d)



Among the females, the proportion of time dedicated to Rest decreased significantly with an increase in dominance rank (Kendall's rank correlation, $\tau = -0.741$, $p < 0.05$), while larger individuals were observed to Sit Alert more often than did relatively smaller females ($\tau = 0.957$, $p < 0.01$). When correlations across behaviours were examined, only the males demonstrated a strong positive correlation between the proportions of time spent in Moving and Resting ($\tau = 1.000$, $p < 0.05$).

Individual behavioural events

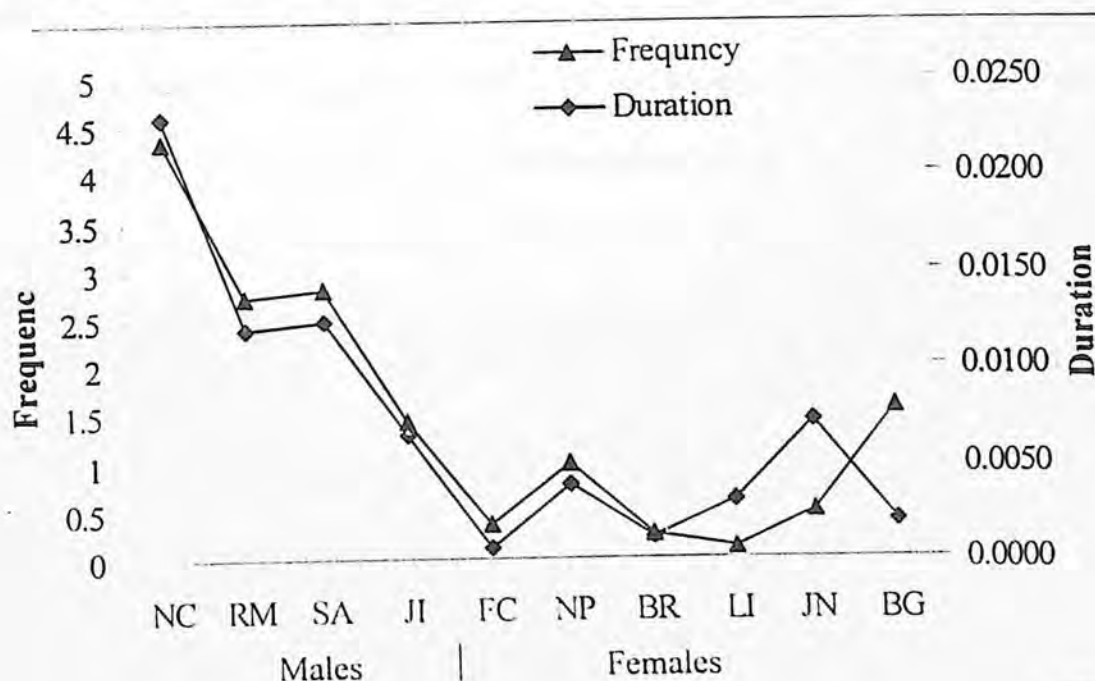
The frequency with which the study individuals displayed the different individual behavioural events has been shown in Table 4.4. What is most remarkable is that the males initiated significantly more events of Autogrooming than did adult females (Kruskal-Wallis test, $KW = 5.500$, $p < 0.02$); as mentioned above, they also spent a relatively greater proportion of time Autogrooming (Figure 4.3; $KW = 6.936$, $p < 0.01$). Males also Scratched themselves more frequently than did females ($KW = 4.545$, $p < 0.05$). In general, there appeared to be significant individual variation among the different study individuals with regard to the display of many of the individual behaviours (Table 4.4), although the small sample sets preclude rigorous statistical analysis.

Table 4.4: Frequency of individual behavioural events displayed by the study individuals.

The frequency has been measured in terms of events/hour

	MALES →					FEMALES →				
ANIMAL → BEHAVIOUR ↓	NC	RM	SA	JI	FC	NP	BR	LI	JN	BG
Alarm Call	0.000	0.000	0.000	0.000	0.000	0.244	0.241	0.585	0.000	0.000
Autogroom	4.350	2.727	2.815	1.432	0.346	0.976	0.241	0.098	0.494	1.570
Body Shake	0.300	0.182	0.148	0.247	0.148	0.195	0.145	0.000	0.198	0.152
Cough	0.000	0.000	0.000	0.247	0.000	0.000	0.048	0.098	0.099	0.000
Defecate	0.250	0.045	0.099	0.198	0.000	0.098	0.096	0.049	0.148	0.101
Lick Hand	0.050	0.182	0.049	0.099	0.494	0.098	0.000	0.000	0.395	0.101
Masturbate	0.000	0.045	0.148	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rub Body	0.400	0.364	0.148	0.642	0.395	0.000	0.048	0.244	0.444	0.152
Scratch Body	6.950	4.864	5.333	2.963	2.815	1.512	1.735	2.537	3.704	3.291
Sneeze	0.100	0.727	0.148	0.346	0.099	0.146	0.048	0.000	0.000	0.000
Stretch	0.000	0.000	0.000	0.049	0.000	0.000	0.000	0.000	0.000	0.000
Swipe at Insect	0.100	0.227	0.148	0.099	0.099	0.049	0.000	0.049	0.000	0.101
Urinate	0.100	0.318	0.198	0.049	0.346	0.293	0.145	0.146	0.346	0.304
Wipe	0.100	0.182	0.049	0.099	0.494	0.000	0.000	0.049	0.444	0.000
Yawn	0.300	0.000	0.296	0.148	0.000	0.000	0.000	0.049	0.148	0.000

Figure 4.3: The frequency (Events per hour) and duration (Proportion time) of Autogrooming exhibited by the study individuals



4.3 SOCIAL RELATIONSHIPS

Dominance ranks were calculated independently for males and females in the study troop on the basis of the frequency of Aggressive Approach and Approach Retreated From, as shown in Table 3.2. While the dominance hierarchy exhibited by the four males was distinct, linear and transitive, that shown by the six females had two pairs of individuals where the relative rank position remained unclear. One of these pairs was that of the two most dominant females – FC and NP – who had not displayed any act of Aggressive Approach or Approach Retreated From towards each other and who were, therefore, assigned the highest rank of 4. The other pair was between the two lowest-ranking females – JN and BG – who had both demonstrated Approach Retreated From towards each other at the same frequency, and who were consequently each assigned the rank 1.

An interesting observation in the study troop was that, among both males and females, rank position in the dominance hierarchy appeared to be influenced strongly by body size as monitored by Body Size Rank. Linear regression analysis (males: $R^2 = 0.89$; females: $R^2 = 0.92$) (Figure 4.4) showed that relatively larger individuals were dominant over smaller individuals, an unusual finding for the females of a cercopithecine primate species. The Body Size Rank also varied considerably across the two sexes although the males in the study troop were significantly larger than the females (Mann-Whitney U test, $U = 1.00$, $p < 0.02$).

The two sexes showed an interesting difference in grooming patterns (Fig. 4.5). Females were observed to Allogroom more than males, and this was consistent for both frequency and duration of Allogrooming. Males, in contrast, Autogroomed much more frequently ($U = 0$, $p = 0.01$) and for longer durations than did the females ($U = 3$, $p =$

Figure 4.4 Relationship between dominance rank and body size rank among (a) males and (b) females in the study troop.

Data are based on an evaluation of all four adult males and six adult females. See Chapter 3 for definitions of dominance rank and body size rank

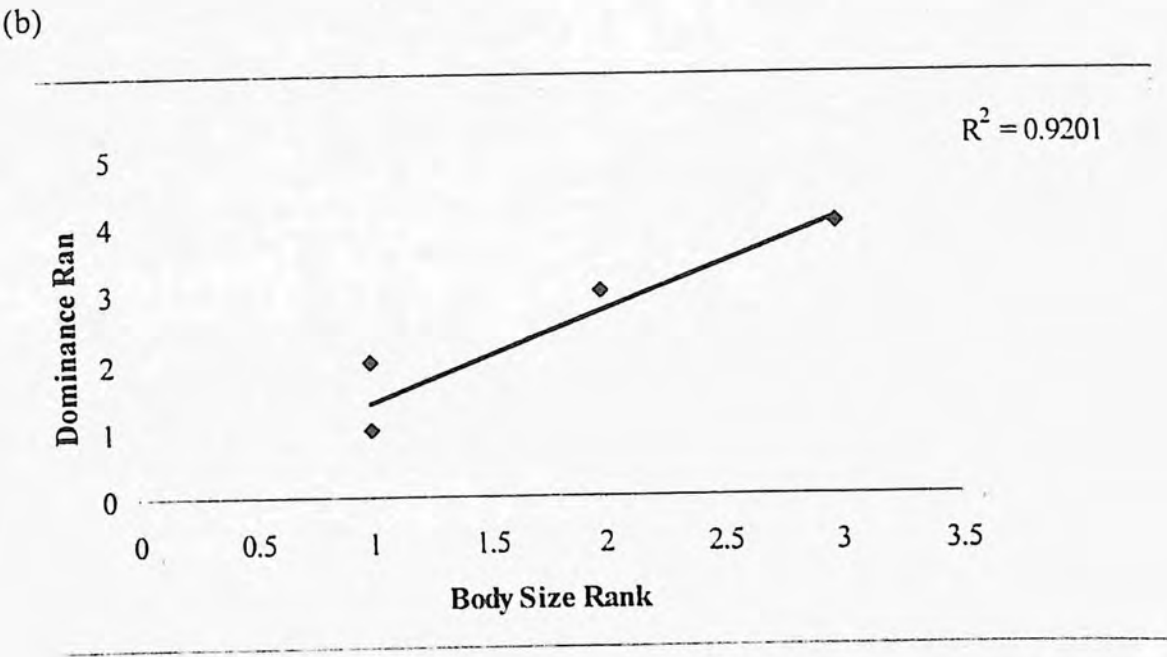
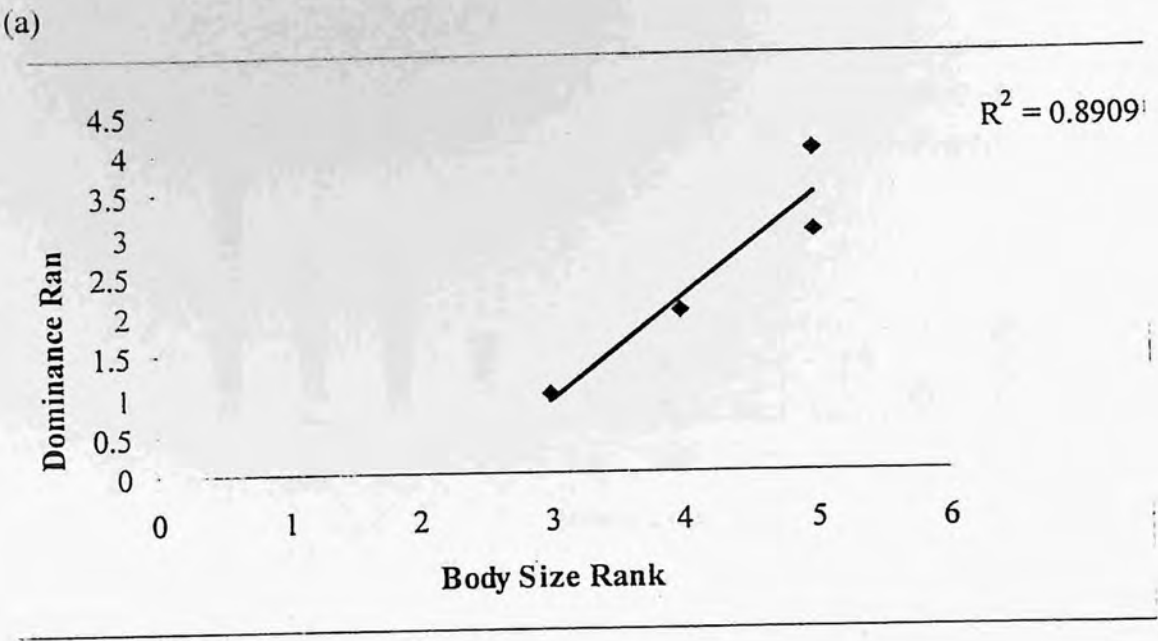
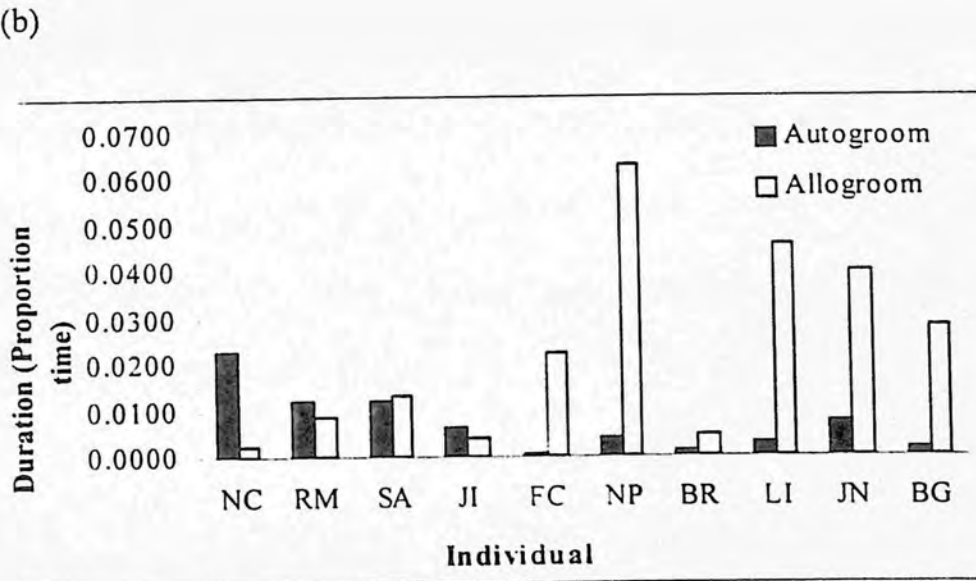
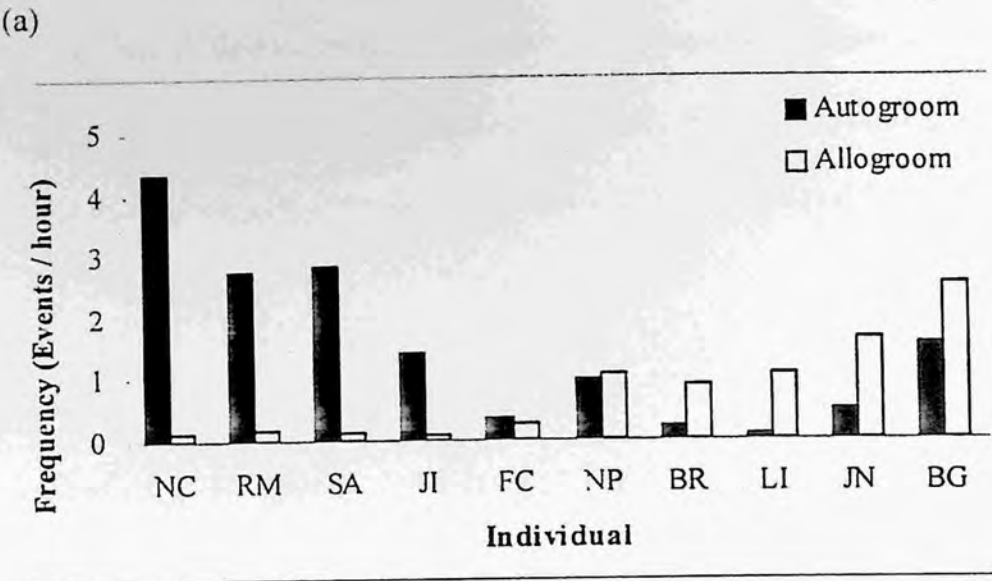


Fig 4.5. Variation of Allogrooming and Autogrooming (a) frequency and (b) duration across individuals.

NC, RM, SA and JI represent the four males and FC, NP, BR, LI, JN and BG the six females in the study



0.03). Moreover, among females, Submission was positively correlated with both Allogrooming frequency ($\tau = 0.393$, $p < 0.005$) and duration ($\tau = 0.400$, $p < 0.002$). Subordinate females were also observed to groom their dominant counterparts for longer durations than the other way around ($U = 40$, $p < 0.05$). Allogrooming frequency also increased as rank difference between the interacting females progressively decreased ($\tau = -0.257$, $p < 0.05$). Finally, Allogrooming duration and Allogrooming frequency were strongly positively correlated to each other ($\tau = 0.791$, $p < 0.001$) (Fig.4.6).

Spatial proximity and social behaviour

When the possible connections between the three proximity classes and the frequency of various social interactions were examined, Allogrooming frequency ($\tau = 0.500$, $p < 0.01$), as well as duration ($\tau = 0.480$, $p < 0.02$) were each positively correlated to the proportion of time spent Sitting in Contact. Aggression ($\tau = -0.410$, $p < 0.05$), Affiliation ($\tau = 0.404$, $p < 0.05$) and one particular submissive behaviour – Mount with Lip-smacking ($\tau = 0.397$, $p < 0.05$) – were correlated to Sitting Within Half Metre of each other. Mount ($\tau = 0.404$, $p < 0.05$) and Present ($\tau = 0.404$, $p < 0.05$) were both observed to correlate with Sitting Between $\frac{1}{2}$ and 3 Metres of each other.

Social relationships among males

Correlations between the various attributes, such as dominance rank and Body Size Rank, and the different behavioural interactions displayed by the males in the study troop are shown in Table 4.5. With regard to dominance and agonistic relationships, larger males induced retreat of smaller individuals at relatively higher frequencies. (Total) Aggression, Contact Aggression and Non-contact Aggression are positively correlated to the display of

Figure 4.6 Relationship between Allogrooming duration and frequency.

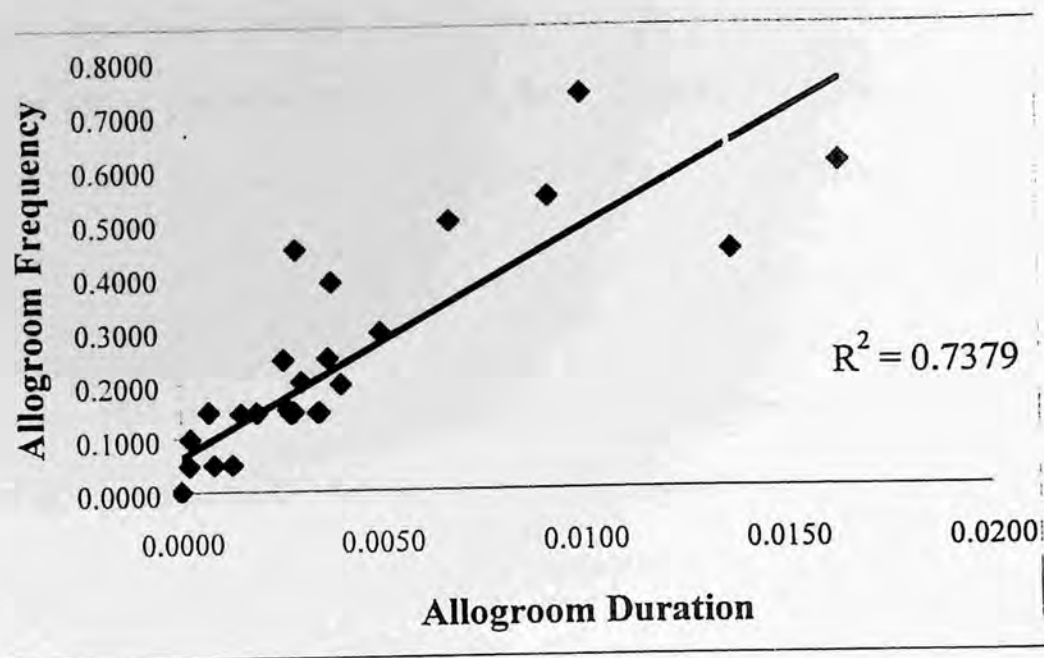


Table 4.5 Correlation between dominance rank, Body Size Rank and various behaviours that characterise social relationships among males.

Note that, for the four males, the number of male-male dyads, N = 12. Only statistically significant results ($p \leq 0.05$) have been shown

Parameters	τ	p
Target Body Size Rank and Retreat	0.459	0.038
Aggression and Dominance	0.689	0.002
Non-Contact Aggression and Dominance	0.689	0.002
Contact Aggression and Dominance	0.494	0.025
Aggression and Submission	-0.706	0.001
Non-Contact Aggression and Submission	-0.706	0.001
Aggression and Retreat	-0.706	0.001
Non-Contact Aggression and Retreat	-0.706	0.001
Dominance and Retreat	-0.626	0.005
Target Dominance Rank and Affiliation	0.503	0.023
Dominance Rank Difference and Seek	0.435	0.049
Grooming – with Positive Response	0.976	0.000
Allogroom duration and Allogroom frequency	0.467	0.034
Allogroom Duration and Friendly Approach	-0.434	0.050
Hinde's Index and Rank Difference	-0.492	0.026
Hinde's Index and Dominance	0.483	0.029
Hinde's Index and Allogroom	0.443	0.045
Hinde's Index and Allogroom duration	0.438	0.048
Hinde's Index and Affiliation		

Dominance, Aggression and Non-contact Aggression were both negatively correlated to Submission as well as to Retreat. Dominance was also negatively correlated to Retreat. When agonistic interactions directed down the dominance hierarchy were considered, actor Body Size Rank alone was positively correlated to Contact Aggression ($\tau = 0.282$, $p < 0.005$).

When affiliative interactions in male-male dyads were investigated, Affiliation was observed to be preferentially directed towards higher-ranking males (Table 4.5). Rank difference was positively correlated to the frequency of Seek Grooming with Positive Response: solicitations for allogrooming were thus favourably responded to as progressively dominant individuals solicited subordinate males. Allogrooming duration was positively correlated to both Allogrooming frequency and Friendly Approach. Hinde's index was negatively correlated to both rank difference as well as Dominance. This indicated that males were averse to maintaining affiliative relationships with males who were increasingly subordinate to them and to those towards whom they display increasing levels of Dominance. As could be predicted, Hinde's index was positively correlated to Affiliation as well as Allogrooming frequency and duration. Interestingly, however, analysis of dyadic interactions failed to reveal any significant difference in the actual levels of different affiliative behaviours interchanged between dominant and subordinate individuals.

Social relationships among females

Correlations between the various attributes, such as dominance rank and Body Size Rank, and the different behavioural interactions displayed by the females in the study troop are shown in Table 4.6. Larger animals were observed to initiate Contact Aggression more

Table 4.6 Correlation between dominance rank, Body Size Rank and various behaviours that characterise social relationships among females.

Note that, for the six females, the number of female-female dyads, $N = 30$. Only statistically significant results ($p \leq 0.05$) have been shown

Parameters	τ	P
Actor Body Size Rank and Contact Aggression	0.271	0.035
Dominance Rank Difference and Aggression	0.644	0.000
Dominance Rank Difference and Non-Contact Aggression	0.661	0.000
Aggression and Dominance	0.430	0.001
Non-Contact Aggression and Dominance	0.427	0.001
Contact Aggression and Mount	0.266	0.039
Submission and Mount with Lip-Smacking	0.263	0.041
Friendly Approach and Move Away	0.359	0.005
Dominance and Move Away	0.267	0.038
Hinde's Index and Affiliation	0.366	0.005

often, and such aggression was preferentially directed towards smaller females. Frequency of both (Total) Aggression and Non-contact Aggression were also correlated to the rank difference between the actor and the target. In general, dominant females typically exhibited Aggression towards their subordinate counterparts. Among the behaviours, the display of Contact Aggression was positively correlated to Mounting, while Submission was positively correlated to Mounting with Lip-smacking.

When affiliative relationships between the females were characterised, the frequency of Friendly Approach was observed to positively correlate with Move Away (Table 4.6). Dominance was also seen to be positively correlated to the act of Move Away. As was expected, Hinde's index was positively correlated to the display of Affiliation.

Social relationships between males and females

Correlations between the various attributes, such as dominance rank and Body Size Rank, and the different behavioural interactions displayed between the males and females in the study troop are shown in Table 4.7. Female Body Size Rank was negatively correlated to the amount of Dominance received by her – males thus tended to Dominate smaller females. Correspondingly, male Body Size Rank was negatively correlated to Submission exhibited by males. As could be expected, the size difference between individuals was negatively correlated to Submission and positively correlated to Dominance. Dominance was also positively correlated to (Total) Aggression, Non-contact Aggression and Contact Aggression.

Table 4.7 Correlation between dominance rank, Body Size Rank and various behaviours that characterise social relationships between males and females.

Note that, for the four males and six females, the number of male-female dyads, $N = 24$. Only statistically significant results ($p \leq 0.05$) have been shown

Parameters	τ	p
Female Body Size Rank and Dominance	-0.391	0.007
Male Body Size Rank and Submission	-0.294	0.044
Body Size Rank Difference and Submission	-0.291	0.046
Body Size Rank Difference and Dominance	0.382	0.009
Aggression and Dominance	0.337	0.021
Non-Contact Aggression and Dominance	0.327	0.025
Contact Aggression and Dominance	0.289	0.048
Hinde's Index and Affiliation	0.296	0.042
Dominance Rank Of Male and Sexual Mount	0.365	0.012
Dominance Rank Of Male and Inspect	0.399	0.006
Body Size Rank Of Male and Inspect	0.407	0.005

Among the affiliative behaviours, the Hinde's index was positively correlated to the display of Affiliation (Table 4.7). Interestingly, females Friendly Approached progressively higher-ranking males at increasing frequency ($\tau = 0.317$, $p < 0.05$).

When interactions directed by males towards females and by females towards males were compared, females showed significantly higher frequencies of Submission ($U = 91$, $p < 0.001$), Retreat ($U = 142.5$, $p < 0.001$) and Present ($U = 150$, $p < 0.001$) towards males than the other way around. Correspondingly, males showed relatively higher levels of Dominance ($U = 148$, $p < 0.01$) as well as Contact Aggression ($U = 240$, $p < 0.05$) than did the females. Males also Mounted females much more often ($U = 118$, $p < 0.001$). It is illuminating that as far as affiliative interactions are considered, males showed relatively greater Affiliation towards females than *vice versa* ($U = 176.5$, $p < 0.05$). This was also true for the display of the Affiliative Bared-teeth Face ($U = 216$, $p < 0.05$). Finally, the Hinde's index for males towards females was greater than that for females towards males ($U = 157.5$, $p < 0.005$).

An analysis of the sexual behaviour of the troop individuals revealed that male dominance rank was positively correlated to the displayed frequency of sexual behaviour including Sexual Mount and Inspection (Table 4.7). Male Body Size Rank was also positively correlated to the frequency of Inspection carried out by males.

4.4 COMMUNICATION

Primate communication has generally been classified into vocal, tactile, chemical and visual systems (Zeller 1987). Visual communication consists principally of gestural communication, which, in turn, includes both body postures and facial expressions. This study has examined patterns of gestural and vocal communication among adult individuals in the study troop of lion-tailed macaques.

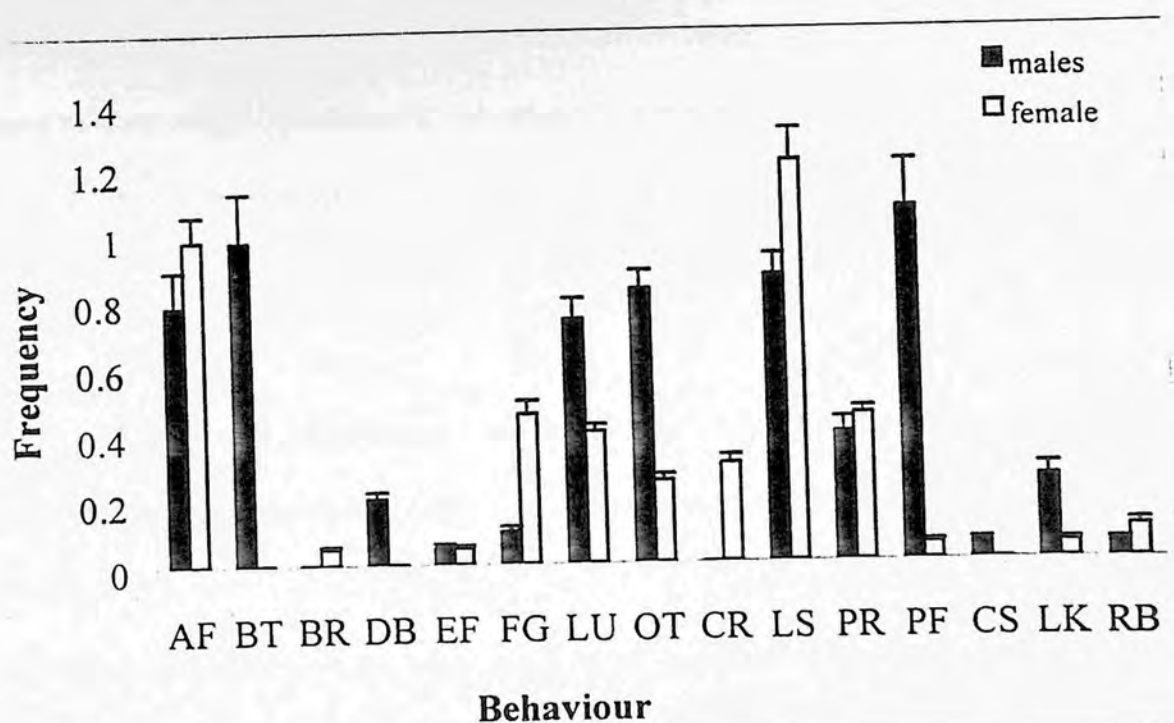
Gestural communication:

The body postures and facial expressions considered in the present analysis include: Crouch, Lip-smack, Present, Affiliative Bared-teeth Face, Play Face, Bared-teeth Display, Branch Shake, Display Bounce, Eye Flash, Fear Grimace, Lunge, Open-mouth Threat, Affiliative Bared-teeth Face, Raise Brow, Copulatory Grimace and Look (for definitions of these gestures, see Appendix 1).

Many of the gestures were differentially displayed by the troop individuals, particularly across the two sexes. A few gestures, for example, were exclusively used by males; these include the Bared-teeth Display (Kruskal-Wallis test, $KW = 5.573$, $p < 0.02$) and Display Bounce ($KW = 5.625$, $P < 0.02$). Open-mouth Threat and display the Play Face was expressed more frequently by males than females (Open-mouth Threat: $KW = 4.257$, $p < 0.05$; Play Face: $KW = 4.168$, $p < 0.050$). None of the other gestures, however, varied significantly between males and females (Figure 4.7).

Figure 4.7 The frequency of various gestures used by males and females in the study troop.

AF = Affiliative Bared-teeth Face; BT = Bared-teeth Display; BS = Branch Shake; DB = Display Bounce; EF = Eye Flash; FG = Fear Grimace; LU = Lunge; OT = Open-mouth Threat; CR = Crouch; LS = Lip-smack; PR = Present; PF = Play Face; CS = Copulatory Grimace; LK = Look; and RB = Raise Brow



Communication between males

Individual males used several gestures to different extents, many of these being correlated with actor or target rank. The frequency of Open-mouth Threats, for example, was positively correlated with actor rank (Kendall's rank correlation, $\tau = 1.000$, $p < 0.05$), as were Lunge ($\tau = 0.467$, $p < 0.05$) and Affiliative Bared-teeth Face ($\tau = 0.436$, $p < 0.05$). Target rank, on the other hand, was positively correlated with the frequency of received Lip-smacking ($\tau = 0.556$, $p < 0.05$) and negatively with Open-mouth Threats received ($\tau = -0.438$, $p < 0.05$). Interestingly, target size was positively correlated with Present ($\tau = 0.474$, $p < 0.05$) – smaller, but not necessarily subordinate, individuals thus Presented more to their larger counterparts. Amongst the gestures themselves, the frequency of Fear Grimace displayed was strongly positively correlated to that of Lip-smacking ($\tau = 0.654$, $p < 0.005$).

When dyadic interactions were considered, subordinate individuals displayed the Fear Grimace and Lip-smack much more frequently than did their dominant counterparts (Mann-Whitney U test; Fear Grimace: $U = 6$, $p < 0.05$; Lip-smack: $U = 1$, $p < 0.01$). Dominant individuals, on the other hand, were observed to Lunge ($U = 3$, $p < 0.01$) and Open-mouth Threat ($U = 0$, $p < 0.005$) significantly more towards subordinate individuals across all dyads.

Communication between females

Amongst females, actor size was positively correlated with the frequency of Open-mouth Threat ($\tau = 0.255$, $p < 0.05$) and negatively correlated with Fear Grimace ($\tau = -0.261$, $p < 0.05$). Target rank, in contrast, was strongly negatively correlated with Lunge ($\tau = -0.423$,

$p < 0.002$) – relatively low-ranking individuals thus received this form of non-contact aggression at fairly high rates. It is noteworthy that both rank difference ($\tau = -0.377$, $p < 0.05$) and size difference ($\tau = -0.524$, $p < 0.05$) were independently negatively correlated with frequency of displayed Fear Grimace, an indication that this behaviour was relatively more used during interactions between females close in rank and body size. The apparently neutral behaviour of Look also seemed to have a definite pattern, being negatively correlated with target rank ($\tau = -0.294$, $P < 0.05$), and also exhibiting a positive correlation with rank difference ($\tau = 0.290$, $P < 0.05$).

Some of the aggressive behaviours were positively correlated with each other, including, for example, Open-mouth Threat and Lunge ($\tau = 0.585$, $p < 0.05$). Lip-smack and Fear Grimace were also observed to be positively correlated to each other ($\tau = 0.554$, $p < 0.05$); both these behaviours being more likely to be expressed by relatively subordinate individuals. Amongst the affiliative behaviours, Affiliative Bared-teeth Face and Affiliative Grunt ($\tau = 0.572$, $p < 0.05$) and Affiliative Bared-teeth Face and Raise Brow ($\tau = 0.309$, $p < 0.012$) were positively correlated with each other.

Analysis of dyadic interactions revealed that, akin to the males, acts of Lunge were initiated more by dominant individuals ($U = 60$, $p < 0.05$), while Fear Grimace ($U = 42$, $p < 0.005$) and Lip-smack ($U = 46$, $p < 0.02$) were preferentially used by subordinates towards dominant individuals.

Male to female communication

Size difference between the actor and the target was negatively correlated to frequency of Present ($\tau = -0.292$, $p < 0.05$) and Lip-smacking ($\tau = -0.310$, $p < 0.05$); males thus Presented and Lip-smacked at females at higher relative frequencies as the latter became progressively larger than them. Amongst the affiliative behaviours, the rank of the actor was positively correlated with frequency of Affiliative Bared-teeth Face ($\tau = 0.287$, $p < 0.05$).

Female to male communication

Target rank was positively correlated to the frequency of displayed Lip-smacking – females thus preferentially Lip-smacked at dominant males. As the size difference between the interacting individuals increased, with the target males becoming relatively larger, the frequency with which females Crouched ($\tau = 0.312$, $p < 0.05$) or Presented ($\tau = 0.366$, $p < 0.02$) to them also increased significantly. In contrast, size difference between the females and the males was negatively correlated with frequency of Open-mouth Threat ($\tau = -0.448$, $p < 0.005$) and Lunge ($\tau = -0.310$, $p < 0.05$); females thus displayed increasing frequencies of non-contact aggression only towards progressively smaller males.

When dyadic interactions between males and females were considered, females were observed to Present ($U = 150$, $p < 0.002$), Crouch ($U = 228$, $p < 0.05$) and Fear Grimace ($U = 240$, $p < 0.05$) more, while males expressed Affiliative Bared-teeth Face at significantly higher frequencies ($U = 216$, $p < 0.05$).

Multi-dimensional scaling (Manley 1985) of the individuals, based on the repertoire and frequency of expression of different gestures, showed that animals separated from each other along three dimensions (Table 4.8) with a stress factor of 0.104. The individuals separated along dimension 1 on the basis of dominance rank, while separation along dimension 2 appeared to be on the basis of sex. All females except one were thus observed to have values above 0 along dimension 2, while all the males lay below. Dimension 3 appeared to have no simple or obvious interpretation and is believed to reflect certain aspects of differential use of gestures by the study individuals.

VOCAL COMMUNICATION:

The calls that have been analysed in this study include: Alarm Call, Affiliative Grunt, Contact Call – with positive response, Contact Call – with negative response, Reply Contact Call, Long Call – with positive response, Long Call – with negative response, Reply Long Call, Aggressive Bark, Warning Growl, Copulatory Call, and Staccato Call.

In general, females tended to vocalise more than the males did ($U = 944.5$, $0.05 < p < 0.07$). Significant differences across the sexes were, however, observed in the frequency of Contact Call ($KW = 6.545$, $p < 0.02$) and Reply Contact Call ($KW = 6.545$, $p < 0.02$) (Figure 4.9).

Communication between males

Actor size was positively correlated with the frequency of Warning Growl ($\tau = 0.467$, $p < 0.05$), while actor rank was positively correlated with the frequency of Reply Contact

Figure 4.8 Multi-dimensional scaling of the study individuals on the basis of the repertoire and frequency of gestures exhibited by them.

Only the first two dimensions have been depicted here

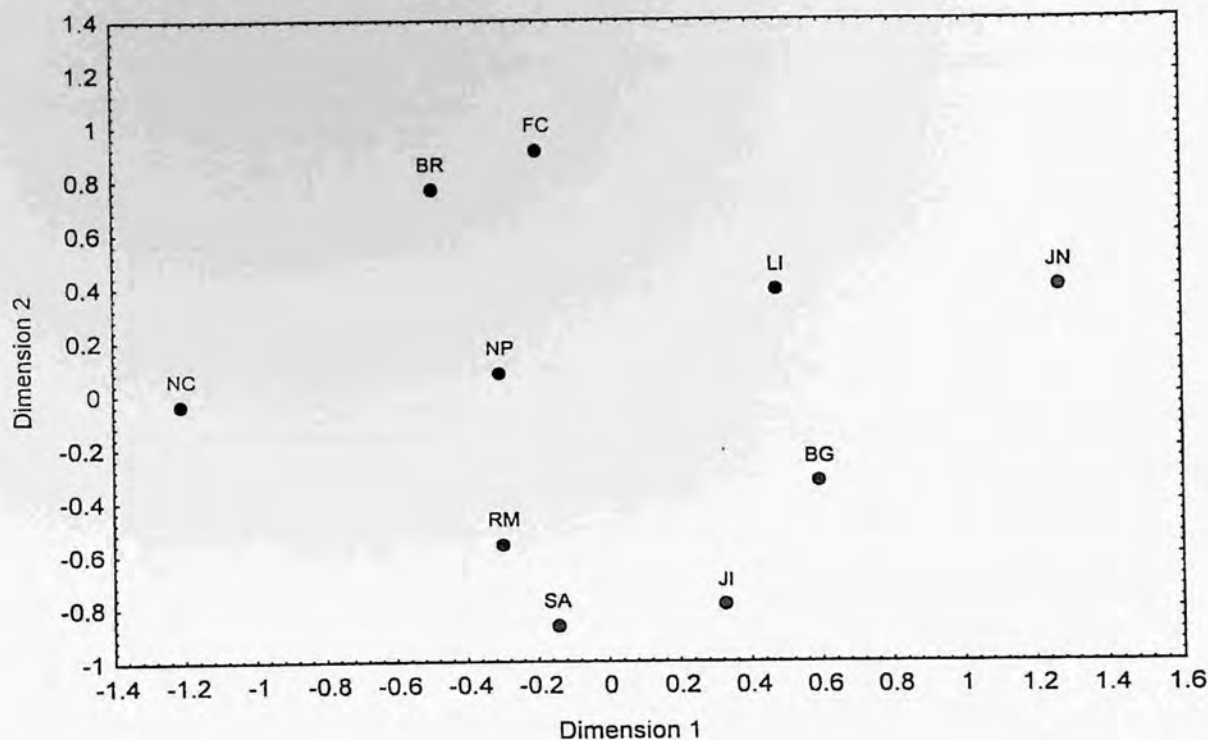
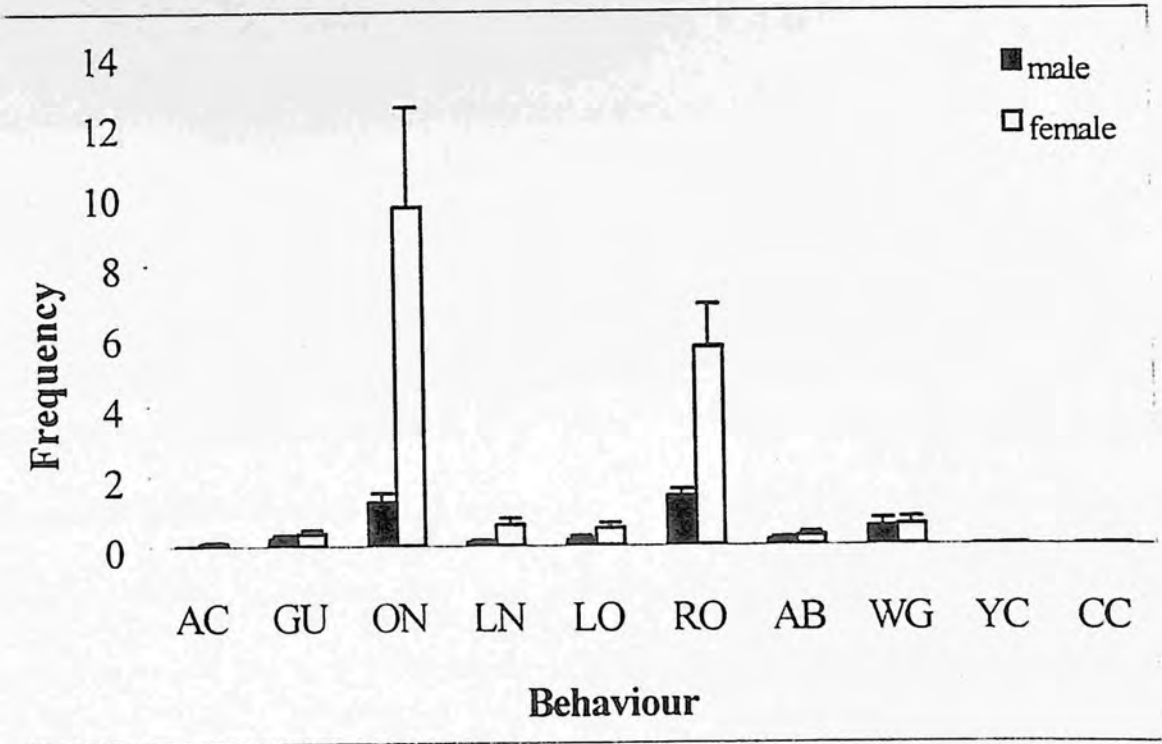


Table 4.8 Dimensions defined by multi-dimensional scaling of the study individuals on the basis of the repertoire and frequency of gestures

	DIM. 1	DIM. 2	DIM. 3
NC	-1.214	-0.032	-0.271
RM	-0.301	-0.557	-0.616
SA	-0.146	-0.864	0.501
JI	0.324	-0.786	-0.248
FC	-0.194	0.915	-0.438
NP	-0.307	0.083	-0.097
BR	-0.496	0.771	0.735
LI	0.475	0.390	0.317
JN	1.267	0.405	-0.490
BG	0.592	-0.325	0.606

Fig. 4.9 Frequency of various vocalisations used by males and females in the study troop.

AC = Alarm Call; GU = Affiliative Grunt; ON = Contact call; LN = Long Call; LO = Reply Long Call; RO = Reply Contact Call; AB = Aggressive Bark; WG = Warning Growl; YC = Copulatory Call; CC = Staccato Call



Calls given ($\tau = 0.487$, $p < 0.05$). Target rank, in contrast, was positively correlated to Contact Calls – with positive response ($\tau = 0.487$, $p < 0.05$).

Communication between females

The frequency of Long Contact Call given was seen to be positively correlated with the rank of calling females ($\tau = 0.964$, $p < 0.05$), while the frequency of Contact Call – with negative response – increased with decrease in the actor body size ($\tau = -0.256$, $p < 0.05$). Lower ranking females progressively received more Aggressive Barks from other females ($\tau = -0.363$, $p < 0.01$, while the rank difference ($\tau = 0.487$, $p < 0.05$) and body size difference ($\tau = 0.428$, $p < 0.05$) between the actor and the target were both observed to be positively correlated with the frequency of Warning Growl.

Amongst the different behaviours, the frequency of Contact Call was positively correlated with Open-mouth Threat ($\tau = 0.701$, $p < 0.05$), but negatively correlated with submissive behaviours such as Lip-smack ($\tau = -1.000$, $p < 0.005$) and Fear Grimace ($\tau = -0.745$, $p < 0.05$). Aggressive Bark and Warning Growl were positively correlated with each other ($\tau = 0.525$, $p < 0.05$), as were Open-mouth Threat and Warning Growl ($\tau = 0.658$, $p < 0.05$), and Lunge and Open-mouth Threat ($\tau = 0.585$, $p < 0.05$). Similarly, frequency of Lip-smack and Fear Grimace were positively correlated to each other ($\tau = 0.625$, $p < 0.05$). Affiliative behaviour like Affiliative Bared-teeth Face and Affiliative Grunt ($\tau = 0.574$, $p < 0.05$), and Affiliative Bared-teeth Face and Raise Brow ($\tau = 0.309$, $p < 0.02$) were also positively correlated to each other.

In dyadic interactions between females, Lunge ($U = 60$, $p < 0.05$) and Warning Growl ($U = 30$, $p < 0.002$) were predominantly directed by dominant individuals to lower ranking females, while subordinate females showed significantly higher frequencies of Fear Grimace ($U = 42$, $p < 0.005$) and Lip-smack ($U = 46$, $p < 0.02$).

Male to female communication

Actor size was observed to be positively correlated with Affiliative Grunt ($\tau = 0.320$, $p < 0.05$) as well as to Contact Call – with positive response ($\tau = 0.386$, $p < 0.01$).

Female to male communication

The frequency of Warning Growl received by an individual was negatively correlated both with its dominance rank ($\tau = -0.425$, $p < 0.005$) and with its body size ($\tau = -0.466$, $p < 0.002$). Target size, on the other hand, was positively correlated to the frequency of Reply Contact Calls ($\tau = 0.314$, $p < 0.05$).

The size difference between females and males was negatively correlated with the frequency of Warning Growl ($\tau = -0.415$, $p < 0.005$) and Aggressive Bark ($\tau = -0.310$, $p < 0.05$); females could thus direct increasing levels of certain agonistic vocalisations only towards progressively smaller males.

Based on the repertoire of vocalisations given as well as the frequency with which these calls were produced, multi-dimensional scaling of the individuals yielded three dimensions (Table 4.9, Stress = 0.063). The first dimension (Fig. 4.10) allowed JL, FC, BR

Figure 4.10 Multi-dimensional scaling of the study individuals on the basis of the repertoire and frequency of vocalisations exhibited by them.

Only the first two dimensions have been shown here.

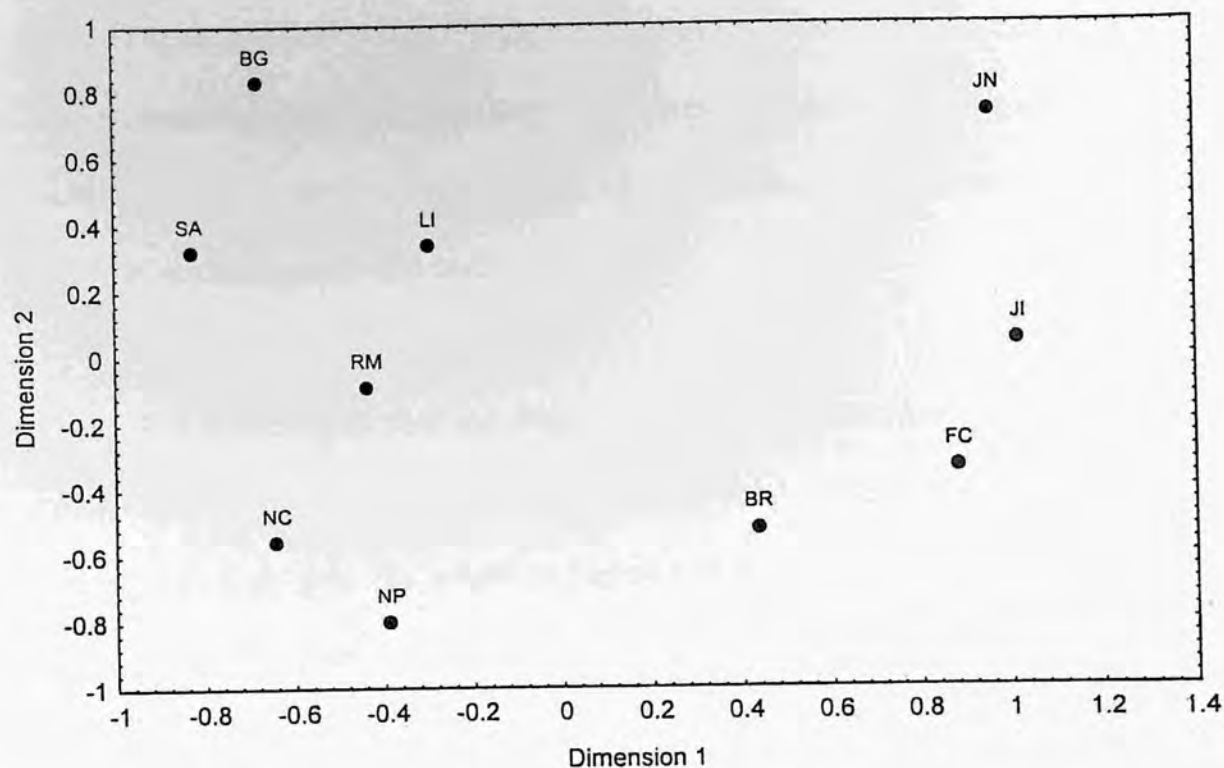


Table. 4.9 Dimensions defined by multi-dimensional scaling of the study individuals on the basis of the repertoire and frequency of vocalisations

	DIM. 1	DIM. 2	DIM. 3
NC	-0.645	-0.553	-0.111
RM	-0.439	-0.086	1.012
SA	-0.830	0.325	-0.588
JI	1.015	0.048	0.313
FC	0.880	-0.334	-0.686
NP	-0.391	-0.795	0.337
BR	0.432	-0.518	-0.331
LI	-0.295	0.340	-0.108
JN	0.952	0.737	0.321
BG	-0.679	0.836	-0.158

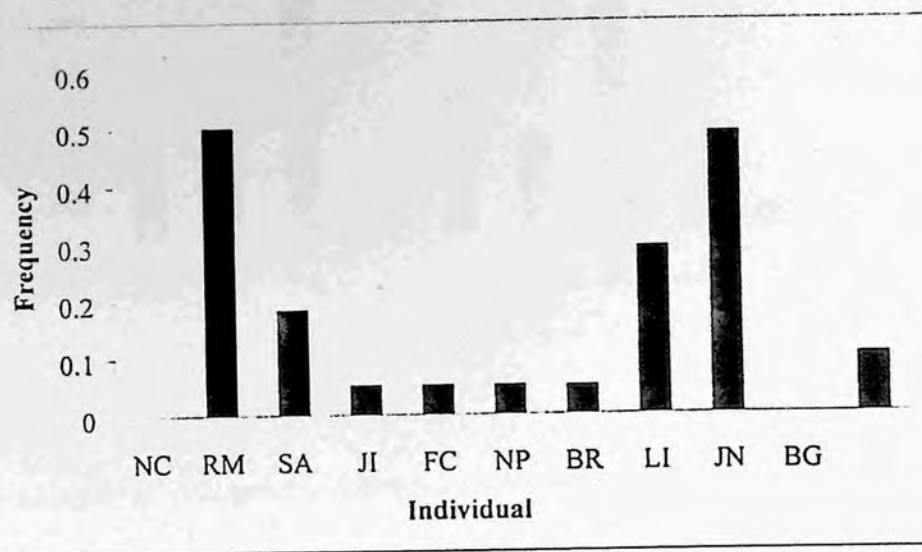
and JN to separate from the other six animals primarily because they displayed Aggressive Bark at levels higher than that of the other individuals in the troop ($U = 2$, $p < 0.05$). Along the second dimension, it was interesting to note that the study individuals separated on the basis of their dominance ranks, with the three most dominant females and two dominant males separating from the remaining subordinate individuals. Dimension 3 appeared to have no simple or obvious interpretation, although it must reflect certain differences in the usage of vocalisations by the study individuals.

It is important to note that there existed, in the study troop, significant individual variation in communication patterns that could not be explained by age, sex, dominance rank or even body size. The graphs in Figure 4.11 depict the variability across individuals in the display of certain gestures (Affiliative Bared-teeth Face) and calls (Affiliative Grunt and Warning Growl). This variability is not restricted to gestures and vocalisations alone. Individual variation was observed in other behaviour too. The Frequency of Allogroom that indicated the initiation of a grooming session between all dyads also showed a pattern that was can not be explained by the dominance rank, body size or age (Figure 4.12). This variability could be either due to individual temperament or due to the situational variation that all individuals are invariably subjected to.

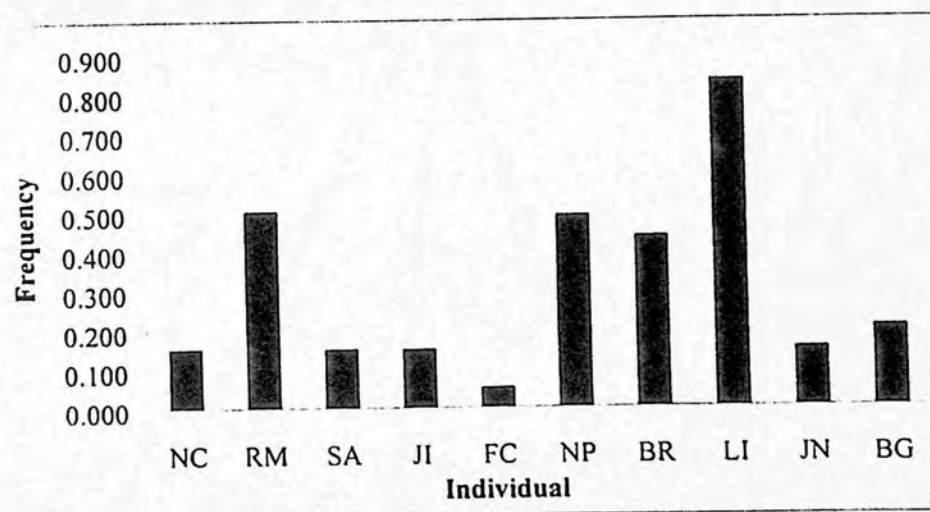
Figure 4.11 Frequency of (a) Affiliative Bared-teeth Face, (b) Affiliative Grunt, and (c) Warning Growl expressed by the individuals in the study troop.

Individuals NC, RM, SA and JI represent the four males, while FC, NP, BR, LI, JN, and BG are the six females

(a)



(b)



(c)

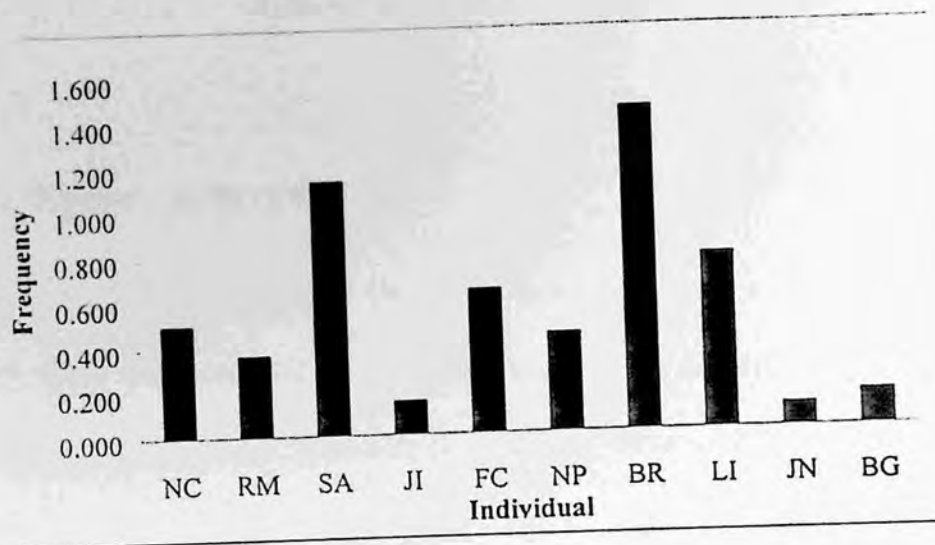
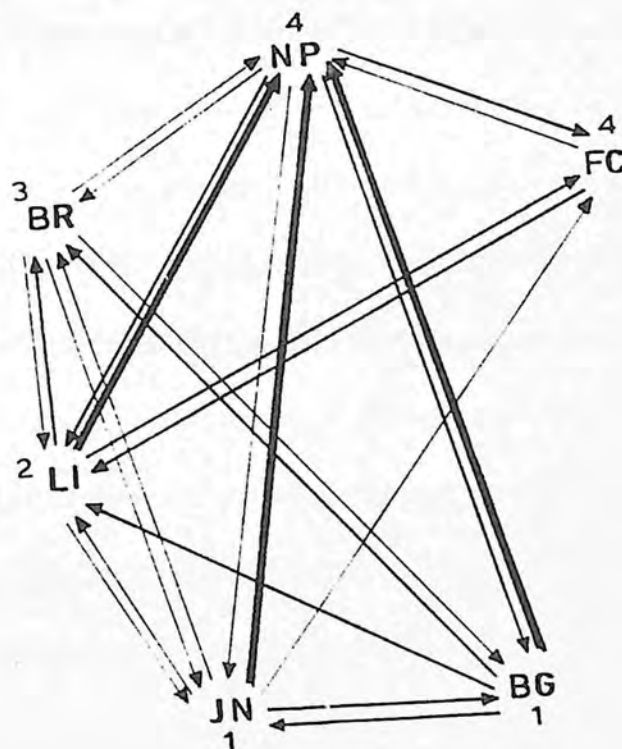


Figure 4.12: Frequency of Allogroom expressed between all dyads of adult females. This shows explicitly the individual variation.

The thickness of the lines are representative of the frequency of allogrooming observed between the individuals in the dyad. Increasing values of allogrooming frequency being depicted with thicker lines.



CHAPTER 5: DISCUSSION

TIME-ACTIVITY BUDGET:

Earlier investigations comparing the study troop to those in other fragments in the Anaimalai Hills indicated that the Puthutotam troop did not differ in some aspects of its general behavioural patterns, including time activity budgets, feeding behaviour and social behaviour (Singh *et al.* 1998; Umapathy and Kumar 2000). Singh *et al.* (1998), for example, also found Move, Feed and Passive states as the predominant behaviours observed. The present study also does not show any significant change with respect to the amount of time spent in Rest (16.6% vs 16%), Forage (22.4% vs 23.7%) and Feed (17% vs 17.9%) over that documented in a study conducted 10 years ago (1990 – 1991) by Menon and Poirier (1996) in the same area. The proportion of time spent in Move (13% Vs 38%), however, seems to have changed considerably over this period of time. This is of particular interest since the level of disturbance within the Puthutotam fragment has definitely increased over this period (Ajith Kumar *pers. comm.*), and there has been a change in the social structure of the group as well, from the original single large troop of 43 animals to two troops at the present time, consisting of 54 and 19 individuals, respectively. The decrease in the amount of time spent in Move can perhaps be explained by the fact that the movement of the study troop is dependent on that of the second and larger troop in the same area. Due to their overlap in home range, this troop would often get displaced during inter-troop encounters and the range of the troop thus appeared to be largely restricted to areas where the other troop was not present. Another implication of the present observations on the lack of change in other activities is that lion-tailed

macaques, in spite of being called habitat specialists (Singh *et al.* 1997), are able to adapt to changes in habitat structure. Further monitoring of the behavioural profile of this nature could perhaps be important in providing insights into the changing status of the habitat, and thus help in the effective management of this highly endangered species.

Adult males in the troop seem to be more active in the defence of the area that the troop ranged in since males were generally observed to Survey more than any other class of individuals in the troop. In addition, the fact that the adult males were all larger in size than adult females would give them a need to spend longer durations of time in obtaining nourishment; males were thus observed to carry out Active Feeding significantly more than did adult females. Males were also observed to Rest more during the day – the positive correlation between Move and Rest among adult males could perhaps be attributed to an energy conservation mechanism.

In general, males spent more time on the ground, and females on intermediate-sized trees and branches, and on the canopy. While moving too, females moved predominantly along intermediate trees while males moved on the ground. This could be due to the fact that three of the six study females had infants during the period of the study, and, as an anti-predatory defence strategy, could have been more wary and remained on relatively higher habitat strata. The females also took much longer to descend to the ground after daybreak; they spent the mornings predominantly foraging on intermediate trees and the canopy, and descend to the ground only later during the day.

The study troop has been known to spend large proportions of time on the ground and in the undergrowth than troops in other less-disturbed areas (Singh *et al.* 1998). The

study individuals, however, were observed to use intermediate-sized trees most frequently for most behavioural states such as Sit, Forage, Feed, Rest, and Allogroom, a reflection once again of the highly arboreal nature of the species. For the purpose of Surveying the area, nevertheless, the animals were observed to use the canopy.

Among females, the larger-bodied individuals were observed to Sit Alert more often; since body and dominance rank were correlated among females in the troop, this could mean that, among females, the more dominant individuals play a role in scanning for predators as well as for neighbouring troops.

An interesting observation regarding the social interactions of the troop members is that males Allogroomed and Received Grooming to much lesser extents than did the females. They were, however, observed to Autogroom and Scratch at much higher levels than the females; could this be a compensatory mechanism and if so, does this imply that there is a general biological requirement for grooming and/or scratching that every individual has to fulfill?

It is important to note that except for allogrooming, no other social interaction was recorded during the instantaneous scans that were conducted on the troop. This illustrates very dramatically the relative rarity of such interactions in this species and raises a very important methodological issue. It would suggest that the use of instantaneous scans to record social interaction data, as has been done by virtually all earlier studies on the behaviour of this species in the wild, is unwise since it would be insufficient and unable to provide an accurate estimate of all such behavioural interactions.

SOCIAL INTERACTIONS:

Following Vehrencamp (1983), the classification of macaque species into "egalitarian" and "despotic" organisations (see also van Schaik 1989, 1996) emphasises the formation of egalitarian societies where resource distribution attenuates the competitive disadvantage of defending resources against other group members. Egalitarian societies typically display weaker differences in dominance ranks among adult females, assuming that they are invariably philopatric. There was a remarkable similarity in the frequency with which dominant and subordinate females displayed virtually all behaviours towards each other in dyadic interactions that were monitored in the study troop. Taken at face value, this provides support to the prevailing view that lion-tailed macaques indeed display an egalitarian nature (Abegg *et al.* 1996).

Assigning dominance ranks to females on the basis of approach-retreat interactions has been a common practice for decades. The ties in the dominance rank of two pairs of females in the study troop could be possibly attributed to two reasons. First, this could result from the low rates of interaction between those particular females, due to the nature of the species, which is known to interact less in comparison to other species of macaques (Bertrand 1969). The second reason for this could be that the dominance hierarchy among lion-tailed macaques, when arranged on a scale from despotic to egalitarian, is more at the egalitarian end of the scale (Abegg *et al.* 1996).

Studies among macaque females have often shown that the dominance ranks of individuals do not correlate to their body size or physical strength (reviewed in Fedigan 1992). The strong relationship between dominance rank and Body Size Rank among the adult females in the study troop is, therefore, particularly interesting. Among macaque

females, dominance rank usually follows a matrilineal pattern of inheritance. This ensures that body size of females do not play any role in rank determination, except for infants and juveniles when body size may decide the outcome of sporadic local agonistic interactions. This gives us reason to believe that, in the study troop, the dominance hierarchy is an individual-based one, more typical of macaque males. Support for this comes from the fact that adult female LI, who is third-ranked (see table 3.2), could be the daughter of FC, the highest-ranked female (A.K. Sharma *pers. comm.*). The fact that FC was observed to initiate Allogrooming at much higher levels and spend longer durations of grooming with LI than with any other female provides further support to this possibility (see Birky 1993 for documentation of preferential kin-based grooming in lion-tailed macaques, and Goosen 1981). Note that in any other macaque society, LI would have occupied a rank position immediately below that of FC. Moreover, there is hardly any allogrooming of BR, the female immediately below FC in the hierarchy, by FC. In a typical macaque group, BR would have been FC's daughter and should have been groomed by her extensively. If the existence of a unique individual-based dominance hierarchy among the study females is indeed confirmed, it could be predicted that the present-day younger smaller females would subsequently gain in rank as they grow older. Continued monitoring of the troop should enable such a confirmation. It must be mentioned here, however, that a study on captive female lion-tailed macaques demonstrated a clear linear matrilineal hierarchy among the adult females, as is typical of macaques (Birky 1993).

An interesting feature of the social relationships displayed by the study troop is that males Allogroomed less than the females did. They, however, Autogroomed significantly more perhaps to remove ectoparasites and debris from their hair that would have otherwise been removed through allogrooming interactions. This could also explain

why they were observed to Scratch more often than females as well. The positive correlation between Allogroom frequency and Allogroom duration indicates that individuals who initiate grooming more also groom for longer durations. The patterns of grooming among the females in the study troop, however, appeared to largely follow the typical macaque pattern. In dyadic interactions, subordinate females thus spent significantly longer durations grooming their dominant counterparts; these females did not, however, initiate allogrooming more. Moreover, relatively high levels of grooming were initiated within dyads consisting of closely ranked females, another typical cercopithecine female grooming characteristic (Wu *et al* 1980; Cheney and Seyfarth 1990, Henzi and Barrett 1999).

An interesting aspect of the analysis of social interactions in the study troop concerns the relationship of the various documented social behaviours and the spatial proximity between the troop members. In general, individuals who sat in contact more also Allogroomed more. Both Affiliation and Aggression also appeared to be correlated to individuals sitting close to each other. Individuals that sat within half a metre of each other, therefore, showed more Affiliation towards each other, but significantly less Aggression. If individuals interacted more, simply because they found themselves in close proximity, even levels of Aggression would have been high. Since this was obviously not the case, sitting close is likely to be the result, rather than a cause, of two individuals interacting affiliatively with each other.

Social relationships among males

The display of Aggression followed a linear pattern among the study males, being preferentially directed down the dominance hierarchy, a fact that appears to belie the

proposed egalitarian nature of the species (Abegg *et al.* 1996). It is also true, however, that most discussions on the despotic and egalitarian nature of macaque societies have typically characterised social relationships among females with the males remaining largely neglected. In the study troop, Affiliation was directed more towards higher-ranking animals. Dominant males also sought grooming successfully from relatively low ranking individuals than from those closer in rank. Analysis of the Hinde's index indicated that lower-ranking males were more active in maintaining affiliative relationships with dominant individuals than they were with closely ranked individuals, a typical cercopithecine feature. Another interesting aspect of the social interactions among the males was that the exhibition of Contact Aggression was correlated to Body Size Rank rather than to the dominance rank of the individual. This could be due to the fact that contact aggression is generally a very costly option for individuals caught in agonistic situations, and, therefore, it is conceivable that only larger individuals, rather than high-ranked ones, can afford to invest in acts of contact aggression.

Social relationships among females

A similar pattern was also observed among the study females, wherein Body Size Rank, rather than dominance rank, was strongly correlated to the frequency of displayed Contact Aggression. As argued for the males, larger females alone would have an advantage if they adopted contact aggression in agonistic encounters and would be taking a lower risk in case of retaliation. Among the behaviours that could signal dominance relations, Mounting was correlated to Contact Aggression and is, therefore, a sign of dominance while Mounting with Lip-smacking is a gesture used typically in submissive contexts.

Since the behavioural acts of Friendly Approach and Move Away were correlated to each other, it indicated that animals that initiated affiliation also appeared to terminate the affiliative interaction. Among dyads with large differences in rank, however, there was a positive correlation between Dominance and Move Away, an indication that dominant individuals more often terminated an affiliative interaction than did the subordinate female.

Social relationships between males and females

Sexual behaviour could not be documented satisfactorily in the study troop because four of the six adult females were either lactating or were pregnant during the period of the study. The two adult females who were cycling did not, however, present many opportunities for the observation of sexual interactions, especially during focal animal sampling. The small data set obtained, however, indicates that the dominant males clearly sexually monopolised the oestrus females, with the frequency of Sexual Mounts and Inspections being highest among the higher-ranking males. A similar pattern was observed by Berard (1999) which was observed to change over time and the joining of new males in the troop. Ananda Kumar *et al.* 2001 have documented the change in social interactions between males and females with migration of males into and away from the troop. Long term studies will be able to give a better idea of the effects of these changes in social structure to the behaviour of the individuals in the troop.

Females were observed to preferentially initiate Friendly Approaches towards high-ranking males. Since affiliation was thus clearly targeted towards dominant individuals, this suggested that female lion-tailed macaques could be using a social strategy to gain alliance partners from among high-ranking males. Given that foraging is a

very important activity for these arboreal rain forest primates and that Seeking Support was not usually observed during aggressive encounters. It could also be possible that females established affiliative social relationships with high-ranking males in order to be tolerated at good quality food resource sites.

Dominance interactions between males and females were characterised by the latter exhibiting more Submission towards males and males displaying relatively more Aggression and Dominance towards females. This does not imply, however, that all females were subordinate to all males. The dominant females FC and NP did show Dominance towards some of the males, especially the younger smaller individuals. Females were also observed to Present at higher rates to males, while males Mounted females more. Interestingly, males appeared to exhibit more Affiliation towards females than the other way around, and also seemed to be interested in maintaining such relationships, as monitored by the Hinde's index. The investment of males to maintain affiliative relationships with females is noteworthy. Disregarding the possibility of kin attraction, which can never be determined in a short-term study such as the present one, this mechanism may be employed for maintaining affiliative social bonds (Cooper and Bernstein 2000). This strategy of males could also represent their efforts at gaining access to females through the establishment of friendships even when the females are not in oestrus and hence, ultimately increasing their chances of reproduction when the females do become sexually receptive (Smuts *et al.* 1983)

COMMUNICATION

Studies have been conducted on gestural communication among primates and include accurate descriptions (Hinde & Rowell 1962; van Hoof 1967; Bertrand 1969; Skinner & Lockard 1979; Johnson 1985), contextual usage of gestures as well as the functional significance of some the behaviour (Preuschoft 1995; Maestriperi 1996a, b; Maestriperi & Wallen 1997). The study of Vocal communication among primates has been of great interest of scientists. A wide range of studies (reviewed by Cheney and Seyfarth 1990) have looked at vocal communication mechanisms in primates, the genus *Macaca* represent the most comprehensively investigated taxonomic group (Hauser 1996). Hohmann and Herzog (1985) have provided a comprehensive list as well as description of the various calls of the lion-tailed macaque.

The communication patterns exhibited by the adult males and females in the study troop appear to be quite distinct. Both sexes seem to display a few gestures or calls that are exclusive – such as the Copulatory Grimace among males and the Staccato Call among females. It is interesting, and perhaps not a simple coincidence, that both these signals are used in a sexual context; sexual situations clearly demand different motivational signals from individuals of the two sexes. There are some behavioural signals that both sexes retain the potential to display, but yet are exhibited very differently under different conditions. Examples of these include the two kinds of Contact Calls by females and the Bared-teeth Display and Display Bounce by males. Many other behaviours such as Lip-smack, Present, Warning Growl, Affiliative Bared-teeth Face, Affiliative Grunt are, on the other hand, used by males and females alike, and at comparable frequencies.

The Bared-teeth Display and Display Bounce exhibited by males are both used during agonistic interactions with extra-troop individuals, emphasising the role played by males in the defense of the home range of the troop. Females, in contrast, seem to Contact Call to a much greater extent than do the males. This may be because, being philopatric, lion-tailed macaque females need to communicate with each other much more and thus ensure group cohesiveness in order to prevent the straying of their infants and other kin. Among males too, the larger individuals were observed to Contact Call and Reply Contact Call at relatively high frequencies, thus indicating a role for certain males in maintaining the cohesiveness of the group as well. Why did only larger males call thus? One possible hypothesis could be that it is in the greatest interest of the dominant males, who tend to monopolise most matings in species like the lion-tailed macaque, that females do not stray from the group and thus expose themselves to contact with extra-troop males. It is also illuminating that among females, only Contact Calls of larger individuals were responded to at higher frequency, and females tended to reply more to the calls of larger males than smaller individuals. It is thus possible that these older, more experienced, individuals served as stable 'centres' for troop cohesion and troop members preferentially responded to the Contact Calls of these individuals.

The display of certain gestures was correlated to the dominance rank of the actors. Among males, for example, dominant individuals invariably used the Open-mouth Threat, an agonistic signal, against low-ranking males – to the extent that this signal could be used as a reliable indicator of the dominance hierarchy. Interestingly, the expression of Open-mouth Threat among females was found to correlate to the body size of the individual. Hence, in addition to rank, body size could also play an important role in patterning aggressive interactions among females. This raises the problem of identifying the precise

contexts in which rank determines the nature of social interactions and those in which size becomes more critical. Lunge is another behaviour that was predominantly used by dominant individuals towards subordinates, among both males and females.

Ambiguous gestures, such as Lip-smack and Present, are generally not used in the context of submission alone, but are also often exhibited by dominant individuals when they need to reconcile after an act of aggression or to reassure their subordinates during other tense social situations. In the study group, however, these signals were predominantly used by subordinate males and females and directed towards dominant individuals of the respective sex. This was true of male-female interactions as well, where Present and Lip-smack were used by males only towards similar-sized females (the smaller subadult male was similar in size to the large dominant females) and by females only towards larger males. The use of these gestures thus appears to be clearly linked with the expression of submission within this troop and their employment in the contexts of reconciliation or reassurance minimal.

Female lion-tailed macaques were occasionally observed to Fear Grimace as an expression of submission, with smaller females grimacing at relatively higher levels. Interestingly, however, the frequency of Fear Grimace was negatively correlated with both rank difference and size difference, indicating that it was exchanged more between closely ranked individuals. This may be due to the fact that the dominance hierarchy among females, probably being individual-based, provides scope for competition among closely ranking animals for higher positions, leading to higher levels of aggression between them.

The positive correlation between the dominance rank of adult males and the frequency of Affiliative Bared-teeth Face directed both at males and females indicates that this signal could be used in the context of reassurance. This expression of affiliation was often found to be employed in the context of a dominant male approaching a subordinate individual in order to ensure that the latter does not retreat. Larger males were also observed to Affiliative Grunt at females more than did smaller males. Could this also be explained simply as has been done for the Affiliative Bared-teeth Face, or could these behaviours together serve in the establishment of long-term affiliative social relationships between adult males and females? Closer examination of individual variation in the display of such affiliative signals could provide clues to these questions.

Larger males were observed to Warning Growl more, but, surprisingly, there was no such correlation between Aggressive Bark and size among the males. A possible explanation for this is that smaller, and subordinate, males could retreat from the Warning Growl of larger, more dominant, males even before the more severe Aggressive Barks could be employed. Dominant females, in contrast, were often observed to use the Aggressive Bark during agonistic interactions, and with higher frequency during dyadic interactions with relatively greater rank or size difference between the interacting pair of individuals.

The separation of individuals upon multi dimensional scaling based on the use of gestures was along differences in both rank and sex, while the separation based on calls was not determined by differences in sex, although it did appear to depend on the dominance rank.

Often the role of dominance and its influence on primate behaviour is acknowledged, however largely ignoring the role of personality in an individual's behaviour (Nash and Chamove 1981). This individual variation is an important aspect governing social relationships and should not be unduly negated.

Close behavioural observations of this troop should, therefore, enable an understanding of not only the needs of the species to cope with severely altered environments, but should also reveal particular behavioural strategies that individuals might adopt to deal with the corresponding social stress. The importance of understanding the behaviour of the species and the role it can play in effective management should not be neglected.

REFERENCE

- ANON. 1992. *The wildlife (protection) act, 1972 (as amended upto 1991)*. Natraj Publishers, Dehra Dun.
- ABEGG, C., THIERRY B. AND KAUMANN W. 1996. Reconciliation in three groups of lion tailed macaques. *International Journal of Primatology* 17: 803-816
- ALI, R. 1985. An overview of the status and distribution of the lion-tailed macaque. In: *Lion-tailed Macaque: Status and Conservation* (ed. P.G. Heltne), Alan R. Liss, New York. pp. 13-25
- ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49: 227- 265
- ANANDA KUMAR, M., SINGH, M., KUMARA, H.N., SHARMA, A.K., AND BERTSCH, C. 2001. Male migration in lion-tailed macaques. *Primate Report*. 59: 5 – 17
- BERARD, J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*) *Primates*. 40: 159 – 175
- BERTRAND, M. 1969. *The behavioural repertoire of the stumptail macaque*, Basel, Karger.*
- BHAT, H.R. 1994. The status of lion-tailed macaque (*Macaca silenus*) in the Western Ghats Crest Zone between Sharavathi and Aghanashini in Karnataka. *Proceedings of the IVth International Symposium on Lion-Tailed Macaque*, Madras, India.
- BIRKY, W.A. 1993. Female-female social relationships in a captive group of lion-tailed macaques (*Macaca silenus*). M.Sc thesis. California State University, Northridge, USA

- CARO, T. 1999. The behaviour-conservation interface. *Trends in Ecology and Evolution* 14: 366-369
- CHENEY, D.L. AND SEYFARTH, R.M. 1990. *How Monkeys See the World*. University of Chicago Press, Chicago. pp 377
- COOPER, M.A. AND BERNSTEIN, I.S. 2000. Social grooming in assamese macaques. (*Macaca assamensis*). *American Journal of Primatology*. 50: 77 – 85
- DUNBAR, R.I.M. 1988. *Primate social systems*. Croom Helm. London. pp. 373
- EASA, P.S., SURENDRANATHAN ASARI, P.K. AND CHAND BASHA, S. 1997. Status and distribution of the endangered lion-tailed macaque *Macaca silenus* in Kerala, India. *Biological Conservation*. 80: 33 –37
- FA, J.E. AND LINDBURG, D.G. 1996. *Evolution and Ecology of Macaque Societies*. Cambridge University Press, Cambridge pp. 597
- FEDIGAN, L.M. 1992. *Primate paradigms: Sex roles and social bonds*. The University of Chicago Press. Chicago. pp. 386
- GOOSEN, C. 1981. On the function of allogrooming in old-world monkeys. In : *Primate behaviour and sociobiology*. (eds. A.B. Chiarelli and R.S. Corruccini). Springer-Verlag. Berlin. pp 110 – 120
- GREEN, S. AND MINKOWSKI, K. 1977. The lion-tailed monkey and its south Indian rain forest habitat. In: *Primate Conservation* (eds. H.S.H. Prince Rainier III of Monaco and G.H. Bourne), Academic Press, New York. pp. 289 – 337
- HAUSER, M.D. 1996. Vocal communication in macaques: Causes of variation. In: *Evolution and ecology of macaque societies*. (eds. J.E.Fa, and D.G.Lindburg).Cambridge University Press. Cambridge. 551 – 578
- HENZI, S.P. AND BARRETT, L. 1999. The value of grooming to female primates. *Primates*. 40: 47 – 59

- HINDE, R.A. 1983. *Primate social relationships: An integrated approach*. Blackwell Scientific Publications. U.K. pp. 384
- HINDE, R.A. AND ATKINSON, S. 1970. Assessing the roles of social partners in maintaining mutual proximity as exemplified by mother – infant relations in rhesus monkeys. *Animal Behaviour*. **18**: 169 – 176
- HINDE, R.A. AND ROWELL, T.E. 1962. Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proceedings of the Zoological Society, London*. **128**: 1 – 21 *
- HOHMANN, G. 1988. A case of simple tool use in wild lion-tailed macaques (*Macaca silenus*). *Primates* **29**: 565-567
- HOHMANN, G. AND SUNDERRAJ, F.S.W. 1990. Survey of niligiri langurs and lion-tailed macaques in Tamil Nadu, South India. *Primate Conservation*. **11**: 49 – 53
- HOHMANN, G.M. AND HERZOG, M.O. 1984. Male loud calls in *Macaca silenus* and *Presbytis johnii*. *Folia Primatologica* **43**: 189-197*
- HOHMANN, G.M. AND HERZOG, M.O. 1985. Vocal communication in lion-tailed macaque (*Macaca silenus*). *Folia Primatologica* **45**: 148-178*
- IUCN, 1996. *IUCN Red List of Threatened Animals*. IUCN, Gland, Switzerland
- JOHNSON, M.J. 1980. The status, ecology and behaviour of lion-tailed macaque (*Macaca silenus*). *Journal of Bombay Natural History Society*. **75**: 1017 – 1027
- JOHNSON, P.C. 1985. Notes on the ethogram of captive lion-tailed macaque. In: *Lion-tailed Macaque: Status and Conservation* (ed. P.G. Heltne), Alan R. Liss, New York. pp. 239 – 263
- KARANTH, K.U. 1984. Conservation Plan for the Lion-tailed Macaque and its Rainforest Habitats in Karnataka. Report to the Government of Karnataka. Bangalore, India.

- KARANTH, K.U. 1985. Ecological status of the lion-tailed macaque and its rainforest habitats in Karnataka, India. *Primate Conservation* 6: 73-84
- KARANTH, K.U. 1992. Conservation prospects for lion-tailed macaques in Karnataka, India. *Zoo Biology* 11: 33-41
- KUMAR, A. 1985. Patterns of extinction in India, Sri Lanka and elsewhere in southeast Asia: Implications for lion-tailed macaque wildlife management and the Indian conservation system. In: *Lion-tailed Macaque: Status and Conservation* (ed. P.G. Heltne), Alan R. Liss, New York. pp. 65-90
- KUMAR, A. 1987. *The Ecology and Population Dynamics of the Lion-tailed Macaque, Macaca silenus, in South India*. PhD Thesis, Cambridge University, Cambridge, UK
- KUMAR, A. 1995 a. The life history, ecology, distribution and conservation problems in the wild. In: *The Lion-tailed Macaque: Population and Habitat Viability Assessment Workshop* (eds. A. Kumar, S. Molur and S. Walker), Zoo Outreach Organisation, Coimbatore, India
- KUMAR, A. 1995 b. Birth rate and survival in relation to group size in the lion-tailed macaque, *Macaca silenus*. *Primates*. 36: 1 – 9
- KUMAR, A. 2000. Sexual harassment among female lion-tailed macaques (*Macaca silenus*) in the wild. *Journal of the Bombay Natural History Society* 97: 42-51
- KUMAR, A. 2001. Mounting pattern in the lion-tailed macaque: An analysis based on inter-mount intervals. *Primate Report*. 59: 19 – 26
- KUMAR, A. AND KURUP, G.U. 1981. Infant development in the lion-tailed macaque, *Macaca silenus* (Linnaeus): The first eight weeks. *Primates*. 22: 512 – 522

- KUMAR, A. AND KURUP, G.U. 1993. The demography of the lion-tailed macaque in the wild. *Proceedings of the IVth International Symposium on Lion-tailed Macaque*, Chennai, India, October 1993
- KUMAR, A., SIVAGANESAN, N., UMAPATHY, G. AND PRABHAKAR, A. 1998. A Study on the Management of Fragmented Rain Forests for the Western Ghats for the Special Conservation of Fauna with Special emphasis on Small Mammals – Final Technical Report, Salim Ali Centre for Ornithology and Natural History, Coimbatore, India
- KUMARA, H.N., SINGH, ME., SHARMA, A.K., SINGH, MR., AND ANANDA KUMAR, M. 2000. Faunal component in the diet of lion-tailed macaque. *Primate Report*. 58: 57 – 65
- KURUP, G.U. 1978. Distribution, habitat and status survey of the lion-tailed macaque, *Macaca silenus*. *Journal of the Bombay Natural History Society* 75: 321-340
- KURUP, G.U. 1988. The present status of the lion-tailed macaque. *Primate Conservation*. 9: 34-36
- LACY, R., BALLOU, J. AND MOLLUR, S. 1996. Small population biology and the tools of recovery: Insitu report. *Zoo's Print*, XI: 9-23
- LINDBURG, D.G. 1990. Proceptive calling by female lion-tailed macaque. *Zoo Biology*. 9: 437 – 466
- MAESTRIPIERI, D. 1996 a. Gestural communication and its cognitive implications in pigtailed macaques (*Macaca nemestrina*). *Behaviour* 133: 997-1022
- MAESTRIPIERI, D. 1996 b. Social communication among captive stump-tailed macaques (*Macaca arctoides*). *International Journal of Primatology* 17: 785 – 802
- MAESTRIPIERI, D. AND WALLEN, K. 1997. Affiliative and submissive communication in rhesus macaques. *Primates* 38: 127 – 138

- MANLY, B.F.J. 1985. Multivariate Statistical Methods – A Primer. Second edition. Chapman and Hall, UK. pp 215
- MENON, S. 1993. *Ecology and Conservation of the Endangered Lion-tailed Macaque (Macaca silenus) in the Landscape Mosaic of the Western Ghats*. Ph.D Dissertation, Ohio State University, Columbus, USA
- MENON, S. AND POIRIER, F.E. 1996. Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: Activity patterns and time budget. *International Journal of Primatology* 17: 967- 985
- NASH, V.J. AND CHAMOVE, A.S. 1981. Personality and dominance behaviour in stumptailed macaques. In : *Primate behaviour and sociobiology*. (eds. A.B. Chiarelli and R.S. Corruccini). Springer-Verlag, Berlin. pp 88 - 92
- PASCAL, J.P. 1988. *Wet evergreen forests of the Western Ghats of India: Ecology, structure, floristic composition and succession*. Institut de Français, Pondichéry, Travaux de la section Scientifique et technique. Pondicherry, India. xx bis. pp 354
- PREUSCHOTT, S. 1995. "Laughter" and "Smiling" in Macaques: An evolutionary perspective. Ph.D. thesis. Rijkuniversiteit Utrecht, Utrecht.
- PROSSER, T.M. 1988. Social relationships in a group of five lion-tailed macaques *Journal of the Minnesota Academy of Science* 53: 32
- RAMACHANDRAN, K.K. 1994. Status of the lion-tailed macaque in Silent Valley National Park and adjacent areas. *Proceedings of the IVth International Symposium on Lion-Tailed Macaque*, Madras, India.
- REDICAN, W.K. 1975. Facial expressions in nonhuman primates. In: *Primate Behaviour: Development in field and laboratory research*. (ed: L.A. Rosenblum). Academic Press, New York. Pp. 103 – 194 *

- ROHLF, F.J., & SOKAL, R.R. 1995. Statistical Tables, Third Edition. W.H. Freeman and Co. New York. pp. 199
- SAKTHIVELU, G. AND KUMAR, A. 1998. Temporary group splitting in the lion-tailed macaque *Macaca silenus* in a forest fragment in Indira Gandhi Wildlife Sanctuary, Tamil Nadu. *Journal of the Bombay Natural History Society* 95: 422 - 425
- SIEGEL, S. 1956, Nonparametric Statistics for the Behavioural Sciences, McGraw-Hill International Book Co., London.UK
- SINGH, M., KUMARA, H.N., ANANDA KUMAR, M., SHARMA, A.K. AND DEFALCO, K. 2000. Status and Conservation of lion-tailed macaque and other arboreal mammals in tropical rainforests of Sringeri forest range, Western Ghats, Karnataka, India. *Primate Report*. 58: 5 - 16
- SINGH, M., SINGH, M., KUMAR, M.A., KUMARA, H.N., AND D'SOUZA, L. 1997 a. Distribution and research potential of non-human primates in the Aliyar-Valparai sector of Indira Gandhi Wildlife Sanctuary, Tamil Nadu, India. *Tropical Biodiversity*. 4: 197 - 208
- SINGH, M., SINGH, M., KUMAR, M.A., KUMARA, H.N., D'SOUZA, L., AND SHARMA, B.A.A.K. 1998. Behaviour of lion-tailed macaque (*Macaca silenus*) in vulnerable and relatively secure habitats in the rain forests of Western Ghats, India. *Tigerpaper* 25: 19 - 25
- SINGH, M., SINGH, M., KUMARA, H.N., KUMAR, M.A., AND D'SOUZA, L. 1997 b. Inter- and intra- specific associations of non-human primates in Anaimalai Hills, South India. *Mammalia* 1: 17 - 28
- SINGH, MR., SINGH, ME., ANANDA KUMAR, M., KUMARA, H.N., SHARMA, A.K., AND SUSHMA, H.S. 2000. Niche separation in sympatric lion-tailed macaque (*Macaca*

silenus) and nilgiri langur (*Presbytis johnii*) in an Indian tropical rain forest.

Primate Report. 58: 83 – 95

SKINNER, S.W. AND LOCKARD, J.S. 1979. An ethogram of the liontail macaque (*Macaca silenus*) in captivity. *Applied Animal Ethology*. 5: 241 – 253

SMUTS, B.B. 1983. Special relationships between adult male and female olive baboons: Selective advantages. In: *Primate social relationships: An integrated approach*. (ed. R.A.Hinde) Blackwell Scientific Publications. U.K. pp. 262 – 266

SMUTS, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Struhsaker, T.T. 1987. *Primate Societies*. University of Chicago Press, Chicago pp. 578

SOKAL, R.R. & ROHLF, F.J. 1995, Biometry, The principles and practice of Statistics in Biological Research. Third Edition, W.H. Freeman and Co., New York. pp. 887

SPSS INC. 1999. SPSS Professional Statistics 8.0. SPSS Inc., Chicago, USA.

STATISTICA. 1994. Statistica for Windows. General Conventions and Statistics, Tulsa, USA

SUGIYAMA, Y. 1968. The ecology of the lion-tailed macaque (*Macaca silenus*): A pilot study. *Journal of the Bombay Natural History Society* 65: 283 - 292

TOMASELLO, M. AND CALL, J. 1997. *Primate Cognition*. Oxford University Press, New York. pp 315

UMAPATHY, G. 1998. *Impacts of Habitat Fragmentation on the Arboreal Mammals in the Wet Evergreen Forests of the Anamalai Hills in the Western Ghats, South India*. PhD Thesis. Bharathiar University, Coimbatore, India

UMAPATHY, G. AND KUMAR, A. 2000. Impacts of the habitat fragmentation on time budget and feeding ecology of lion-tailed macaque (*Macaca silenus*) in rainforest fragments of Anamalai Hills, South India. *Primate Report*. 58: 67 – 82

VAN HOOFF, J.A.R.A.M. 1967. The facial displays of the Catarrhine monkeys and apes. In: *Primate Ethology* (ed: D.Morris.) Weidenfield, London. pp. 7 – 68 *

- VAN SCHAİK, C.P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: The behavioural ecology of humans and other animals*. (ed: V.Standen, R.A.Foley.)Blackwell. Oxford. pp. 241 –269
- VAN SCHAİK, C.P. 1996. Social evolution in primates: the role of ecological factors and male behaviour. In: *Evolution of social behaviour patterns in primates and man*. (ed: W.G.Runciman, J. Maynard-Smith, R.I.M.Dunbar, Oxford University Press. Oxford. Pp 9 – 32
- VEHRENCAMP, S. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* **31**: 667 – 682
- WU, H.M.H., HOLMES, W.G. MEDINA, M.R. AND SACKETT, G.P. 1980. Kin preference in infant *Macaca nemestrina*. *Nature*. **285**: 225 – 227
- ZELLER, A.C. 1987. Communication by sight and smell. In: *Primate Societies*.Ed: B.B.Smuts, D.L.Cheny, R.M.Seyfarth, R.W.Wragham, T.T.Strusaker. The University of Chicago Press. Chicago. pp. 433 – 439

* Not referred to in original.

APPENDIX 1: ETHOGRAM

The complete behavioural repertoire of a wild troop of lion-tailed macaques has been documented and described in this section. Although two earlier studies have presented ethograms for the species, both of these described the behaviour of captively housed groups (Skinner and Lockard 1979; Johnson 1985). The few behavioural studies, conducted on the species in its natural habitat, did not, however, document a comprehensive ethogram.

The behavioural repertoire of lion-tailed macaques, described here, is based on observations *ad libitum*, instantaneous scans and focal animal sampling of Troop 2, the smaller troop that occurs in the Puthuthottam fragment of the Indira Gandhi Wildlife Sanctuary, Anaimalai hills, Tamil Nadu, during the period from November 2000 to April 2001.

BEHAVIOURAL STATES refer to those behaviours that occur over a well-defined period of time. Since these are not instantaneous events, such behaviours are usually measured in terms of the proportion of time that an individual dedicates to them in course of its activity regime. The behavioural states that have been enumerated in the study troop are listed here.

1. *Absent from Troop*: Occasionally, certain individuals may not be with the rest of the troop, but could be ranging away from the main activity centres of the group. Care should be taken, however, to ensure that the absence of the individual from the troop is genuine, and that it is not simply at the periphery of the troop and hence, not easily visible to the observer. Adult males in particular were often found to move away from the rest of the troop while foraging in, or surveying certain areas of the home range.
2. *Autogroom*: The animal grooms any part on its own body, actively searching for insects, seeds, dirt, ectoparasites or any other object that might be entangled in its hair and focusing its attention on that particular part of the body. This is a common behaviour exhibited by both males and females, but to a relatively larger extent by males. In the study troop, adult males displayed a higher frequency of initiated

autogrooming and also spent relatively greater proportions of time in the activity than did the adult females.

3. *Drink*: Individuals usually drink by either lying flat, or by simply bending over and placing their mouths directly on the source of water. Occasionally, water may also be scooped out with the hands and drops licked up from the palm. Drinking behaviour is usually observed when the individuals are foraging and chance upon a hollow with water collected therein, or when the troop moves across a stream.
4. *Feed*: This behaviour usually involves the process of handling the food item, active ingestion and the process of chewing while consuming it. Feeding can be further classified into *Active Feeding*, whereby the individual feeds directly from the food source, and *Passive Feeding*, which involves the act of regurgitation of material stored in the cheek pouches and its subsequent ingestion.
5. *Forage*: The individual searches actively for food on various substrates. This behaviour can be divided into two classes. *Active Foraging* involves the active searching for food items among twigs, branches, green leaves, dry leaves, hollows on trees as well as on the ground, and the subsequent handling and manipulation of a food item. *Passive Foraging*, on the other hand, consists of the individual sitting alertly and looking around for potential food items. Adult females were observed to spend a larger proportion of their time foraging as compared to adult males in the study troop.
6. *Move*: Individuals may move continuously along tree branches or on the ground, usually in a specific direction, often not displaying any particular interest to objects along the way. This behaviour was typically observed during troop movements, when the entire group moved from one particular area to another.
7. *Play*: This behaviour involves the acts of mock biting, chasing, lunging, and wrestling between two or more individuals. Although play behaviour was usually observed frequently among infants, juveniles and subadults of both sexes, adult males too occasionally participated in play bouts. Adult females, in contrast, were almost never observed to play, a few exceptions being certain mothers who played with their own infants or with those of other adult females.

8. *Rest*: Individuals usually rest with their feet up on a branch and with the head down on the chest, or by slouching with the head hanging off the branch. During such resting periods, the eyes usually remain open and the individual may be completely awake. Resting has been observed more frequently among adult males than adult females in the study troop.
9. *Sit*: Individuals may sit in a relaxed fashion on any substratum, often without exhibiting a specific interest in any object, individual or event. This has been observed commonly among all individuals of all age and sex classes in the troop.
10. *Sit Alert*: An individual may sit on any substratum and looks attentively at a particular object, individual or event in the surrounding area. This behaviour is exhibited more commonly by adult individuals, with males usually sitting alert more often than do females.
11. *Sleep*: Individuals sleep either in the sitting position or while lying supine – with eyes closed in either situation. Apart from being observed during the late evening or early morning owing to the diurnal nature of the species, sleeping is also met with during afternoons when certain individuals may fall asleep during rests between bouts of foraging.
12. *Stand*: The individual stands on all four limbs on any particular substratum, without necessarily being attentive to any particular object, individual or event in the immediate environment.
13. *Stand Alert*: Individuals may often stand on any substratum and look attentively at a particular object, individual or event in the immediate or distant environment. This behaviour is usually exhibited during inter-troop encounters with members of neighbouring groups or when a predator is sensed.
14. *Survey*: An individual stands attentively, sits alertly or stands erect bipedally on any substratum, but usually on high branches, and scans the neighbourhood intently. This

is a behaviour almost exclusively exhibited by adult and subadult males, although certain dominant females also surveyed the surrounding area on occasions.

BEHAVIOURAL EVENTS are instantaneous behaviours or those that occur with a certain frequency, but do not occupy any significant span of time. The behavioural events have been further divided into *individual events* and *social interactions*.

Individual events comprise those behavioural acts that are not directed towards any other individual within the social group. These behaviours may be self-directed, directed towards members of other species, and may be performed in the absence of any other individual or animal.

1. *Alarm Call*: Short gruff bark-like vocalisations are often given when an individual is startled, or in response to alarm calls given by other individuals. Such calls may be directed towards potential predators, as when a raptor flies overhead, or even to human beings. Alarm calls may be given by both males and females, belonging to different age classes.
2. *Body Shake*: An individual, while sitting or standing, may shake its torso vigorously, often to dislodge twigs, fragments of leaves and dust, and also occasionally to shake off water after the rains. This is a common behaviour exhibited by individuals of all age and sex classes.
3. *Cough*: This behaviour, very reminiscent of a human cough, may result from a temporary choking during feeding bouts, during regurgitation, or as a result of a suspected ailment or infection.
4. *Defecate*: Individuals may defecate while sitting or standing on any substratum.
5. *Inspect Penis*: Sexually mature males often inspect their penis, sometimes visually but often with their hands: they may then smell their fingers or lick their palms after such inspection.

6. *Lick Hand*: Individual males and females often lick the palms and fingers of the hand, after the inspection of a bodily wound or of any part of the body.
7. *Masturbate*: Sexually mature males often manipulate their genital organs by rubbing the penis with their hands, often resulting in a visible erection of the penis. Masturbation has been reported by Skinner and Lockard (1979) and Johnson (1985), but neither study has reported ejaculation. Since conditions in field did not facilitate observations of ejaculation, whether masturbation terminates in ejaculation remains uncertain.
8. *Rub Body or Object*: An individual may rub any part of its body, or may rub any other object that it is holding against the substratum. An interesting behaviour in this connection is that of rubbing a food item such as a caterpillar against a branch, often after enclosing it within a leaf, in order to remove its hairs.
9. *Scratch Body*: Individuals often scratch different parts of their bodies, sometimes without even being overtly attentive to the act. Scratching is usually performed by individuals of all age and sex classes, although adult males were observed to scratch more frequently than did adult females.
10. *Sneeze*: This behaviour, very reminiscent of the human sneeze, is not restricted to individuals of any particular age or sex class.
11. *Stretch*: The individual stretches its body, while standing. Although not very common, it can be performed by all classes of individuals.
12. *Swipe at Insect*: An individual often vigorously moves its hand in front of its face, presumably to drive away flies or other hovering insects. This is a common behaviour exhibited by all individuals but at higher frequencies during certain seasons or in certain habitats.
13. *Urinate*: Individuals may urinate while sitting or standing on any substratum.

14. *Wipe Mouth or Nose*: An individual uses its palm to wipe any object or any part of its body: the mouth is often wiped, for example, after an active feeding session.
15. *Yawn*: Individuals usually yawn while sitting on any substratum. This behaviour needs to be distinguished from the rather similar-appearing *Bared-teeth Display*, which is usually performed during episodes of aggression. Yawning is usually performed at higher frequencies following periods of rest or sleep.

Social interactions include behavioural events that are directed by an individual towards one or more members of the same social group; occasionally such events may also occur between individuals belonging to different, often neighbouring, troops of lion-tailed macaques. Social behavioural events have been further classified into Affiliation, Aggression, Dominance, Play, Sexual Behaviours, Infant-related Behaviours and Neutral Behaviours.

Affiliation: This category of behaviours includes those that are employed in an affiliative context during social interactions between individuals.

1. *Affiliative Bared-teeth Face*: This is a communicative gesture in which an individual displays its teeth by pulling apart its lips, with the corners drawn backwards. The mouth is also held partially open. A common behaviour displayed in a variety of non-agonistic situations including, for example, as a greeting display between adult females, it is often accompanied by the *Affiliative Grunt*. This gesture has also been referred to as an Open Bare-teeth Display by Preuschoft (1995)
2. *Affiliative Grunt*: A short grunt-like vocalisation usually made by an individual when encountering another individual in a non-agonistic situation. Exhibited by both males and females alike, it is more common among older individuals and not observed as often among juveniles and infants.
3. *Allogroom*: In this most common of all social interactions, an individual grooms any part of the body of another individual, actively looking for and picking out dirt, ectoparasites and other foreign particles from the hair. Allogrooming is usually performed by individuals of all age and sex classes except infants, who were never

observe to allogroom. In the study troop, this behaviour was most frequently directed by adult females towards other females, male-male allogrooming being relatively rare. Occasionally, allogrooming may be accompanied by active lip-smacking.

4. *Contact Call*: A "coo" vocalisation made by an individual, this call is usually made when individuals are moving or foraging in close proximity to each other. Contact calls may or may not, however, receive an immediate response from another individual. Often the contact call may be responded to with a similar-sounding call – this has been referred to as the *Reply Contact Call*. The frequency of contact calls made by adult females was seen to be higher than that given by males in the study troop.
5. *Follow*: One individual may follow a second individual as the latter moves, typically using the same path. This behaviour, used almost invariably with the purpose of approaching the second animal, was displayed by all classes of individuals, but at relatively higher frequencies by infants and juveniles moving with their mothers or siblings.
6. *Friendly Approach*: This refers to an approach made by an individual towards another, followed by the display of any of the affiliative behaviours towards each other.
7. *Hold*: An individual holds another individual by any part of the latter's body. Although used in an affiliative context, this was of rare occurrence, at least among the members of the study troop.
8. *Hug*: Also referred to by Skinner and Lockard (1979) as an Embrace, the individual stands erect bipedally and embraces a second individual ventro-ventrally. Like the *Hug*, this behaviour too was of rare occurrence in the study troop.
9. *Long Call*: This is a loud long vocalisation made by an individual when the troop begins to move after spending significant time foraging, feeding or resting in a particular area. Although there may not be an immediate response, the call is sometimes responded to with a similar-sounding call, referred to as the *Reply Long Call*. While adult females gave the long call more frequently than did adult males, the

frequency of long calls displayed was observed to be positively correlated to that of *Contact Calls*, described above.

10. *Mouth Touch*: An individual touches the mouth of another individual with its own mouth in an affiliative gesture, although, occasionally the head of the target individual may also be touched. This behaviour is performed by both males and females of all age classes.
11. *Move Away*: The actor moves away from the target individual, terminating an affiliative interaction between the two of them. It must be noted that moving away is never in response to any aggressive act or behaviour displayed by the involved individuals, but a decision made by the actor to simply terminate the affiliative interaction. Although not strictly an affiliative behaviour by itself, this behaviour has been included in this category because it is shown in the context of affiliative interactions alone.
12. *Pat*: The individual gently pats any part of the body of another individual. An affiliative gesture, the pat was rarely performed among the members of the study troop.
13. *Raise Brow*: An affiliative gesture, the actor lifts its eyebrows at another individual, displaying the upper eyelids in the process. The head is also lifted slightly and held up at an angle during the act, while the lifted eyebrows are held in that position for a while. Often repeated in quick succession, this behaviour is usually displayed when an individual approaches another. This appears to be a relatively rare behaviour, observed by Johnson (1985), but not by Skinner and Lockard (1979).
14. *Seek Allogrooming*: An individual often approaches another animal and either lies down, bends, sits or stands in front of the latter, usually looking away from it. This behaviour could either result in the actor being allogroomed by the target individual, or in the latter moving away or otherwise ignoring the request for allogrooming. Observed alike among males and females, higher ranked and larger body-sized individuals in the study troop were more likely to be groomed on seeking allogrooming than were smaller individuals of lower rank.

15. *Seek Support*: During agonistic interactions, one or more of the protagonists may look at an hitherto uninvolved individual and perform an affiliative gesture such as *Affiliative Bared-teeth Face* or *Lip-smack*. The target individual may or may not respond to this behaviour by subsequently participating in the encounter and providing agonistic support to the actor.
16. *Sit Close*: An individual sits at a distance less than half a metre from a second individual. A common affiliative behaviour observed among individuals of all age and sex classes. It usually follows the act of an individual making a *Friendly Approach* towards another individual.
17. *Sit in Contact*: An individual sits with all or some part of its body touching that of a second individual. Although not very common, it has been most frequently observed among certain dyads and particularly during resting periods.
18. *Sleep Together*: The actor sits in contact with or close to the target individual and both fall asleep in this situation. Although common in mother-infant or mother-juvenile dyads, this behaviour is of rare occurrence among adult individuals, particularly adult males.
19. *Touch*: An individual reaches out its hand and touches any part of the body of another individual. This behaviour is often directed toward new or very young infants that arouse the curiosity of other members of the troop.

Aggression: This category of behaviours includes those that are employed during agonistic interactions between individuals.

1. *Aggressive Bark*: Sharp bark-like vocalisation that an individual directs towards a target individual during relatively highly aggressive encounters. This call may be given by animals of all age and sex classes.
2. *Aggressive Bite*: The actor may hold tight the body or a body part of the target and bite hard into its flesh. Although occasionally mildly performed during certain within-troop

agonistic interactions, the bite may be rather severe during intense aggressive bouts or during inter-troop encounters, often drawing blood in the process.

3. *Bared-teeth Display*: A prolonged deliberate yawn that fully exposes the canines of the individual, this aggressive display gesture is often not directed towards any particular individual. Performed by males much more frequently than by females, this behaviour has also been referred to as a Tension Yawn or Threat Yawn by Skinner and Lockard (1979).
4. *Branch Shake*: Performed more frequently by males than by females, this aggressive gesture consists of an individual holding a branch with its hands and shaking it vigorously. The visual display and the noise produced by this behaviour typically serves to attract attention towards the actor – particularly when performed during within-group and inter-troop agonistic encounters.
5. *Chase*: During aggressive interactions, an individual may rush towards the target individual and follow it closely for some distance. During particularly aggressive encounters, the chase may terminate in an act of contact aggression. The target individual necessarily *Flees* during a chase; this may subsequently be followed by a *Fear Grimace* or *Lip-smack* directed at the chasing individual.
6. *Display Bounce*: An individual stands on a branch and jumps on it causing it to shake vigorously and occasionally break and fall, thus creating a loud commotion during the process. A common display during inter-troop encounters, this behaviour is invariably performed by males and almost always in tense or aggressive situations. A milder version of this act is often by juveniles to initiate play.
7. *Eye Flash*: The individual lifts its eyebrows and pulls back its forehead exposing the upper eyelids in a sudden jerky motion. A behaviour observed only very rarely, it is used in aggressive contexts and is often accompanied by a *Warning Growl* or other aggressive behaviour.
8. *Fear Grimace*: The individual opens its mouth slightly, with the corners of the lips pulled back so as to expose both rows of teeth. The jaws are not held open and the

teeth are parted only very slightly. Displayed by both males and females when receiving aggression, lower ranking individuals perform this gesture much more often than do relatively higher ranked animals. This behaviour has also been referred to as Silent Bared-teeth Display by Skinner and Lockard (1979), and as Grimace by Johnson (1985).

9. *Fear Scream*: A loud high-pitched screech-like vocalisation usually made by an individual in response to received aggression or in fear. This call can be given by individuals of all age and sex classes, but is rarely observed among adult males.
10. *Flee*: An individual runs away quickly from another animal in response to a *Chase* or any other aggression directed towards it. Juveniles and subadults were observed to flee more often than did adults. This behaviour was also noted during inter-troop encounters when individuals of one troop were displaced by those of a more dominant troop.
11. *Lunge*: During certain agonistic interactions, the actor may suddenly rush towards another individual but may stop short before making contact. The torso of the aggressor is often held forward in a directed manner towards the victim of aggression during this behaviour. Displayed most commonly by adult males and females and less often by juveniles, it is almost never exhibited by infants.
12. *Open-mouth Threat*: During this gesture, the mouth of the actor is held wide open displaying the canines for a relatively long duration of time. The head is usually held up such that the chin protrudes forward – towards the victim of aggression. Occasionally, the eyebrows are also raised so as to expose the eyelids. Exhibited by both adult males and females alike, this behaviour is more often directed by higher ranking individuals towards their subordinate counterparts.
13. *Pull Roughly*: An individual forcefully pulls any part of the body of a second individual. This behaviour was invariably used as an aggressive act by members of the study troop, in response to which the recipient was observed to either *Fear Scream*, *Fear Grimace* or *Lip-smack*. Johnson (1985) has, however, classified a similar behaviour as one used to 'reduce tension' during agonistic interactions: the display of

this behaviour apparently involved the pulling of another individual followed by acts of presenting or lip-smacking.

14. *Push Away*: The actor roughly pushes another individual or any part of its body away from itself, often in an effort to avoid unwanted attention. Performed by both males and females, this behaviour is frequently used by adult females to keep away other individuals from their infants. On rare occasions, it was used in the context of active aggression whereby an animal approached another and pushed it away roughly.
15. *Strike with Contact*: A hard hit or slap delivered by the actor on any part of the body of the target individual. Occasionally, a strike did not terminate in contact especially when the target was not physically close enough to the actor (*Strike without Contact*). A rare behaviour, the strike was observed only during highly aggressive interactions.
16. *Warning Growl*: A low growl-like vocalisation directed by an individual towards another during agonistic encounters, the warning growl is used by both males and females alike. Larger, more dominant individuals were, however, observed to direct this behaviour at relatively higher frequencies towards smaller lower ranking animals.

Dominance: This category of behaviours includes all interactions related to the establishment and maintenance of dominance-subordination relationships. These have been classified into three groups:

- (1) *Dominance*: Behaviours that are indicative of the actor's relative dominance over the target individual and, accordingly, invariably directed by dominant individuals towards their subordinate counterparts.
- (2) *Submission*: Behaviours that are displayed by subordinate individuals towards their dominant counterparts, and are usually indicative (to the observer) of their subordinate status.
- (3) *Ambiguous*: Behaviours that are often exhibited during dominance-subordination interactions, out which remain ambiguous with respect to the direction in which they are displayed.

Dominance

1. *Aggressive Approach*: The actor approaches a target individual and subsequently displays an aggressive act or gesture towards this individual. This behaviour was used as an indicator of dominance-subordination relationships since a dominant individual alone, by definition, exhibited aggressive approach towards subordinate individuals.
2. *Approach Retreated From*: The actor approaches the target individual but the latter moves away from the former without any subsequent interaction occurring. A clear indicator of dominance, this spontaneous moving away from the approaching individual is displayed, by definition, only by a subordinate animal.

Submission

1. *Crouch*: The actor physically bends down and often lies low on the substratum or otherwise cowers from a second individual. The head is usually held forward during this act and the fore limbs tucked under the trunk. Johnson (1985) has classified this behaviour as a 'tension reducing action'.
2. *Retreat*: An individual moves away from an approaching animal in order to maintain a definite distance between them or to move away from it altogether. This behaviour is typically observed during dominance-subordination interactions when the subordinate often spontaneously moves away, or during agonistic interactions when the victim of aggression retreats from the aggressor.

Ambiguous

1. *Avoid*: The actor moves or turns its body around in order to avoid facing an approaching individual or any other animal in the vicinity. Although subordinate individuals often actively avoid their dominant counterparts, this behaviour may also be exhibited by relatively high ranking individuals in an effort to deflect unwanted attention: for example, females with infants often turned away from lower ranking females to avoid their infants being handled by the latter.

2. *Avoid Mount*: An individual moves away just as a second individual is about to mount it. Both males and females are known to avoid being mounted by certain individuals, but the relationship of this behaviour to dominance-subordination interactions remains unclear.
3. *Lip-smack*: The actor vigorously opens and closes its mouth in rapid succession, pressing the lips firmly against each other during the closed mouth phase of the act – this invariably leads to a clearly audible smacking sound. Although subordinate animals showed a higher frequency of lip-smacking towards their dominant counterparts in the study troop, higher ranking individuals were also observed to lip-smack, particularly while reassuring lower ranking animals. Lip-smacking can also be used as a gesture of appeasement or reassurance during acts of *Allogroom*, *Present*, *Simple Mount* and *Thrusting Mount*.
4. *Present*: The actor approaches and/or stands in front of the target individual and presents its hindquarters to it. In response to this act, the target individual could mount the actor, inspect its genital area or ignore the act completely. Subordinate individuals were usually observed to present to dominant individuals with lip-smacking (*Present with Lip-smacking*). Males and females in the troop were observed to present to individuals of their own sex as well as to those of the opposite sex. In general, females in the study troop presented relatively much more to the males; on some occasions, however, these were of a sexual nature (see *Sexual Mount* below).
5. *Simple mount*: The actor mounts or partly climbs and clasps the hindquarters of the target individual but without any thrusting movement of the abdomen. In the study troop, males simple-mounted each other more often than females did. Juvenile and female-female mounts were more likely to be simple mounts than *Thrusting Mounts*. Occasionally, simple mounts were observed to be accompanied by lip-smacking (*Simple Mount with Lip-smacking*).
6. *Thrusting mount*: An individual mounts the hindquarters of the target individual and accompanies this act with a thrusting motion of its abdomen; often the genitalia of the actor may be rubbed against that of the target. In the study troop, adult males were more likely to thrusting-mount other males and females than were adult females.

Occasionally, the target individual moved away and avoided being mounted by the actor. Subordinate individuals typically accompanied their thrusting mounts of dominant animals with vigorous lip-smacks (*Thrusting Mount with Lip-smacking*).

Play: This category includes all acts of play behaviour indulged in by the different individuals of the troop. Play was most common among subadults, juveniles and infants, although certain adult males were occasionally observed to participate in some play bouts. Adult females, in contrast, almost never played except occasionally with their own infants.

1. *Initiate Play*: An individual may charge another individual, jump on a branch in front of it, or mock chase it, occasionally even approaching and striking out playfully at the animal, with the purpose of initiating play with the second individual.
2. *Play Bite*: The individual gently bites another individual on any part of the body, occasionally holding onto it with its mouth for a short period of time. Most bouts of *Play Wrestle* were accompanied by acts of play bite.
3. *Play Chase*: An individual runs at another animal and chases it around playfully. This could terminate in a wrestling bout or in the target individual turning around and play chasing the actor.
4. *Play Face*: The actor opens its mouth wide and holds it in that position for a short period of time, displaying the teeth during the process. This behaviour is often used to *Initiate Play*. The *Affiliative Bared-teeth Face* and the *Play Face*, described here, have been combined together and referred to as Grin by Johnson (1985). Skinner and Lockard (1979) have not mentioned a gesture equivalent to the *Affiliative Bared-teeth Face*, but have described a Relaxed Open-mouth Face or Play Face. Preuschoft (1995), on the other hand, have used the term Open-mouth Bared-teeth Display to refer to this particular behaviour.
5. *Play Jump*: The actor jumps at or very close to the target individual in order to initiate play or in the middle of a play session.

6. *Play Slap*: An individual reaches out and strikes at the target individual, with whom it had been playing, during a play session. This behaviour, although not very common, is often followed by a Play Chase between the same pair of individuals.
7. *Play Wrestle*: Two individuals grapple each other and wrestle, often tumbling off in the process. This is a very common behaviour during play sessions.

Sexual Behaviours: This category includes all sexual behaviours that occur between sexually mature males and females in oestrus.

1. *Avoid Sexual Mount*: This refers to the act of an oestrus female in moving away from a male as he prepares to mount her in order to avoid being mounted.
2. *Copulatory Call*: A repeated abrupt "ugh" vocalisation made predominantly by the female while the male is copulating with her or just after he dismounts. Most events of *Sexual Mount* are accompanied by the copulatory call.
3. *Copulatory Grimace*: This gesture is usually made by a copulating male when he lifts his head upwards and parts his lips to display the teeth, although the jaws are not opened too wide. This behaviour has been observed during most acts of *Sexual Mount*.
4. *Inspect*: The male lifts the tail of the female and examines her genitalia. Such inspection may be simply visual (*Visual Inspection*), or it may involve the male smelling the genitalia of the female or smelling his fingers after removing some secretions from the female's genitalia (*Olfactory Inspection*). Occasionally, the male may also taste the secretions that he has collected from the genital region of the female (*Gustatory Inspection*).
5. *Sexual Approach*: This behaviour refers to the approach made by a male towards an oestrus female, occasionally followed a *Sexual Mount*.
6. *Sexual Mount*: This behaviour involves the mounting of an oestrus female by a male who then thrusts his abdomen repeatedly in order to copulate with her. Since the lion-tailed macaque is known to be a multiple-mount ejaculator, not all sexual mounts

necessarily terminate in ejaculation. It is, however, extremely difficult to observe the actual act of ejaculation, following a sexual mount, under field conditions.

Infant-related Behaviours: This category includes behaviours that usually characterise mother-infant relationships or those between infants and other adult females. Adult males were virtually never observed to show any interest towards infants.

1. *Carry Infant:* An individual carries an infant as it moves from one place to another. In most cases, it is the mother who carries the infant, although as the infant grows older and less dependent on its mother, it may be carried by other adult females or juveniles for short periods of time.
2. *Groom Infant:* The actor allogrooms any part of the body of an infant, actively looking for and picking out dirt, ectoparasites and other foreign particles from the hair.
3. *Hold Infant:* The individual holds the infant close to its own body, supporting it with both hands.
4. *Nuzzle Infant:* The actor takes its face close to the infant and rubs its face against the infant. Although very rare, this behaviour appears to signify an affiliative relationship between the infant and the actor.
5. *Pull Infant:* An individual pulls the infant close to itself either from another individual or from where the infant is sitting or standing. Adult females were often observed to pull their own infants towards themselves – either just prior to moving or during periods of rest.
6. *Push Infant:* The actor pushes away the infant or any part of the body of the infant away from itself. This behaviour was often observed when an infant interfered with its mother's feeding, or when an infant attempted to reach out for some object held by the actor.

7. *Touch Infant*: An individual reaches out and touches any part of the body of an infant with its hands. One particular, frequently observed variant of this behaviour is the mouth-touch of an infant.

Neutral Behaviours: This category of behaviours includes those that appear to be functionally neutral with regard to agonistic and affiliative relationships, dominance-subordination interactions or sexual relationships.

1. *Ignore*: The actor does not any attention or chooses to look away from any act directed towards it by the target individual. This behaviour has often been observed as a response to the acts of *Present*, *Seek Allogrooming* or *Seek Support*.
2. *Look*: An individual looks directly at the target individual, usually making eye contact in the process. Not seen in the context of aggression or seeking support, the underlying motivation for this behaviour remains unclear.
3. *Lost Call*: A long, loud, wail or moan made by an individual that has become isolated from the rest of the troop and appears to be unable to detect any of the group members. Other individuals from the troop almost invariably respond to the lost call immediately by giving long calls (*Reply Lost Call*) – these calls are given until actor finds its way back to the troop.
4. *Loud Call*: A loud vocalisation comprising a long initial part followed by repeated calls of a shorter duration. This vocalisation is given only by adult males when they move away from the rest of the troop.
5. *Neutral Approach*: The actor approaches another individual and sits within a metre of the latter without any further interaction. This approach is not followed subsequently by the display of any affiliative or aggressive behaviour. Neutral approaches were often made in the context of foraging in an effort to reach a particular food resource.
6. *Observe*: An individual looks at another individual casually and follows its actions or movement for a short period of time. This behaviour could be associated with the target individual failing to realise that it was being observed.

7. *Staccato Call*: Loud repeated short "aah" vocalisation, given only by females. This call has been described as a proceptive call given by oestrus females with the purpose of attracting males (Lindburg 1990). In the study troop, however, this call was made by a dominant female when she did not appear to be in oestrus.
8. *Walk Past*: The actor, while moving, walks past the target individual either brushing against it or moving within $\frac{1}{2}$ metre of it. This behaviour is commonly observed when individuals are foraging together at a clumped food resource.