

THE UNIVERSITY OF CALGARY

ADULT MALE INTRAGROUP BEHAVIOUR
IN JAPANESE MACAQUES (*Macaca fuscata*)

by

Sasrika Neelakshi Tillekeratne

A THESIS

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Pathology 0419
Pharmacology 0572
Pharmacy 0382
Physical Therapy 0573
Public Health 0574
Radiology 0575
Recreation 0460
Speech Pathology 0383
Toxicology 0386
Home Economics 0386

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Biochemistry 0488
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Nuclear 0490
Organic 0491
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Physical 0495
Polymer 0754
Radiation 0405
Mathematics 0605
Physics 0986
General 0606
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Radiation 0611
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Marketing	0338
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Histoire générale	0578

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Médiévale	0581
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Histoire des noirs	0328
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Transports	0709
Travail social	0452

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Culture	0479
Élevage et alimentation	0475
Exploitation des pâturages	0777
Pathologie animale	0476
Pathologie végétale	0480
Physiologie végétale	0817
Sylviculture et faune	0478
Technologie du bois	0746
Biologie	
Généralités	0306
Anatomie	0287
Biologie (Statistiques)	0308
Biologie moléculaire	0307
Botanique	0309
Cellule	0379
Écologie	0329
Entomologie	0353
Génétique	0369
Limnologie	0793
Microbiologie	0410
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Océanographie	0416
Physiologie	0433
Radiation	0821
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Zoologie	0472
Biophysique	
Généralités	0786
Médicale	0760

Géologie	0372
Géophysique	0373
Hydrologie	0388
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Paléocologie	0426
Paléontologie	0418
Paléozoologie	0985
Palynologie	0427

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Sciences de la santé	
Généralités	0566
Administration des hôpitaux	0769
Alimentation et nutrition	0570
Audiologie	0300
Chimiothérapie	0992
Dentisterie	0567
Développement humain	0758
Enseignement	0350
Immunologie	0982
Loisirs	0575
Médecine du travail et thérapie	0354
Médecine et chirurgie	0564
Obstétrique et gynécologie	0380
Ophtalmologie	0381
Orthophonie	0460
Pathologie	0571
Pharmacie	0572
Pharmacologie	0419
Physiothérapie	0382
Radiologie	0574
Santé mentale	0347
Santé publique	0573
Soins infirmiers	0569
Toxicologie	0383

SCIENCES PHYSIQUES

Sciences Pures	
Chimie	
Généralités	0485
Biochimie	0487
Chimie agricole	0749
Chimie analytique	0486
Chimie minérale	0488
Chimie nucléaire	0738
Chimie organique	0490
Chimie pharmaceutique	0491
Physique	0494
Polymères	0495
Radiation	0754
Mathématiques	0405
Physique	
Généralités	0605
Acoustique	0986
Astronomie et astrophysique	0606
Électronique et électricité	0607
Fluides et plasma	0759
Météorologie	0608
Optique	0752
Particules (Physique nucléaire)	0798
Physique atomique	0748
Physique de l'état solide	0611
Physique moléculaire	0609
Physique nucléaire	0610
Radiation	0756
Statistiques	0463

Sciences Appliquées Et Technologie

Informatique	0984
Ingénierie	
Généralités	0537
Agricole	0539
Automobile	0540

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Génie aérospatial	0538
Génie chimique	0542
Génie civil	0543
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Génie industriel	0546
Génie mécanique	0548
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Métallurgie	0743
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Technique minière	0551
Techniques sanitaires et municipales	0554
Technologie hydraulique	0545
Mécanique appliquée	0346
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Matériaux plastiques (Technologie)	0795
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Textiles et tissus (Technologie)	0794

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Personnalité	0625
Psychobiologie	0349
Psychologie clinique	0622
Psychologie du comportement	0384
Psychologie du développement	0620
Psychologie expérimentale	0623
Psychologie industrielle	0624
Psychologie physiologique	0989
Psychologie sociale	0451
Psychométrie	0632

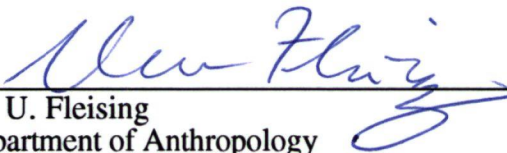


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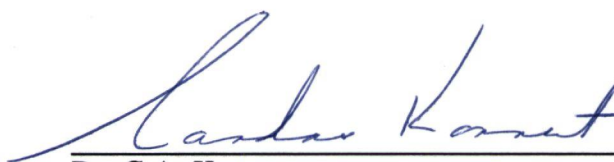
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Date: July 29, 1994

ABSTRACT

In this study, adult male daily activity patterns and social interactions were examined in the two troops of Japanese macaques (*Macaca fuscata*) at The South Texas Primate Observatory: Arashiyama West Snow Monkey Sanctuary, Dilley, Texas. A total of 161.5 hours of focal animal data was collected in the nonmating season from June to September, 1994. Out of all age/sex classes, adult males seem to preferentially affiliate with adult females, and also direct aggression at them the most. There was little overall aggression involving adult males in this colony, and it usually was low-intensity in quality. The age, dominance rank and troop membership of the subject animals were analyzed to discover whether they caused any variation in behaviour. It was established that these variables had little effect on adult male behaviour.

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Finally, I am grateful to the Department of Graduate Studies at the University of Calgary for giving me the funding that permitted me to conduct my study.

DEDICATION

I would like to dedicate this thesis to two very special people who have inspired me and continue to be invaluable in my life - my partner, Roelof-Jan Steenstra, and my mother, Sriya Tillekeratne.

TABLE OF CONTENTS

Approval Page.	ii
Abstract.	iii
Acknowledgments.	iv
Dedication.	v
Table of Contents.	vi
List of Tables.	ix
List of Figures.	xii

CHAPTER ONE - ADULT MALE INTRAGROUP SOCIAL BEHAVIOUR IN FEMALE-BONDED OLD WORLD MONKEYS

Introduction.	1
Dispersal and Philopatry.	3
Adult Male Intragroup Social Interactions: Macaques and Savanna Baboons.	5
Entrance into a Bisexual Group	6
Affiliative Interactions.	7
Agonistic Interactions.	10
The Dominance Hierarchy.	11
A Nonfemale Bonded Species: The Chimpanzee.	14
Research Objectives.	18

CHAPTER TWO - METHODS

The Study Species: Japanese Monkeys (<i>Macaca fuscata</i>).	20
Social Organization.	20
The Study Group.	21
Subject Animals.	23
Data Collection Methods.	26
Ethogram.	26
State Behaviours.	27
Event Behaviours.	28
Data Analysis Methods.	33
Introduction.	33
General State Behaviours.	33
Affiliative Interactions	33
Agonistic Interactions	34
Relatedness of Adult Interactants	34
Overview of Thesis.	35

CHAPTER THREE - RESULTS: GENERAL STATE BEHAVIOURS AND THE NATURE OF SOCIAL INTERACTIONS OF ALL SUBJECT ANIMALS

Introduction.	37
General State Behaviours.	37
Affiliative Interactions.	39
Nature of Affiliative State Behaviours.	39
Age/Sex Class of Interactants - Affiliative State Behaviours	42
Age/Sex Class of Interactants - Affiliative Event Behaviours	45

Agonistic Interactions.	45
Age/Sex Class of Interactants - Agonistic Event Behaviours	45
Relatedness of Adult Interactants.	48
Affiliative State Behaviours	48
Affiliative Event Behaviours.	51
Agonistic Event Behaviours	54
Summary of Results	57
Case Studies	59

CHAPTER FOUR - RESULTS: OVERALL DIFFERENCES ACCORDING TO AGE

Introduction.	65
General State Behaviours.	67
Affiliative Interactions.	67
Affiliative State Behaviours	67
Affiliative Event Behaviours	70
Agonistic Interactions.	72
Relatedness of Adult Interactants.	72
Affiliative State Behaviours	72
Affiliative Event Behaviours	72
Agonistic Event Behaviours	78
Summary of Results.	81

CHAPTER FIVE - RESULTS: OVERALL DIFFERENCES ACCORDING TO RANK

Introduction.	82
General State Behaviours.	84
Affiliative Interactions.	84
Affiliative State Behaviours	84
Affiliative Event Behaviours	87
Agonistic Interactions.	87
Relatedness of Adult Interactants.	92
Affiliative State Behaviours	92
Affiliative Event Behaviours	92
Agonistic Event Behaviours	92
Summary of Results.	97

CHAPTER SIX - RESULTS: OVERALL DIFFERENCES ACCORDING TO TROOP MEMBERSHIP

Introduction.	98
General State Behaviours.	99
Affiliative Interactions.	99
Affiliative State Behaviours	99
Affiliative Event Behaviours	99
Agonistic Interactions.	104
Relatedness of Adult Interactants.	104
Affiliative State Behaviours	104
Affiliative Event Behaviours	104
Agonistic Event Behaviours	104
Summary of Results.	111

CHAPTER SEVEN - DISCUSSION

General State Behaviours and Nature of Social Interactions.	112
General State Behaviours	112
Affiliative Interactions.	113
Agonistic Interactions.	118
Variation in Adult Male Behaviour	121
Variation due to Age.	121
Variation due to Dominance Rank.	122
Variation due to Troop Membership	123
Comment on Integration of Qualitative and Quantitative Data.	125
Limitations and Practical Considerations of Study.	127
Conclusion.	128
 REFERENCES.	 130
 APPENDIX A.	 140

LIST OF TABLES

Table 2.1 -	Adult Male Subject Animals.	25
Table 4.1 -	Results of Spearman's Rho Test: Age and General State Behaviours of Adult Males	68
Table 4.2 -	Results of Spearman's Rho Test: Age and Affiliative State Behaviours of Adult Males	69
Table 4.3 -	Results of Spearman's Rho Test: Age and General Categories of Affiliative Event Behaviours of Adult Males.	71
Table 4.4 -	Results of Spearman's Rho Test: Age and Affiliative Event Behaviours of Adult Males	71
Table 4.5 -	Results of Spearman's Rho Test: Age and General Categories of Agonistic Event Behaviours of Adult Males.	73
Table 4.6 -	Results of Spearman's Rho Test: Age and Agonistic Event Behaviours of Adult Males	74
Table 4.7 -	Results of Spearman's Rho Test: Age and Affiliative State Behaviours of Adult Males with Related and Unrelated Adults.	76
Table 4.8 -	Results of Spearman's Rho Test: Age and Affiliative Event Behaviours of Adult Males with Related and Unrelated Adults.	77
Table 4.9 -	Results of Spearman's Rho Test: Age and Agonistic Event Behaviours of Adult Males with Related and Unrelated Adults.	79
Table 5.1 -	Results of Kruskal-Wallis Test: Dominance Rank and General State Behaviours of Adult Males.	85
Table 5.2 -	Results of Kruskal-Wallis Test: Dominance Rank and Affiliative State Behaviours of Adult Males.	86
Table 5.3 -	Results of Kruskal-Wallis Test: Dominance Rank and General Categories of Affiliative Event Behaviours of Adult Males.	88

Table 5.4 -	Results of Kruskal-Wallis Test: Dominance Rank and Affiliative Event Behaviours of Adult Males	88
Table 5.5 -	Results of Kruskal-Wallis Test: Dominance Rank and General Categories of Agonistic Event Behaviours of Adult Males.	89
Table 5.6 -	Results of Kruskal-Wallis Test: Dominance Rank and Agonistic Event Behaviours of Adult Males.	90
Table 5.7 -	Results of Kruskal-Wallis Test: Dominance Rank and Affiliative State Behaviours of Adult Males with Related and Unrelated Adults.	93
Table 5.8 -	Results of Kruskal-Wallis Test: Dominance Rank and Affiliative Event Behaviours of Adult Males with Related and Unrelated Adults.	94
Table 5.9 -	Results of Kruskal-Wallis Test: Dominance Rank and Agonistic Event Behaviours of Adult Males with Related and Unrelated Adults.	95
Table 6.1 -	Results of Mann-Whitney Test: Troop Membership and General State Behaviours of Adult Males.	100
Table 6.2 -	Results of Mann-Whitney Test: Troop Membership and Affiliative State Behaviours of Adult Males.	101
Table 6.3 -	Results of Mann-Whitney Test: Troop Membership and General Categories of Affiliative Event Behaviours of Adult Males.	102
Table 6.4 -	Results of Mann-Whitney Test: Troop Membership and Affiliative Event Behaviours of Adult Males.	103
Table 6.5 -	Results of Mann-Whitney Test: Troop Membership and General Categories of Agonistic Event Behaviours of Adult Males.	105
Table 6.6 -	Results of Mann-Whitney Test: Troop Membership and Agonistic Event Behaviours of Adult Males	106
Table 6.7 -	Results of Mann-Whitney Test: Troop Membership and Affiliative State Behaviours of Adult Males with Related and Unrelated Adults.	108

Table 6.8 -	Results of Mann-Whitney Test: Troop Membership and Affiliative Event Behaviours of Adult Males with Related and Unrelated Adults.	109
Table 6.9 -	Results of Mann-Whitney Test: Troop Membership and Agonistic Event Behaviours of Adult Males with Related and Unrelated Adults	109

LIST OF FIGURES

Figure 3.1 -	Percentage of Time Adult Males Spent in General State Behaviours.	38
Figure 3.2 -	Percentage of Total Time Adult Males Spent in Social vs. Nonsocial Activity	40
Figure 3.3 -	Percentage of Total Social Time Adult Males Spent in Affiliative State Behaviours.	41
Figure 3.4 -	Percentage of Time Adult Males Spent in Social Grooming Activity with each Age/Sex Class.	43
Figure 3.5 -	Percentage of Time Adult Males Spent in Body Contact with each Age/Sex Class.	44
Figure 3.6 -	Frequency of Approaches Adult Males Directed toward and Received from each Age/Sex Class	46
Figure 3.7 -	Frequency of Directed Aggression by Adult Males toward each Age/Sex Class	47
Figure 3.8 -	Frequency of Received Aggression by Adult Males from each Age/Sex Class.	49
Figure 3.9 -	Percentage of Time Adult Males Spent in Social Grooming Activity with Related and Unrelated Adults	50
Fig. 3.10 -	Percentage of Time Adult Males Spent in Body Contact with Related and Unrelated Adults.	52
Fig. 3.11 -	Frequency of Approaches Adult Males Directed toward and Received from Related and Unrelated Adults.	53
Fig. 3.12 -	Frequency of Directed Aggression by Adult Males toward Related and Unrelated Adults	55
Fig. 3.13 -	Frequency of Received Aggression by Adult Males from Related and Unrelated Adults.	56

CHAPTER ONE - ADULT MALE INTRAGROUP SOCIAL BEHAVIOUR IN FEMALE-BONDED OLD WORLD MONKEYS

INTRODUCTION

Early cross-sectional studies of Old World monkeys focused on male dominance hierarchies, while there was little research conducted on how females were significant members of their social groups (Fedigan and Fedigan, 1989; Fedigan, 1992). Males were thought to be socially-central, powerful, and competitive, and male relationships were described as being dyadic, linear, and constant. Female primates were described as being dedicated mothers and sexually receptive to males, but otherwise of little social significance (Fedigan and Fedigan, 1989). In these early studies, the interpretations of males in a society were faulty. These studies were cross-sectional and of a short-term basis, and there were inherent problems in their methodology. For example, pioneering studies of baboons (Washburn and DeVore, 1961; DeVore, 1964; Hall and DeVore, 1965) identified only the few adult males, while females and infants were lumped together by age and sex (Strum, 1987).

With methodological improvements (Altmann, 1974), a necessity for longitudinal studies (as emphasized by Japanese primatologists), the understanding of patterns of dispersal and philopatry, theory driven questions (e.g. sociobiological), and more women researchers entering the field of primatology, these early biased models of primate social organization were challenged (Fedigan and Fedigan, 1989). After an early overemphasis on males came a redressing of the balance by an emphasis on females. The social dynamics of females in female-bonded Old World monkey societies are now well known. The basic structure of a female-bonded Old World monkey social group consists of "matrilineal" systems based on lifelong bonds of females who form the stable core of the group, and unrelated adult males (Pusey and Packer, 1987). Primatologists now know

that for females, kinship bonds are among the most important determinants of behaviours such as grooming, agonistic aiding, the ontogeny of social behaviour in infants, as well as the acquisition and maintenance of dominance rank, and mate choice (Gouzoules and Gouzoules, 1987).

In the 1980's, a number of studies emerged documenting the lives of female nonhuman primates (e.g. Altmann, 1980; Hrdy, 1981; Fedigan, 1982; Small, 1984; Smuts, 1985). A male's social position in a social group, however, has not been redressed or well delineated. Our understanding of monkey life history is more complete for females than for males. This lack of research conducted on the social life of males may be because males are more difficult to study (Pavelka, 1993). There are problems associated with following and observing the dispersing sex; in almost all primate species, most migrants are adult or subadult males (Altmann and Altmann, 1979). Also, there is a tendency for researchers studying the social dynamics in a group to focus on females since they are often the permanent residents in the social group. Another reason why males are more difficult to study is that determination of paternity in free-ranging groups is problematic (Sade, 1972).

Studies that have focused on male interaction patterns within a social group have tended to focus on behaviours that deal with reproduction (de Waal, 1986; Fedigan, 1992), while little is known about male social activity outside of reproduction. Most female-bonded Old World monkeys have sexual relationships that are confined to a limited mating season (for example, Melnick and Pearl, 1987). Mating in these species is short-term and highly seasonal - most fertile females spend the greatest part of their reproductive years either pregnant or lactating. Mating itself is a relatively minor activity; in many primate species, mating occurs within temporary social bonds called "sexual consort relationships" or "consortships" (Hill, 1987). Therefore, mating cannot alone account for the cohesiveness of males to the group (see Hill, 1990).

This chapter will focus on what has been reported on the social dynamics of adult males in female-bonded Old World monkeys *outside* of the mating season. Most Old World monkey species are female-bonded - females in these species are philopatric and form the stable core of the social group, while males are the dispersing sex (they leave their natal group at maturity and join other groups). In these species, females remain closely bonded to their mothers and sisters even after they have their own offspring. Groups are comprised of closely related females and unrelated males (immigrant males). Patterns of dispersal and philopatry will be reviewed, and adult male intra-group social interactions in female-bonded nonhuman primates will be examined by focusing on macaque and savanna baboon (including olive, yellow and chacma) societies. These species share many characteristics in social structure and organization. Chimpanzees, on the other hand, are non-female bonded (males are philopatric and females are the dispersing sex), and groups are comprised of related males and unrelated females (immigrant females). Chimpanzee societies will be discussed in order to contrast their intragroup adult male social interactions with those of female-bonded societies. Lastly, the research objectives of this thesis will be presented.

DISPERSAL AND PHILOPATRY

In all living nonhuman primates, there is intergroup transfer by one or both sexes (Pusey and Packer, 1987). In most Old World monkeys, almost all males emigrate at the time they have reached full size (exceptions: hamadryas baboons, red colobus monkeys, and black and white colobus monkeys) and it is noteworthy when a male remains to breed in his natal group (Chapais, 1983; Pusey and Packer, 1987). According to Pusey and Packer (1987), natal emigration is associated with an increased mortality risk due to predation, starvation, and aggression from unfamiliar conspecifics. Males in many of these species also show considerable secondary emigration and transfer. For example, it has

been documented that in some groups of Japanese macaques, complete replacement of males has occurred in only 2 years (Sugiyama, 1976). Although males in many species may transfer several times, they almost never return to their natal group (for example, rhesus macaques: Drickamer and Vessey, 1973; Japanese macaques: Fedigan, 1976; Sugiyama, 1976).

There is inter- and intraspecific variation in the age and stage of maturation at which natal emigration occurs. In most species, males generally emigrate at puberty, but there are exceptions. For example, male savanna baboons remain in their natal group for several years after puberty (Pusey and Packer, 1987). Even though males may occasionally remain and breed in their natal group (Smuts, 1985), the great majority do not breed until after they have left their natal group or area (Pusey and Packer, 1987). Several factors influence the variation in age of natal emigration. In some species, males who have high-ranking mothers emigrate at older ages than other males (rhesus and Japanese macaques: Colvin, 1983b). Provisioning (Sugiyama and Ohsawa, 1974) and a lack of adjacent groups (Drickamer and Vessey, 1973; Sugiyama, 1976) also inhibit male emigration in Japanese and rhesus macaques. As well, group size may influence the age at which males leave. For example, some male Japanese macaques in abnormally large provisioned groups remain in their natal group longer than males born in smaller provisioned groups (Sugiyama, 1976). In Old World monkeys, related males sometimes emigrate together from their natal group (Boelkins and Wilson, 1972; Drickamer and Vessey, 1973; Colvin, 1983a; Vessey and Meikle, 1978). Kinship, therefore, may influence both the timing and distribution of male transfer (Gouzoules and Gouzoules, 1987).

In nonhuman primates, patterns of intergroup transfer appear to have important effects on intrasexual relationships within groups. Among animals in which there is considerable variability between species or groups in dispersal, this process of emigration and transfer may be a major cause of differences in social structure. As an aspect of social

dynamics, natal emigration is a particularly striking phenomenon as it entails a radical restructuring of all of the emigrant's social relationships (Colvin, 1986). In species where males are philopatric (for example, chimpanzees and red colobus), males form strong bonds characterized by grooming, proximity, and support through coalitions. In these species, male-male bonds appear stronger than female-female bonds. In species in which males transfer, male-male bonds are generally weaker than those female-female bonds (Smuts, 1987). It has been suggested that the need for security and protection during pregnancy, and child-bearing and rearing serves to foster the stable position of the female within the matrifocal family. Males, on the other hand, unencumbered by motherhood, are thought to maintain fewer family ties as they mature (Miller, Kling, and Dicks, 1973).

ADULT MALE INTRAGROUP SOCIAL INTERACTIONS: MACAQUES AND SAVANNA BABOONS

There is a vast amount of data available for most macaques and savanna baboon species (see Fedigan, 1992). Most macaques and savanna baboons are characteristic of many Old World monkey species in that they have relatively short breeding seasons and are composed of multi-male multi-female troops. These troops consist of matrilineal groups that are closely associated (Fedigan, 1976; Chapais, 1983) and grooming occurs most frequently with close kin (for macaques: Sade, 1972; Missakian, 1974; Mori, 1975). Females are often found near and in contact with one another and may travel, feed, and sleep together (e.g.: pigtail macaques: Rosenblum, 1971; Japanese macaques: Yamada 1963; Kurland, 1977; yellow baboons: Altmann, 1980).

In most cases all females within a natural group will be kin. By contrast, males tend to leave their natal groups upon reaching sexual maturity and may transfer several times during adulthood (for macaques: Sugiyama, 1976; Meikle and Vessey, 1981). With the possible exceptions of brothers and adult daughters of long-term residents, adult males

do not have adult kin within their resident group (Hill, 1990). Therefore, typical troops consist of two very distinctive subsets, namely kinship groups and adult central males. Each subset has relatively independent characteristics (Grewal, 1980). Members of a kinship group are closely associated with one another (Yamada, 1963; Koyama, 1970), while direct associations among adult central males are reported to be relatively infrequent (Grewal, 1980).

Grewal (1980) described Japanese monkey troops as characterized by the presence of adult central males who associate continuously with adult females as well as the offspring of various kinship groups. Most of the members of any kinship group associate directly or indirectly with the adult central males, and through them, with other kinship groups. However, the number of individuals with whom an adult central male can associate, in a particular period, is limited. In his study of Japanese macaques Grewal (1980) found that there was a tendency of almost no associations between a particular adult central male and his kin, while the bonds among females are very strong throughout their lives. Therefore, breaking the associations of kinship ties is a basic characteristic of the relationships between a male and his kin.

Entrance into a Bisexual Group

Typically in several Old World monkey species, at puberty, adolescent males join the peripheral male subgroup of a troop (composed of juvenile, subadult, and adult males). The term "peripheral" is used to describe these males because in terms of spatial distribution, they live on the edge of the troop, unlike central adult males and females who are more dominant (Sugiyama, 1976). Then, after finally leaving the natal group, males have several choices: they can remain solitary for a period of time (in Japanese macaques, but not olive baboons), become a member of an all-male band (composed of mainly immature males), or directly join a heterosexual troop (Fukuda, 1982). Although adult

males generally have no adult kin within the heterosexual groups they join, they may become well-integrated into the social structures.

It seems likely that their relationships with adult females, who form the stable core of the social group, will be the key to their acceptance (see Smuts, 1985). Aggression from females directed toward males has been found to have an important effect on the extent to which males are able to associate with females in several species of primates who live in multi-male multi-female groups (Pusey and Packer, 1987). However, among various Old World monkey species, there are differences in the amount of aggression that males receive from females. Packer and Pusey (1979) found that immigrating male Japanese macaques received considerably more aggression from adult females in the new group than did male olive baboons.

In some cases, most aggression in the new group comes from same-sexed individuals, and in olive baboons immigrating males receive the most intense aggression from males of the same age (Packer, 1979). Immigrating males may also face aggression from opposite-sexed individuals, and in species where sexual dimorphism is slight, female aggression can even deter males from entering groups. For example, Japanese macaque females often chase solitary males away from the group (Sugiyama, 1976). Eventually, peripheral males may be gradually tolerated into the vicinity of the troop. A peripheral male may do this by attaching himself to a peripheral female and her matrilineage. Then the male begins to try and gain entrance into the central male hierarchy (Fedigan, 1976).

Affiliative Interactions

Most studies of male-female interactions in nonhuman primates focus on sexual behaviour (see Smuts, 1983). However, some studies have shown that in savanna baboons and macaques, adult males and females may form long-term affiliative bonds that persist in the absence of any immediate sexual relationship (Ransom and Ransom, 1971; Ransom and Rowell, 1972; Seyfarth, 1978; Altmann, 1980; Strum, 1987).

A number of early studies of macaques and baboons have reported the occurrence of affiliative relationships between adult males and anestrus females (Altmann, 1962; Kaufmann, 1967; Reynolds, 1970; Loy, 1971; Ransom and Ransom, 1971; Saayman, 1971). More recently, the nature and extent of such relationships have been studied in three species. In a feral troop of olive baboons Smuts (1983, 1985) found that almost all adult females had "special relationships", or what she called "friendships" with one or two adult males. Smuts (1985) first coined the term "friendship" to distinguish longer-term associations between anestrus females and adult males from the more transitory and sexual associations that are called "consortships". Smuts (1985) and Strum (1987) reported that in olive baboons, females and males form long-term special relationships or "friendships" that are easily distinguishable from ordinary male-female relationships evidenced by more frequent grooming, proximity, and the relaxed, friendly quality of most of their interactions. Friendships between males and females were much stronger and longer lasting than male-male relationships, but they were much shorter and more ephemeral than female friendships (Strum, 1987). Takahata (1982a) used the term "peculiar-proximate relation" (PPR) to describe bisexual dyads observed in frequent and prolonged association. Among Japanese macaques, Takahata observed PPR's between adult males and females, some of which were apparent in three consecutive birth seasons. Lastly, in a group of rhesus macaques at the Cayo Santiago colony, Chapais (1983, 1986) found persistent grooming relationships between central males and adult females within a single birth season.

Smuts (1985) provided a summary of the distribution and nature of the relationships found by the three studies, and considered the ways in which males and females might benefit from them. Savanna baboons who have an affiliative relationship in nonsexual contexts are found to be more likely to mate than those who do not (Packer, 1979; Smuts, 1985). Chapais (1986) did not find such an effect in his study on rhesus

macaques, and Takahata (1982a, 1982b) found mating to be less likely among pairs with persistent birth season relationships. All three of these studies found that protection or agonistic aid was given primarily to female partners in affiliative relationships, and in rhesus monkeys, the females also aided their male partners (Chapais, 1983, 1986). There were also some indications that a female's immature offspring may receive protection from her "friend" (Smuts, 1985).

The existing research on adult male social behaviour in Old World monkey species has concentrated on the competitive relationship between males and the close association between males and females, but the positive association (proximity, grooming, etc.) between adult troop males has not been adequately examined. Furuichi (1985) found that for most macaque species, there are two discrete forms of male-male association patterns. In some species, adult troop males frequently associate with one another in a symmetrical pattern, where each type of social behaviour is exchanged with a similar frequency. For example, among bonnet macaques adult troop males frequently slept together and exchanged grooming with one another, and the quantitative asymmetry related to dominance was not found (Koyama, 1973). In other species, adult troop males infrequently associate with one another and social behaviours are exchanged in asymmetrical patterns related to the dominant-subordinate relationship. For example, Kaufmann (1967) reported that grooming was frequently observed between adult central male rhesus macaques in a Cayo Santiago troop, but was mostly restricted to the nonmating season and the subordinate male tended to groom the dominant much more than the dominant groomed the subordinate.

Although male-male interactions are usually more aggressive than those among females (Smuts, 1987), this does not mean that males never cooperate (see Harcourt, 1992). Male macaques frequently emigrate in the company of brothers or natal group peers (Pusey and Packer, 1987) and rhesus macaque brothers have been observed to form

alliances in their adopted groups that increase or maintain their dominance rank (Meikle and Vessey, 1981; Mizuhara, 1964). Alliances among male savanna baboons more often involve unrelated males, probably because baboons are less likely to emigrate with brothers or natal group peers (Pusey and Packer, 1987; Smuts, 1987).

Grooming among adult male macaques is usually less common than among females, although it occurs at low rates, especially during the nonmating season (e.g. Japanese macaques: Sugiyama, 1976). Male baboons groom each other only rarely (Smuts, 1985) but engage in "greeting behaviour", a display characterized by stereotypic vocalizations, facial expressions, mounts, and touches. Such behaviour is thought to be related to the establishment and maintenance of alliances (see Smuts, 1985), or long-term cooperative relationships that form coalitions on a regular basis (Harcourt and de Waal, 1992). Similar greeting displays have been reported to occur among male bonnet macaques (Sugiyama, 1971).

Agonistic Interactions

As stated by Walters and Seyfarth (1987), aggressive behaviours of male and female nonhuman primates vary depending on the species, social context and individual. Aggression in nonhuman primates takes a variety of forms, varying in intensity, from subtle stares to outright physical combat. However, nonhuman primates do not consistently fight over resources, but exhibit both ritualized displays and relatively stable dominance relationships that allow most disputes to be resolved without physical violence.

Although females show aggressive behaviour as often as males do, males generally wound one another more often than do females (Smuts, 1987). It is important to note that in the Order *Primates*, there is a widespread occurrence of male sexual aggression toward females (see Smuts and Smuts, 1992). Male aggression directed toward females often occurs in a sexual context. In macaques and baboons, males have been observed to occasionally attack females who would not mate with them. Estrous females usually

receive more aggression and more wounds than do anestrus females. Although females are vulnerable to male aggression, they have means of protecting themselves; for example, they often join forces against males (Smuts, 1987).

Furuichi (1985) found that in macaques the suppression of inter-male aggression in the mating season may be one of the factors which may encourage males to choose to reside in the troop throughout the year. Furthermore, in the nonmating season, agonistic interaction between males (and between males and females) occurs less frequently in comparison to the mating season. Strum (1987) reported that in olive baboons, males were much less aggressive than had been previously reported. Generally, olive baboons use nonaggressive social strategies to achieve their aims. Also, a male's sheer size and strength made them dominant to all the females and offspring, but their sphere of influence was actually reported as being much narrower than predicted. In fact, Strum (1987) found that aggression in olive baboons was stated to be a function of residency. Newcomers (less than 1 1/2 years residency in a group) were very aggressive, short-term residents (at least 1 1/2 years residency in a group) less so, and long-term residents (at least 3 years in a group) were almost devoid of aggression.

The Dominance Hierarchy

Female-bonded Old World monkey species have been the subject of some of the best known studies of dominance and it is generally held that female and male dominance hierarchies (based on the direction of agonistic and submissive signals) should be considered separately (Fedigan, 1992). Females develop highly differentiated dominance relationships that are based largely on coalitions, a one-time cooperative action by at least two individuals or units against at least one other individual or unit (Harcourt and de Waal, 1992), with other female kin (Smuts, 1987). In female-bonded Old-World monkey species, the acquisition and maintenance of dominance rank among females is closely related to kinship (Datta, 1983). However, adult male rank in general is probably less

effected by kinship than it is for adult females, especially as males usually leave their natal group and live with non-relatives (for Japanese and rhesus macaques: Fedigan, 1992).

The female hierarchy in female-bonded Old World monkeys species is stable (see Strum, 1987): the general rule is that the mother outranks her female offspring and sisters rank in reverse order of their ages (the youngest having the highest rank). The social development of immature males is quite different from that of immature females. In female-bonded Old World monkey species, among male peers of similar size, maternal rank is an important determinant of immature rank (juvenile males tend to occupy a position close to that of their mothers in the social hierarchy), but maternal rank seems to become progressively less important with age (olive baboons: Pereira and Altmann, 1985; rhesus macaques: Datta, 1983). Because males emigrate from their natal groups, adult male dominance rank cannot usually be predicted from maternal rank (Melnick and Pearl, 1987). Moreover, a male's dominance relationships change over his lifetime and during his reproductive years (e.g. Itani, 1975; Bygott, 1979). Generally, however, in Old World monkey species males usually dominate females individually, but females can dominate males, sometimes individually and sometimes as the result of female-female coalitions (Smuts, 1987).

In most groups that contain more than one adult male, some males consistently win agonistic interactions against others. Adult males in a macaque troop can be ranked in a linear dominance hierarchy. Although, the hierarchy among male macaques can be difficult to detect - many male-male dyads are rarely or never seen interacting. A male's relative rank is obvious for the first four or five in the hierarchy, but becomes blurred after that (Pavelka, 1993). Nevertheless, male macaques can be grouped roughly into three discrete rank levels: 1) the central hierarchy, 2) the 4-year old central males, and 3) the peripheral males (Kaufmann, 1967). Males in the central part of the group are often dominant to

those in the periphery (Norikoshi and Koyama, 1974). Thus, spatial distance from the center of the troop is believed also to indicate the social distance from it (Sugiyama, 1976).

Most researchers state that for Japanese and rhesus macaques age, body size, and other individual characteristics have little effect on rank; only the length of tenure in the group is important (Drickamer and Vessey, 1973; Norikoshi and Koyama, 1974; Sugiyama, 1976; Furuichi, 1985; Mcmillan, 1989). Sprague (1992), however, noted that dominance rank among males in a troop is related to age. He stated that the rank acquired by a male joining a troop and the social tactics used to enter a troop are also related to age. Occasionally, an older male moving into a group during the breeding season may rank above some of the younger males who have longer tenure. However, the rule appears to be that when males join a group, they are at or very near the bottom of the male hierarchy and move up in rank only as higher-ranking males leave or die (Vessey and Meikle, 1978).

van Noordwijk and van Schaik (1985) proposed that for long-tailed macaques, males attained their highest lifetime rank as a "young adult" (also see Mcmillan, 1989), when they tried to take "top dominance" by aggressively challenging the dominant male either in their own or another troop. They distinguished between two types of immigrating males: unobtrusive immigrants who behaved inconspicuously and acquired low rank and "bluff" immigrants who behaved self-confidently and who challenged the resident males, and acquired "top dominance" in the troop.

In olive baboons, Strum (1987) could not detect a linear or stable dominance hierarchy in males. What ranking she could find was predicted to be of little or no importance. Dominance rankings, although not stable or linear, could be predicted from residency class. Residency, dominance, and aggression were found to be all inextricably linked. Social strategies, skills, and experience helped to explain why dominance and aggression were of little use to a powerful male baboon. "Newcomers", in olive baboons were the most dominant males in the troop, followed by "short-term residents", with the

"long-term residents" last. The most socially successful males (they received the most cooperation and support from females) were the long-term residents of the troop: the lowest-ranking and least aggressive individuals. Newcomers were high-ranking, aggressive males who received very little in terms of privileges (sexual, food), while the short-term residents fell somewhere between the two extremes. While the length of time spent in the group (residency, or tenure) has been reported to be positively correlated with dominance rank in the case of macaques (Drickamer and Vessey, 1973; Norikoshi and Koyama, 1974), it is negatively correlated with dominance rank for baboons (Strum, 1982).

However, coalitions can have a marked effect on a low-ranking male's ability to gain access to resources from which he might otherwise be excluded. For example, among baboons, two allied low-ranking males can drive away a male who normally ranks higher than either of them (Packer, 1977; Noë, 1992). Male-male alliances among baboons differ from female-female alliances, which seldom result in even temporary reversals of the existing dominance hierarchy. Given that there is a prevalence of male-male alliances in many baboon populations, as well as the clear advantages that low ranking males potentially derive from them, it is surprising that these alliances are extremely rare among macaques (Cheney and Seyfarth, 1990).

A NONFEMALE BONDED SPECIES: THE CHIMPANZEE

A community of chimpanzees is described as a bisexual social group consisting of approximately 15-80 individuals, with roughly equal numbers of males and females. Chimpanzees generally tend to forage and travel together in small temporary associations called "parties", which are subsets of the larger communities (Goodall, 1973). There are several different "types" of these smaller, temporary parties: all-male parties, nursery parties (adult females and offspring), bisexual parties consisting of only adults, matrifocal

parties (one female and her dependent offspring - the only long-term party), and mixed parties. Both females and males have been reported to travel alone (Fedigan, 1992).

Chimpanzees are nonfemale-bonded: female chimpanzees show a strong tendency for migration between communities, while males usually remain in their natal groups (Pusey and Packer, 1987). The core of the community is described as a cluster of strongly-bonded related adult males who are closely associated and inhabit a large range with a number of unrelated mature adult females and their dependent offspring. The community is less associated with a number of younger females (Fedigan, 1992). As males mature, they begin to increasingly travel with all-male parties instead of with their matrifocal parties. A male and his mother are still in the same community, unlike many adolescent females who leave the community and live at some distance away from their mothers (Goodall, 1975). Adult males are often described as being more strongly bonded to one another than adult females are to each other. On the other hand, females are closely bonded to their mothers and then to their own dependent offspring, but seldom associate closely with other adult females (Nishida and Hiraiwa-Hasegawa, 1987).

Females tend to transfer when they are in estrus and are often attracted to high-ranking males, especially the alpha male (Nishida, 1979). Males have differing reactions toward immigrants: some protect them eagerly, while others are aggressive (Nishida and Hiraiwa-Hasegawa, 1987). Resident females usually engage in few interactions with new immigrants. However, sometimes the resident females show hostility, and make threats and displays or bark at them (Nishida, 1979).

Unrelated adult female chimpanzees show little evidence of mutual attraction (Nishida, 1979). For instance, they rarely engage in long grooming bouts, and aggressive coalitions are uncommon (Nishida and Hiraiwa-Hasegawa, 1987). There has been no evidence to show that there are long-term relationships between particular females and particular males (Nishida and Hiraiwa-Hasegawa, 1987). In addition to spending more

time with each other than with females, males have frequent affiliative interactions in a variety of contexts. For example, in Mahale, Nishida (1979) found that grooming among adult males was observed more than four times as frequently as among adult females. Also, greeting behaviours (pant-grunting or kissing), embracing, meat sharing (Teleki, 1973a, 1973b), joint charging displays, and food calling occur most among adult males (Nishida and Hiraiwa-Hasegawa, 1987). Such behaviour stresses the high degree of tolerance among males in chimpanzee society (Nishida and Hiraiwa-Hasegawa, 1987).

However, their relationships are also characterized by intense competition (Nishida and Hiraiwa-Hasegawa, 1987). These apes were originally described as living quite peacefully with one another and having a frugivorous diet (Goodall, 1965), but with further study, they have been found to prey on other primate species and other mammals quite regularly for meat (Teleki, 1973b). Nishida and Hiraiwa-Hasegawa (1987) reported that encounters between different chimpanzee communities often carry a risk of severe aggression, except when a party encounters an estrous female in the process of transfer. Also, chimpanzees have been found to kill and eat chimpanzee infants, as well as to gang-attack and beat to death other adult chimpanzees. These killings can be categorized as attacks on individuals of neighboring communities by adult males, and attacks on young infants of the same community by a mother-daughter pair (Goodall, 1977; Nishida and Hiraiwa-Hasegawa, 1987).

It is important to note that aggressive behaviour does not normally lead to physical violence. Chimpanzees have complex systems of gestural and vocal communication, such as kissing, embracing, and touching, used for greeting, appeasement, reassurance, and display (Nishida and Hiraiwa-Hasegawa, 1987). These behaviours are performed in contexts of reunions, reconciliations, dominance interactions, excitement, fear, pleasure, and grief (Goodall, 1968; Nishida, 1979; de Waal, 1982).

Male chimpanzees living in small communities form a linear dominance hierarchy (Nishida, 1979), but if there are 10 or more males, their dyadic relationships are less clear. In large communities, a dyadic male-male interaction rarely occurs without the presence of others, and the relation between a male's dominance when alone and when with allies is complex (Nishida and Hiraiwa-Hasegawa, 1987). The dominance relationship between males is detectable from the direction of pant-grunting, which is never reversed over the short term (de Waal, 1982), as well as by other interactions such as an attack by the individual who is dominant (Bygott, 1979). For example, there is typically one adult male in the community recognized as the alpha - he never pant-grunts to others, while all pant-grunt to him. In chimpanzees, age is reportedly the best predictor of dominance rank (Nishida and Hiraiwa-Hasegawa, 1987). Adult males outrank adolescent males, and by the time they reach adult size, males are dominant to all females and are then integrated into the male hierarchy (Nishida and Hiraiwa-Hasegawa, 1987). Other than age, additional important factors involved in dominance are size, physical condition, and personality traits, including the ability to form cooperative coalitions with other males (Goodall, 1975; Bygott, 1979; de Waal, 1989).

Unlike in macaques where the support of females is sufficient in itself, in chimpanzees, the tendency toward coalition among males is so strong that incidental reversals in the male dominance hierarchy are more common than in other animal species (de Waal, 1982). That is why the chimpanzee hierarchy is often characterized as being flexible and plastic. Also, the male hierarchy is stated to be heavily formalized. In other words, males frequently communicate their status to one another (de Waal, 1989). The female hierarchy is reported to be rather vague and less clear-cut in comparison (Nishida and Hiraiwa-Hasegawa, 1987; de Waal, 1989). However, older females are generally dominant to younger ones (Nishida and Hiraiwa-Hasegawa, 1987), and newly immigrated females have the lowest status (Nishida, 1979). Relations among females are less

hierarchically organized and much less stable than they are among males (de Waal, 1982). It should be recognized that the role of females in chimpanzee social life, apart from mothering, has not yet been adequately studied or considered (Fedigan, 1992).

RESEARCH OBJECTIVES OF THESIS

In the past twenty years, a male's social position in a group has not been well described. The studies that have been conducted on males in female-bonded Old World monkeys have focused mainly on their tendency to disperse from their natal group (see Pusey and Packer, 1987), or have largely concentrated on reproduction (Fedigan, 1992). The social life of males in a bisexual group in a nonreproductive context have not been well documented.

This study consisted of observing two natural troops of semi-free-ranging Japanese macaques (*Macaca fuscata*) for five months to examine and explore the nature and extent of the daily activity patterns and social interactions of adult males in a social group outside of the mating season. The first goal of this study was to generally describe the behaviour of the total sample of adult males. In Chapter 3, the percentage of time spent in general state behaviours and the percentage of time that is spent in social versus nonsocial activity is presented. The nature of adult male social interactions (affiliative/aggressive, initiated/received), and the age/sex composition of interactants are then discussed. As well, the relatedness of adult interactants is analyzed. Additionally, in this chapter, the different lifestyle patterns of several subject adult males is examined.

The second goal was to investigate variation in adult male behaviour based on male age, dominance rank, and troop membership. The possible effects that the age, dominance rank and troop membership of the adult males have on their general state behaviours and social interactions was analyzed in Chapter 4, 5, and 6 with respect to the durations of general state behaviours, the durations and frequencies of affiliative behaviours

(directed/received), and frequencies of aggressive behaviour. Lastly, a discussion of the results is presented in Chapter 7.

CHAPTER 2 - METHODS

THE STUDY SPECIES: JAPANESE MONKEYS (*Macaca fuscata*)

Japanese macaques, or "snow monkeys" as they are sometimes called, are medium-sized, quadrupedal monkeys indigenous to the islands of Japan, where they range from 31-41 degrees latitude (Fedigan, 1992). These monkeys are very adaptable, as they can tolerate a cold winter (temperatures in their most northerly distribution falling to -5 degrees Celsius) (Izawa, 1978) and temperatures up to 37 degrees Celsius (in one troop's adaptation to their new home in Texas) (Fedigan, 1992). In fact, Japanese macaques are the most northerly-ranging nonhuman primate (Napier and Napier, 1985). Other characteristics of this species are: a moderate degree of sexual dimorphism, a partially-terrestrial, partially-arboreal lifestyle (Fedigan, 1992), and an omnivorous diet. Their diet consists of nuts, buds, berries, shoots, leaves and bark (Itani, 1956), and they also eat insects, crustaceans and bird eggs (Fedigan, 1992).

Social Organization

A social group of Japanese macaques is structured around sets of closely associated matrilineal kin groups with a small number of unrelated central adult males. These kin groups also associate with a larger number of peripheral males of mixed ages. In this multi-male multi-female species, breeding is highly seasonal; both males and females form consortships for the purpose of mating. While there is no evidence that paternity is recognized by these monkeys, intense bonds are formed between mothers and offspring. Group membership is stable and constant for females - they remain bonded for life with their matriline. For males, group membership is unstable and they have a life-long tendency to roam. Males may live a solitary or semi-solitary life for a number of years before entering a non-natal group at a later date (Fedigan, 1992).

THE STUDY GROUP

Fedigan (1976, 1992) described the history of the Arashiyama West Japanese macaques in Texas. A troop of Japanese monkeys known as the "Arashiyama" troop was first contacted, provisioned, and studied in 1954. They ranged on the slopes of Mount Arashiyama near Kyoto, Japan. The population of monkeys grew from 34 in 1954, to approximately 163 in 1966, when a fission occurred. The two daughter troops were named "Arashiyama A" and "Arashiyama B" troops. Several years later, when the Arashiyama A troop became a nuisance to the residents of the Kyoto suburbs, a new home was sought for them. In February 1972, 150 of the 158 members of the Arashiyama A troop were moved to a 108-acre enclosure on a ranch 50 kilometers northwest of Laredo, Texas, locally known as "La Moca". The troop was then renamed "Arashiyama West". In 1980, the monkey troop was moved a second time to a 58-acre enclosure near the town of Dilley, Texas. Dilley is approximately halfway between San Antonio and Laredo. The official name of the organization that preserves and protects these animals is: The South Texas Primate Observatory: Arashiyama West Snow Monkey Sanctuary.

The number of monkeys in this colony increased steadily from 150 in 1972 to approximately 450 in 1989. In 1989, this colony fissioned into two groups. This fission is described in detail by Pavelka (1993). While this would seem to be a very large troop in the wild, this is not an unusually large size for a provisioned troop. The population growth in the colony was by itself not a sufficient condition to cause the fission. Additional conditions which may have precipitated the fission were the environmental and social circumstances in 1988 and 1989.

Membership in the new splinter troop is typical of the normal social organization of Japanese macaque society: related adult females and unrelated adult males. Since the fission, the two groups remain distinct and there have been numerous transfer males from the main troop entering the splinter troop. There are now four identifiable subgroups of

Japanese macaques in Arashiyama West: the main troop, the peripheral males of the main troop, the splinter troop, and the peripheral males of the splinter troop. All four subgroups move freely about the area, but the spatial separation between them is always maintained. An obvious 10 metre (approximately) buffer zone between the peripheral males of the main troop and members of the splinter troop is clearly visible (Pavelka, 1993).

The Arashiyama West troop lives in an enclosure that is surrounded by an 8 foot wire fence, but the monkeys are capable of climbing in and out of the area freely. They forage on the local arid brushland and vegetation, such as mesquite, cactus, and wildflowers. In addition to this, the monkeys are fed corn, milo, cattle cubes, and monkey chow once a day and on occasion are fed fresh produce brought in from San Antonio. They have access to two large annually planted fields, a bushy ravine running the length of the enclosure, two ponds (one seasonal and one permanent), and several water spigots, for swimming and drinking. Artificial wooden structures are present on the site for climbing activities. Human intervention is minimized, but the monkeys are habituated to the presence of observers.

This study was conducted from May to September, 1993 on the colony of semi-free-ranging Japanese macaques (*Macaca fuscata*) at the South Texas Primate Observatory: Arashiyama West Snow Monkey Sanctuary, near the town of Dilley, Texas. In Japanese macaques, the mating season occurs in the fall, starting in late September or early October, and lasting until late January or early February (Pavelka, 1993). This study was undertaken in the nonmating season and included part of the birthing season (the birthing season is roughly April through June). The site near Dilley, an area that is predominantly scrub-brush, is now home to over 600 monkeys. Since these monkeys have been studied in Japan since 1954, genealogies, individual identification (most of the monkeys have facial and leg tattoos), and information on individual and troop history are available for them (Fedigan, 1976).

Subject Animals

Twenty adult males were chosen as subject animals. There are variations in the definitions of "adult" for male Japanese macaques. Females are defined as adult when they bear their first infant, usually at the age of five (McDonald, 1988). Adult males produce sperm at the age of five-years (Griffin, pers. comm., 1993) and are therefore "sexually adult" at this age. However, they are not fully-grown until they are approximately ten years of age. Different studies consider males as reaching adulthood at different ages. There is no cutoff age at which a male Japanese macaque is considered an adult. It is not an abrupt or well demarcated transition as it is for females. Females jump from being a juvenile (1-4 years) to being an adult.

In this study, infants of both sexes were defined as being < 1 year of age, juveniles of both sexes as 1-4 years old, and subadult males as being 5-7 years old. As stated earlier, there is no corresponding subadult category for females. Males were considered adult if they were 8 years of age or older (see Masui, *et. al.*, 1974; Ehardt, 1991). At the age of eight, males are almost full-grown. In the wild, males peripheralize from their natal group between three and seven years of age. Most male immigrants who approach groups are judged to be between seven and ten years old (Fedigan, 1992). Therefore this is the time period in which ties with maternal kin are severed - an important change in their social network.

Eleven central adult males were selected from the main troop and nine were chosen from the splinter troop as subjects. An equal number of males were not chosen from each troop because no other qualifying individuals were available in the splinter troop. All splinter and main troop males nine years of age and older were chosen as subject animals, with the exception of one nine year old male whose behaviour was radically effected when followed by researchers. There were more males who were eight years of age existing in the main troop, but not all were chosen. Males were chosen according to availability and

ease of observation. Therefore, almost the entire population (with the exception of one nine year old male) of splinter group adult males were chosen as subjects, while only a sample of the entire population of adult males in the main group were selected. No peripheral males were chosen as subject animals, since they constitute an entirely different subgroup.

During the early phase of this study, Teresa, an eight-year old subject animal in the splinter troop, died. He was found dead, lying slumped in the fork of a tree in the splinter troop area. He bared no obvious external signs of injury or illness and was presumed to be healthy prior to his death. No autopsy was performed. Since Teresa died early on in the study, the focal animal data collected on him were not included in the analysis. The number of subject animals, therefore, was reduced to nineteen - eleven in the main troop and eight in the splinter troop. A complete list of all subject animals is presented in Table 2.1. Their nickname, troop, i.d. number (tattoo number), unique name (their genealogical name that provides life history information), age in years, and dominance rank (provided by the director of the site) are also presented in this table. As in the case of other provisioned semi-free-ranging troops of Japanese macaques, there are gaps in the representation of certain age categories of adult males (for example, see Koyama, *et. al.*, 1974; Sugiyama and Ohsawa, 1974).

Table 2.1 - Adult Male Subject Animals

Nickname	Troop	I.D. Number	Unique Name	Age in Years	Dominance Rank
Ran	Main	#134	RAN68	25	High
Tree Betta	Splinter	#22	BE6377	16	Medium
Solo	Main	#260	PK6579	14	Low
Horse	Splinter	#306	RO6380	13	Low
Punk	Splinter	#510	BE59667580	13	Low
Skeletor	Main	#706	SH6481	12	Low
Bouncer	Splinter	#487	MA646981	12	Low
Kamster	Main	#426	KU657082	11	Medium
Leon	Splinter	#470	BE596682	11	High
Doc	Main	#790	MI647783	10	Low
Kujiro 500	Splinter	#500	KU677783	10	Low
Binky	Main	#493	BE59667784	9	High
Dexter	Main	#485	DE6584	9	Medium
Indiana	Main	#602	MA60687684	9	Low
Obe	Splinter	#435	MI6484	9	High
Barcley	Splinter	#733	BE556585	8	High
Homey	Splinter	Untattooed	BE586885	8	Medium
Randy	Main	#654	BE596685	8	High
Bippy	Splinter	#662	MA58637485	8	Medium

Data Collection Methods

Systematic data collection was undertaken from June through September, 1993. The month of May, 1993 was used in order to become familiar with the individuals and their behaviour. A total of 161.5 hours of focal animal data (Altmann, 1974) was collected from June 11, 1993 to September 17, 1993, in the morning and early afternoon (07:00-14:00) and the evening (17:00-20:00), 6 days per week. Samples were collected in non-feeding times, and a session was not started until at least 30 minutes had elapsed after provisioning.

All occurrences of specified behaviours of an individual, as well as the time of onset of state behaviours and sequence of event behaviors (see below) were recorded during each focal animal sample period. Focal animal sessions were 30 minutes in duration and were recorded on specific focal sheets that were created for this study (see Appendix A for a sample data sheet). Subject animals were observed from a distance of approximately 6 meters allowing for excellent visibility without interference. All data were collected using paper and pencil format. A digital stopwatch displaying minutes and seconds was used to record time accurately, and binoculars were used to identify individuals. Data were collected in rounds - one round consisted of a 30 minute focal animal sample on each of the 20 adult male subject animals. Seventeen rounds were collected on each subject. Subjects were selected within each round according to availability.

Ethogram

A modified version of Fedigan's (1976) ethogram was used for this study. Fedigan's ethogram was designed for all age-sex classes and included nonmating and mating season behaviour; only those behaviours characteristic of adult males were used for this study. Individuals interacting with the subject animals were identified by tattoo number or nickname and age-sex class (i.e. adult/subadult/juvenile/infant female, adult/subadult/juvenile/infant male), and interactions (if applicable) were coded as either

directed or received. If individuals could not be identified by tattoo number or nickname, they were still categorized by age-sex class.

The ethogram consists of behavioural units: 17 state behaviours, and 42 event behaviours. State behaviours require more than a few seconds to perform (e.g. sitting in body contact or grooming), while events are instantaneous and required no prolonged time (e.g. a threat or vocalization). State behaviours are measured in durations and events are measured in frequencies of occurrence. Also, state behaviours are hierarchically arranged and are mutually exclusive. For example, if the subject was sitting and being groomed by another individual, only grooming (and not sitting) would be recorded. Most event behaviours are mutually exclusive but their occurrence may coincide with state behaviours. Many behaviours have a "direct" and "receive" form, i.e. they can be performed by or be performed toward the subject. The following are behavioural units used in this study.

STATE BEHAVIOURS

<u>Term</u>	<u>Definition</u>
Groom	
(direct/receive):	the manipulation and inspection of pelage and skin of another. This includes picking, scraping, spreading, and licking of any particular parts of the body (Kurland, 1977).
Self-groom:	the manipulation and inspection of pelage and skin of the self.
Social Play:	any combination of cuffing, chasing, mouthing, pulling, jumping, or wrestling, and with accompanying play face expression with one or more individuals.
Travel:	to move on the ground at walking speed.
Body Contact:	inactive, and the individual's fur is touching the fur of another individual.
Forage:	the search for and the preparation of edible non-provisioned items.

Feed:	the ingestion of provisioned food items.
Drink:	to swallow water.
Masturbate:	self-manipulation of the genitals.
Watch	
(direct/receive):	when one individual pays deliberate visual attention to another.
Manipulate Object:	sustained handling of an object in the environment which is not a food item.
Sleep:	in a sitting or lying body posture the individual closes its eyes and is assumed to be asleep.
Stand:	four-legged stance, with all four limbs balanced on ground.
Lie:	resting in a recumbent or prostrate position, stretching out horizontally.
Sit:	inactive in an upright posture.
Out of Sight:	when the subject animal is not visible to the observer.
Surveillance:	an individual sits for a sustained period of time in an elevated position mainly facing away from the body of the troop, and monitors the environment.

EVENT BEHAVIOURS

<u>Term</u>	<u>Definition</u>
Bipedal:	when an individual stands up on their two hind limbs, either standing or locomoting.
Startle:	a sudden almost involuntary-like movement of the body upon being surprised by an action or noise in the environment.
Run Startle:	a sudden explosive movement of the body across space.

Run with Troop:	often after an alarm, the majority of the troop runs in fright, usually all in the same direction toward trees or shelter.
Climb (up/down):	ascension/descension using the hands and feet.
Swim:	movement in the water.
Approach	
(direct/receive):	an initiation of interaction by a direct advance by one individual toward another, or the reduction of social distance between individuals.
Leave	
(direct/receive):	when an individual moves away from an individual with whom it was previously interacting.
Groom solicitation	
(direct/receive):	an individual presents a portion of its body to another at close range. This gesture is often followed by a grooming bout (the presenter being groomed by the presentee).
Contact Calling:	a soft vocalization, sometimes uttered several times in a row. Individuals often respond to the contact calls of other individuals by "replying" with one or sometimes a sequence of several contact calls.
Food Call:	a vocalization similar to a contact call, but ending in a higher-pitch (that lasts several seconds). This vocalization is uttered when there is food nearby or when, as in the case of provisioned groups, feeding time is near.

Approach

Vocalization

(direct/receive): vocalizations of tremulous quality. Usually occurs when two individuals encounter one another.

Muzzle

(direct/receive): when an individual places its mouth directly on another's mouth and sniffs intently.

Smell

(direct/receive): an individual places its nose close to an object and sniffs.

Carry infant: holding an infant ventrally or dorsally, and traveling at the same time.

Charge

(direct/receive): a sudden, vigorous, aimed movement towards another individual.

Lunge: a sharp movement forward toward an opponent in an agonistic encounter, followed by a quick retreat.

Cuff or Slap

(direct/receive): when an individual hits another with the flat of its hand.

Lid (direct/receive): an individual directs its face toward another with eyebrows raised and eyes wide open.

Gape

(direct/receive): eyebrows raised, eyes wide open and mouth open, an individual stretches its head toward an opponent.

Pinch or Grab

(direct/receive): to take hold of another's body by the hand and squeezing hard.

Pull (direct/receive): an individual uses one or both hands to forcefully move another individual toward itself.

Push (direct/receive): an individual uses one or both hands to forcefully move another individual away from itself.

Bite (direct/receive): to seize another with the teeth.

Chase

(direct/receive): the vigorous and high-speed pursuit of one individual by another. It is commonly uni-directional and rarely lasts more than a few seconds, but a large area of ground may be covered (Baldwin and Teleki, 1976).

Jump On

(direct/receive): when an individual pounces on another individual.

Displace

(direct/receive): one individual moves toward another who immediately moves out of the former's way. Frequently the displacer will sit down or stand in the exact location of the displaced individual.

Fear Scream

(direct/receive): a loud shrill vocalization indicating distress.

Threat Scream

(direct/receive): a barking or woofing vocalization made by an aggressor. It varies in frequency and loudness, depending on the severity of conflict (Pavelka, 1993).

Fight: when two or more individuals are engaged in actual physical combat.

Fear Grimace

(direct/receive): a submissive signal in which the lips are retracted from the teeth, with the teeth clenched.

Seek Aid

(direct/receive): in a dispute, an individual screams and repeatedly looks toward an uninvolved individual for support, or else moves to put the uninvolved individual between itself and the opponent.

Support

(direct/receive): an individual enters an ongoing dispute and directs aggressive signals at the opponent, thereby actively siding with the aggressee.

Mount

(direct/receive): an individual stands up against another's back, bracing.

Thrust

(direct/receive): a forward-backward movement of the pelvis by the mounter. Performed both in the presence and absence of intromission.

Lip Quiver

(direct/receive): a rapid up and down movement of the lips over the teeth with the lips slightly pouted.

Body Jerks

(direct/receive): a rapid, repeated twitching of the entire body.

Play Solicitation

(direct/receive): one individual closely and deliberately approaches another and usually performs one of a group of fairly stereotyped behaviours: cuffing, chasing, mouthing, pulling, jumping, or wrestling, and with accompanying play face expression.

Display: a vigorous shaking of some large flexible item in the environment, such as branches, poles, etc.

Vomit: regurgitation of stomach contents, often accompanied by gagging.

Shake: a rapid side-to-side twitching of the torso.

DATA ANALYSIS METHODS

Introduction

In order to be able to analyze the data on a computer, each individual focal animal data sheet was tabulated by hand. These raw scores were then input into a Minitab v.8.1 spreadsheet, and then analyzed using the same program. Cricket Graph v.1.3.2 was used to generate the graphs in this thesis.

The findings of this study are presented in four large sections within each of the results chapters. The sections are: general state behaviours, affiliative interactions, agonistic interactions, and relatedness of adult interactions. Each are introduced and explained below.

General State Behaviours

To examine the general state behaviours of adult male activity, most of the seventeen state behaviours listed in the ethogram were grouped together into ten meaningful general categories. The following are the general state behaviours used in this thesis: inactive (the combined categories of sit, lie, stand and sleep), feed (including the categories of feed, forage, and drink), out of sight, travel, other (the combined nonsocial categories of manipulate object, masturbate, surveillance, and watch), self-groom, direct groom, receive groom, body contact, and social play. The state behaviours were lumped together in a similar manner as Maruhashi (1981) did in his study of the activity patterns of a troop of wild Japanese macaques on Yakushima Island, Japan.

Affiliative Interactions

As stated earlier, state behaviours are measured in durations and event behaviours are measured in frequencies. There are two kinds of affiliative behaviours: affiliative state behaviours and affiliative event behaviours. Affiliative state behaviours include: social grooming (directed and received grooming), body contact, and social play. Affiliative event behaviours refer to all approaches (directed and received).

Agonistic Interactions

Since all agonistic behaviours are instantaneous and require no prolonged time, there are no agonistic state behaviours. Therefore, all agonistic behaviours are measured as event behaviours. Agonistic event behaviours (directed and received) are categorized into four levels. Frequencies of aggression are classified into the following four levels (increasing in intensity) (Alexander and Roth, 1971; Eaton, 1974; Norman, pers. comm., 1993).

1) Noncontact Stationary Aggression - Low-intensity noncontact aggressive threats (agonistic signals) including visual and vocal threats such as stares, lids, gapes, and growls.

2) Noncontact Aggression with Movement - Low-intensity noncontact aggressive threats including lunges, charges, and chases.

3) Contact Aggression without Observed Wounding - Medium-intensity contact aggression without observed wounding including cuffs, slaps, grabs, pinches, pulls, pushes, and jump ons.

4) Contact Aggression with Observed Wounding - Highest-intensity contact aggression with observed wounding including biting that results in injury.

Only the highest level of aggression was scored in a rapid sequence of aggression, and was only scored once. For example, if animal A (the subject animal at the time) was to lid, growl, and then chase and slap animal B in rapid sequence, the entire interaction would be tabulated as one count of level 3 aggression.

Relatedness of Adult Interactants

Only interactions with adults in this society are considered since infants and juveniles were not all distinguishable to the researcher. Some adult female interactants were not identifiable (all adult males were), and thus their relationship to the subject could

not be discerned. It should be mentioned that for all of the results chapters in this thesis, the data collected on unidentified adult females are presented, but not discussed.

For all identified adult interactants, relatedness to the subject could be traced using the observatory's records. Kinship was analyzed in terms of the probable proportion of shared genetic material between two individuals, or a coefficient of relationship (adapted from McDonald, 1988). Scores can range from 1.0 (identical twins) to 0.0 (non-relatives). Where paternity is known (e.g. in humans), parents and siblings are considered to be first degree relatives, and are both assigned a 0.50 degree of relationship with the ego. Since paternity is not known in this analysis, kinship was traced through the female line. Only maternal relationships were considered. Therefore, siblings are likely to be only half siblings and are assigned a 0.25 coefficient of relationship. Only the mother-offspring pair is assigned the full first degree score of 0.50. The coefficients of relationship for the following dyads are as follows:

Mother-son	0.50
Siblings	0.25
Grandmother-grandson	0.25
Aunt-nephew	0.125
Cousin	0.0625
1 1/2 Cousin	0.03125
Great Aunt-Nephew	0.03125
Second Cousin	0.0156

An interactant was considered kin if they had a 0.5 to 0.0156 relationship to the subject.

OVERVIEW OF THESIS

In this exploratory study, the daily activity patterns and intragroup social interactions of males are described. As well, the possible influences that age, dominance

rank, and troop membership have on male behaviour are examined. The results of this study are presented in chapters three through six. General state behaviours are presented in Chapter three. Counts of affiliative and agonistic behaviours using the frequency of event behaviours are also presented in this chapter. In Chapters four, five, and six, the findings presented in Chapter three are analyzed to discover if males display any significant variations in behaviour according to their rank, age, and troop membership, respectively. Therefore, behaviours are dependent variables, while dominance rank, age, and troop are independent variables. Since the assumptions of parametric tests were not made, the nonparametric equivalents are employed. To examine possible differences of the subject animals according to age (Chapter four), a Spearman's rho correlation (rank correlation) is conducted between age and behaviour. The Kruskal-Wallis test is performed to test for differences in behaviour according to the dominance rank of the adult male subjects (Chapter five). The Mann-Whitney test is performed to analyze troop differences in behaviour (Chapter six). For all of these tests, a *p* value of anything less than 0.05 is considered to be significant.

In this thesis, adult interactants are broken down into age/sex class, while juveniles and infants are lumped together by only age class. Since many juveniles were often indistinguishable, and sometimes difficult to sex, they were categorized in this manner. Subadult males were easily distinguishable and constitute an age/sex class, and as stated earlier, there is no corresponding category for females. Adult interactants are categorized into age/sex/kinship classes. It should be noted that for the graphs in this thesis, the interactants are abbreviated as follows: AM (adult males), AF (adult females), SM (subadult males), JV (juveniles of both sexes), INF (infants of both sexes), RAM (related adult males), UAM (unrelated adult males), RAF (related adult females), UAF (unrelated adult females), and UNIDAF (unidentified adult females).

CHAPTER THREE - RESULTS: GENERAL STATE BEHAVIOURS AND THE NATURE OF SOCIAL INTERACTIONS OF ALL SUBJECT ANIMALS

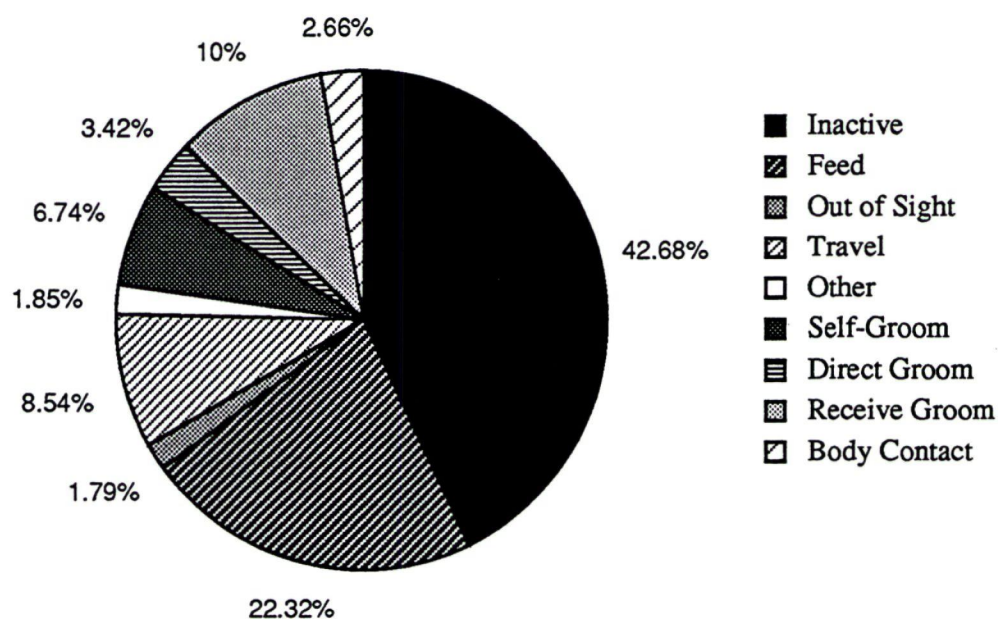
INTRODUCTION

In Chapter three, a description of the general state behaviours and the nature of social interactions for all subject animals is presented. First, general state behaviours and the percentage of total time spent in social vs. nonsocial activity is examined. Next, affiliative and agonistic interactions (directed and received where applicable) are analyzed. This is followed by a discussion of affiliative state behaviours (e.g. grooming) and affiliative event behaviours (e.g. approaches). The nature of affiliative interactions are broadly described, and then specifically presented in terms of the age/sex class of interactants. Agonistic event behaviours (directed and received) are then examined and are described according to the age/sex class of interactants. Lastly, the relatedness of adult interactants is investigated according to the same categories of affiliative state behaviours, affiliative event behaviours, and agonistic event behaviours.

GENERAL STATE BEHAVIOURS

As illustrated in Fig. 3.1, the males spent most of their time inactive (42.68%), 22.32% of their time feeding (eating provisioned food items and native flora), and received grooming (10.00%) more than twice as much than they directed it (3.42%). A total of 6.74% of their time was used in the nonsocial activity of self-grooming. Traveling constituted 8.54% of the adult males' time. The two smallest categories are the categories of out of sight (1.79%) and other (1.85%). Since samples were discarded if the subject animal disappeared for more than five minutes at any time during the sample, this explains why the category of out of sight is so small. Adult males spent very little time in social

Fig. 3.1 - Percentage of Time Adult Males Spent in General State Behaviours



play yielding its very small score. The total amount of time that adult males spent in social activity (social grooming and body contact) constituted 16.10% of their time, while they spent 83.9% of their time in nonsocial activity (all other state behaviour categories combined) (see Fig. 3.2).

AFFILIATIVE INTERACTIONS

In this section, the nature of affiliative state and event behaviours are described. Since all agonistic behaviours are instantaneous, all social activity that required duration was affiliative in nature (as in the case of social grooming, body contact, and social play). As stated previously, the adult males in this study spent only 16.10% of their total time in social activity. The nature of affiliative state behaviours is explored below. In other words, the amount of time adult males spent in each affiliative state behaviour is presented. Other affiliative behaviours (i.e. approaches) are similar to agonistic behaviours in that they were measured in terms of number of occurrences. These are called affiliative event behaviours. Affiliative event behaviours, as well as affiliative state behaviours, are examined according to the age/sex class of interactants involved in these interactions.

Nature of Affiliative State Behaviours

Fig. 3.3 illustrates the duration of affiliative state behaviours expressed in terms of percentage of total social time. This social activity was comprised of the duration of the following categories of affiliative state behaviour: direct groom (21.23%), receive groom (62.16%), body contact (16.58%), and social play (0.03%). The great majority of social activity, then, is spent in receiving grooming, while very little time is spent in social play. In fact, only one adult male, Doc, was observed in social play (with a juvenile) on two brief occasions.

Fig. 3.2 - Percentage of Total Time Adult Males Spent in Social vs. Nonsocial Activity

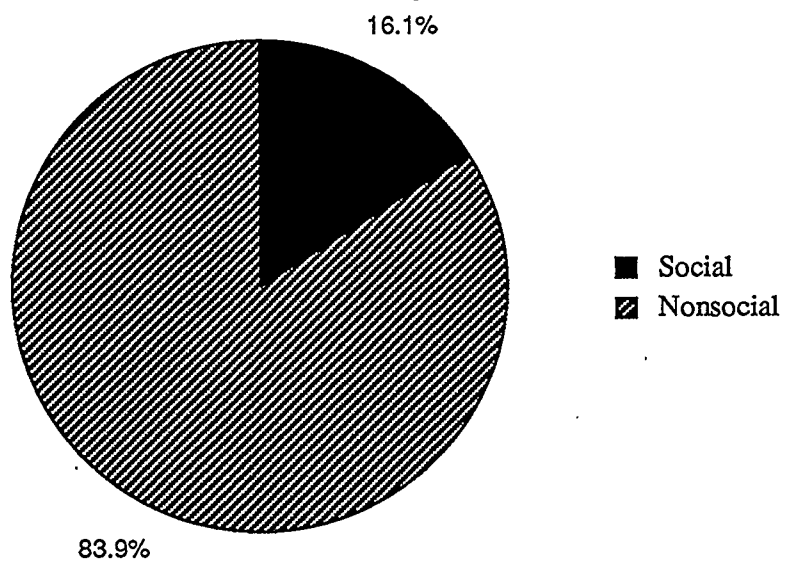
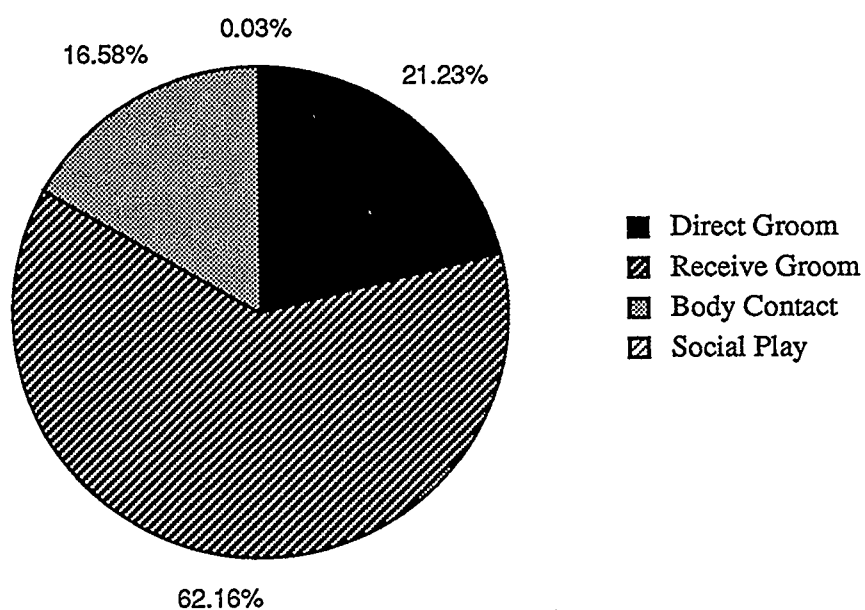


Fig. 3.3 - Percentage of Total Social Time Adult Males Spent in Affiliative State Behaviours



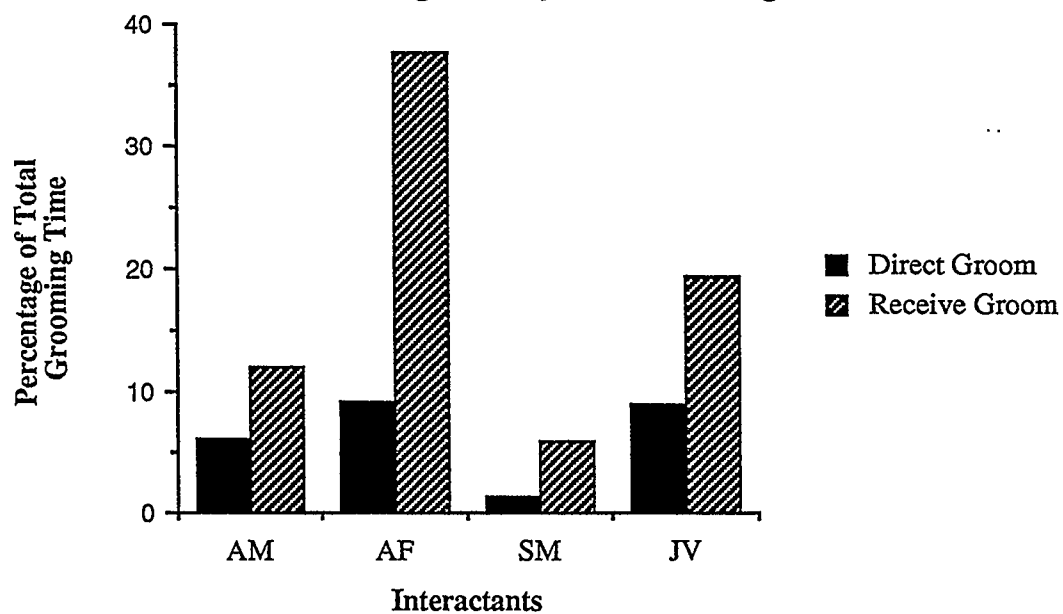
Age/Sex Class of Interactants - Affiliative State Behaviours

In this section, affiliative state behaviours are presented with respect to the age/sex class interactants. Directing and receiving grooming, and body contact time are discussed in this section. Durations of affiliative state activities are expressed in terms of the percentage of total time of the behaviour being examined. For example, if adult males spent 6.14% of their time directing grooming toward other adult males, the score 6.14% is the percentage of total social grooming time spent in this activity.

Fig. 3.4 displays the amount of time that the adult males spent in social grooming activity (directing/receiving) with each age/sex class. Adult males spent most of their time receiving grooming from adult females (37.53%) and directing grooming toward adult females (9.09%). Juveniles were the next favoured grooming partner. Adult males received grooming from juveniles 19.31% of the time, and directed grooming toward them for 8.92%. Adult males also directed grooming toward other adult males (6.14%) and also received grooming from them (11.88%). Adult males spent little time in grooming activity with subadult males - they directed grooming toward them 1.30% of the time, and received grooming from them for 5.83% of the time. The subjects were never observed directing grooming toward infants or receiving grooming from them.

Sitting near another animal may be an indication of social interaction between two animals, but there is a possibility that nearness was a function of a third factor, such as food, water, shade, or another animal (McDonald, 1988). Therefore, only unequivocal social contact expressed by sitting in direct body contact was analyzed. Fig. 3.5 displays the percentage of time that adult males spent in body contact with each age/sex class, as expressed in percentages of total body contact time. Adult males spent more than half of total body contact time with juveniles (53.21%). Adult females were next - adult males spent 33.92% of total body contact time with them. Comparatively, adult males spent very little time in body contact with other adult males (5.18%), infants (4.15%), and subadult

Fig. 3.4 - Percentage of Time Adult Males Spent in Social Grooming Activity with each Age/Sex Class



KEY:

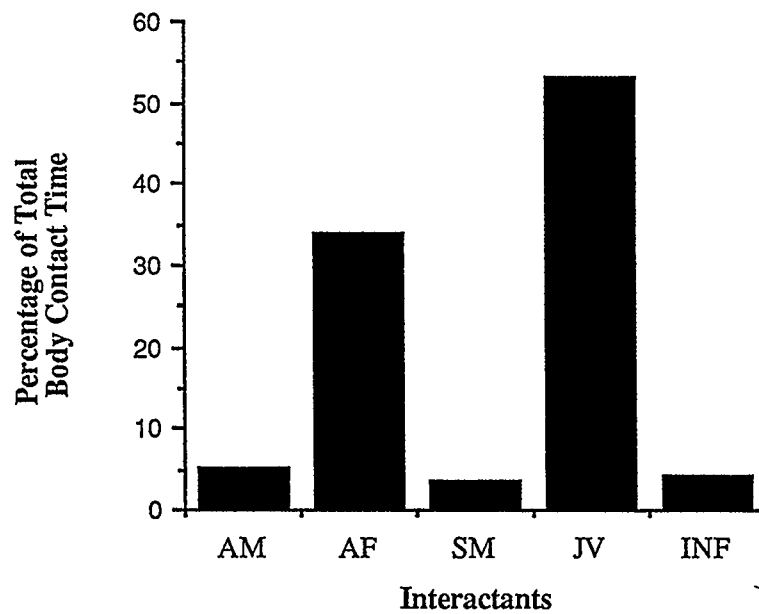
AM - Adult Males

AF - Adult Females

SM - Subadult Males

JV - Juveniles

Fig. 3.5 - Percentage of Time Adult Males Spent in Body Contact with each Age/Sex Class



KEY:

AM - Adult Males

AF - Adult Females

SM - Subadult Males

JV - Juveniles

INF - Infants

males (who had the lowest score of 3.54%).

Age/Sex Class of Interactants - Affiliative Event Behaviours

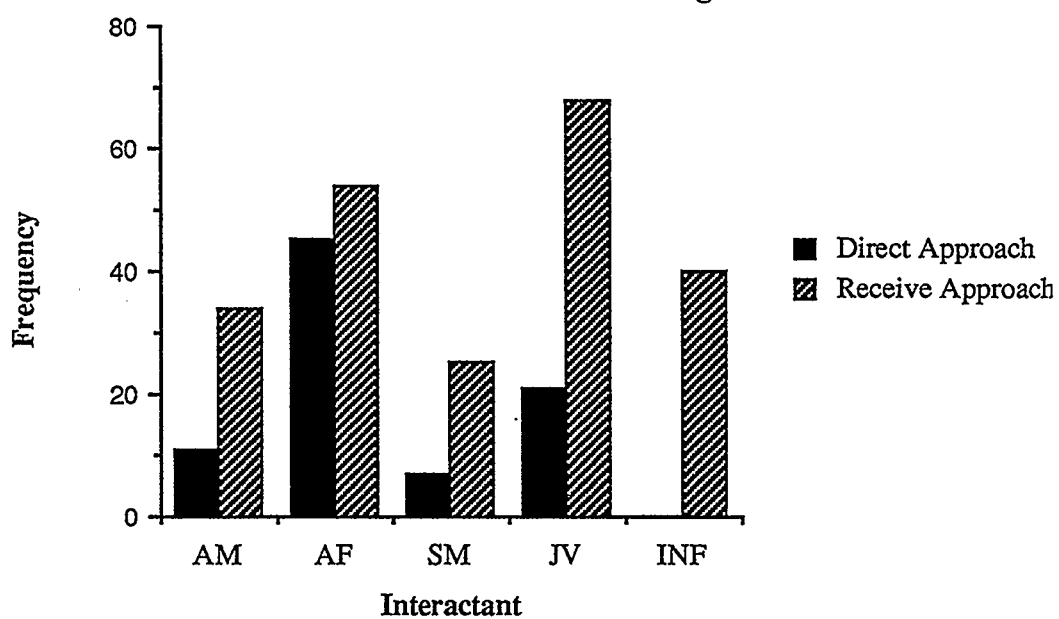
In this section, affiliative event behaviours are presented with respect to the age/sex class of interactants. To determine the initiator of social interactions, the frequency of directed and received approaches is examined (see figure 3.6). Adult males received approaches from juveniles the most out of all other age/sex categories (68 times). Adult males directed approaches toward juveniles only 21 times. The subjects most commonly directed approaches toward adult females (45 times). Adult males also frequently received approaches from adult females (54 times). Adult male subjects directed approaches toward other adult males (11 times) more often than they directed them toward subadult males (7 times). Also, adult males received approaches more frequently from other adult males (34 times) than they did from subadult males (25 times). Adult males received approaches from infants (40 times), but never directed approaches toward them. It is interesting to note that adult males received approaches more frequently than they directed them for all of the age/sex classes.

AGONISTIC INTERACTIONS

Age/Sex Class of Interactants - Agonistic Event Behaviours

Fig. 3.7 graphically illustrates the frequencies of the four levels of aggression adult males directed toward each age/sex class. Overall, the most frequent type of aggression directed by adult males is level 1 and 2, or low-intensity noncontact aggression. It should be noted that only one adult male, Binky, directed one count of level 4 aggression (contact aggression with observed wounding) toward an unrelated adult female. No other incidence of level 4 aggression either directed or received was observed. Adult males directed aggression at the first three levels toward juveniles the most (level 1=33 times, level 2=57 times, and level 3=23 times) out of all other age/sex classes. Adult females also frequently

Fig. 3.6 - Frequency of Approaches Adult Males Directed toward and Received from each Age/Sex Class



KEY:

AM - Adult Males

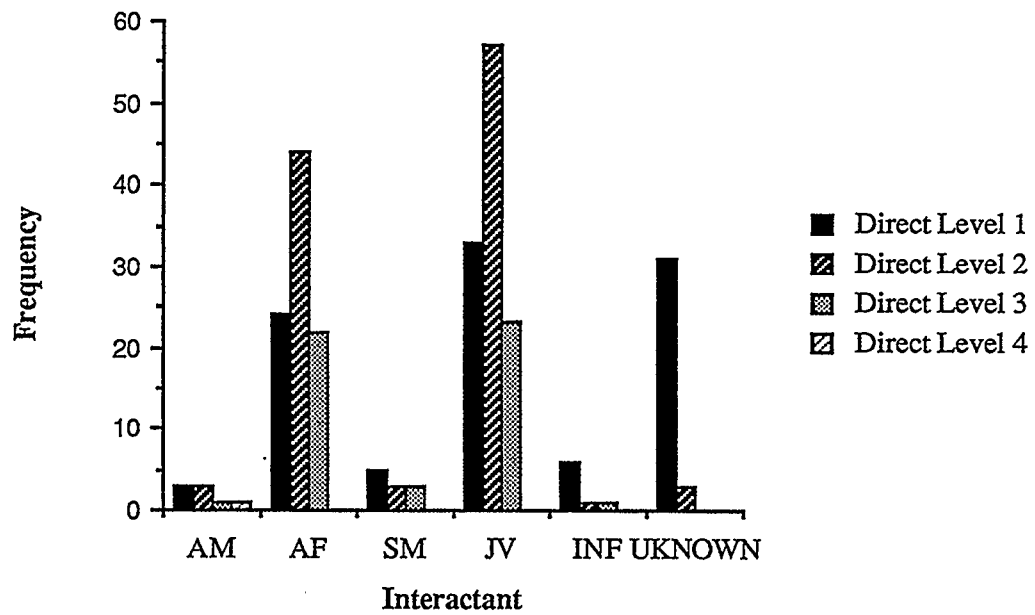
AF - Adult Females

SM - Subadult Males

JV - Juveniles

INF - Infants

Fig. 3.7 - Frequency of Directed Aggression by Adult Males toward each Age/Sex Class



KEY:

AM - Adult Males

AF - Adult Females

SM - Subadult Males

JV - Juveniles

INF - Infants

UNKNOWN - Interactant Unknown

had aggression directed toward them (level 1=24 times, level 2=44 times, and level 3=22 times). It is interesting that level 2 aggression (noncontact aggression with movement) was the most common form of aggression directed toward both juveniles and adult females by adult males. Adult males directed the first three levels of aggression to a much lesser degree toward other adult males (level 1=3 times, level 2=3 times, and level 3=1time), subadult males (level 1=5 times, level 2=3 times, and level 3=3 times), and infants (level 1=6 times, level 2=1time, and level 3=1time). While adult males directed level 2 aggression at a high frequency toward juveniles and adult females, they directed a relatively high frequency of level 1 aggression toward subadult males and infants.

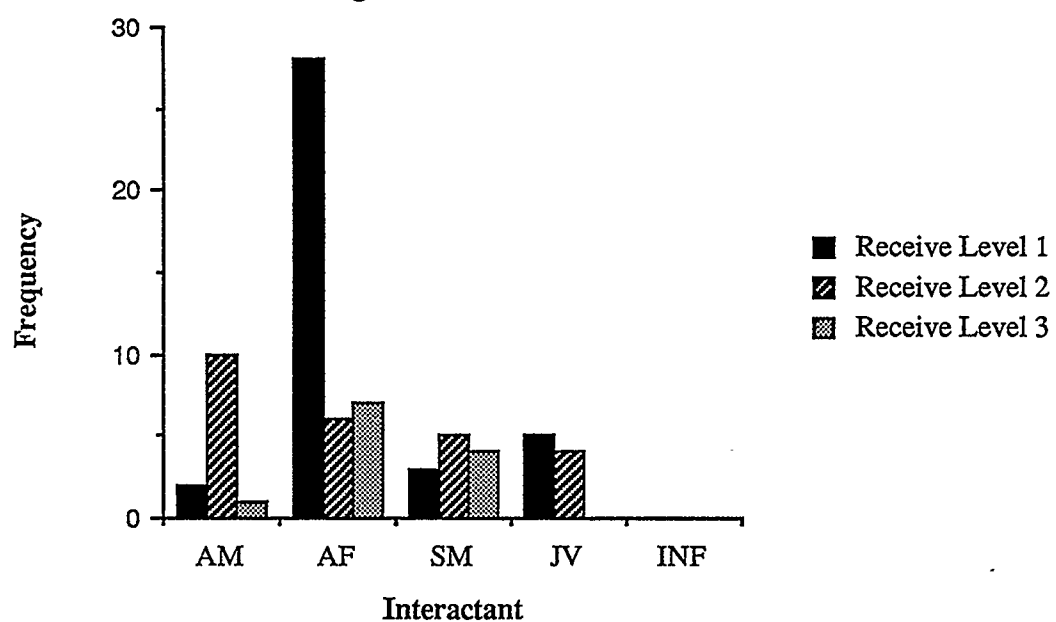
In fig. 3.8, the frequencies of the three levels of aggression that adult males received from each age/sex class is shown. With the exception of level 2 aggression, adult males received the most aggression from adult females (level 1=28 times, level 2=6 times, and level 3=7 times). The form of aggression that adult males received from adult females is clearly observable; they received a high amount of level 1 aggression (noncontact stationary aggression) from adult females. Adult males received the first three levels of aggression from other adult males (level 1=2 times, level 2=10 times, and level 3=1 time) and subadult males (level 1=3 times, level 2=5 times, and level 3=4 times). Adult males only received level 1 (5 times) and level 2 (4 times) from juveniles, and did not receive level 3 (contact aggression without observed wounding) from them. Not surprisingly, adult males never received aggression at any level from infants.

RELATEDNESS OF ADULT INTERACTANTS

Affiliative State Behaviours

In fig. 3.9, the amount of time adult males spent in social grooming activity with related and unrelated adults is presented. Scores are expressed in percentages of total social grooming time. Even though some subjects had adult male relatives residing in their troop,

Fig. 3.8 - Frequency of Received Aggression by Adult Males from each Age/Sex Class



KEY:

AM - Adult Males

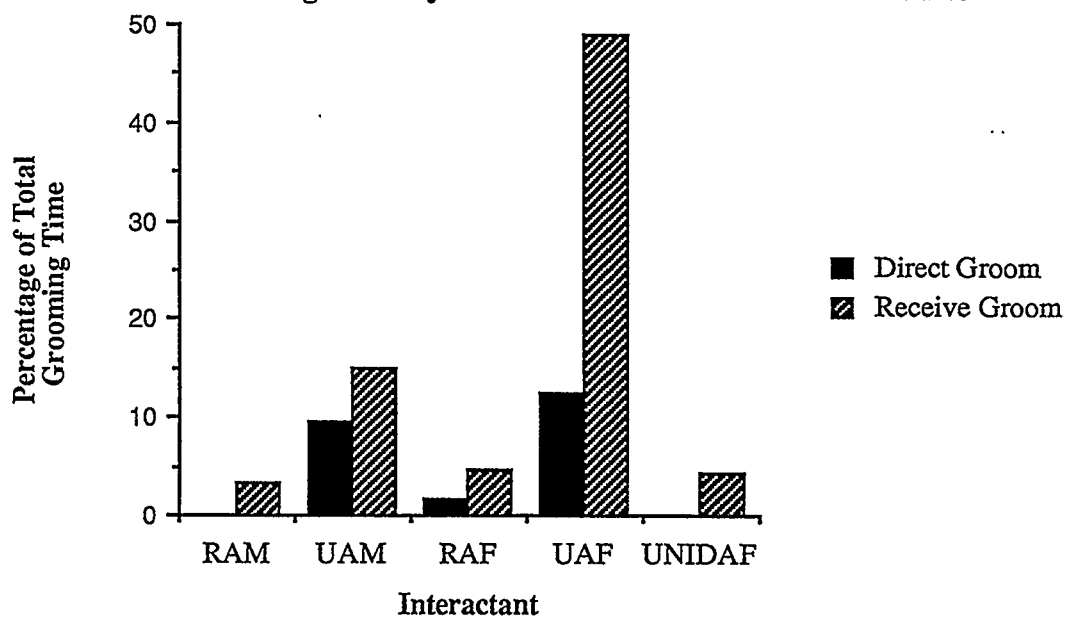
AF - Adult Females

SM - Subadult Males

JV - Juveniles

INF - Infants

Fig. 3.9 - Percentage of Time Adult Males Spent in Social Grooming Activity with Related and Unrelated Adults



KEY:

RAM - Related Adult Males

UAM - Unrelated Adult Males

RAF - Related Adult Females

UAF - Unrelated Adult Females

UNIDAF - Unidentified Adult Females

only one incidence of grooming between related adult males was observed (yielding the score of 3.38% received grooming from a related adult male). Randy received grooming from his maternal nephew, Binky. Subjects more commonly received grooming from unrelated adult males (15.00%), and also directed grooming toward them (9.50%). Related adult females were chosen as grooming partners to a lesser degree than were unrelated adult males. Subjects directed grooming toward related adult females 1.54% of the time and received grooming from them 4.61% of the time. Unrelated adult females were by far the favoured grooming partner. Subjects directed grooming toward them 12.53% of the time and received grooming from them 48.98% of the time. From all categories of adult interactants, adult male subjects received grooming more than they directed it. Also, in general, adult males spent more time in grooming bouts with unrelated adults than with related ones.

Fig. 3.10 graphically depicts the amount of time that subjects spent in body contact with related and unrelated adults, as expressed in percentage of total body contact time. Related adult males were not seen in direct body contact with the subject, while unrelated adult males were observed in this social behaviour for 13.24%. Females were observed to be in body contact with the subjects more so than were males. For body contact time, related adult females had a score of 18.70%, while unrelated adult females had the highest score of 68.06%. Therefore, adult males spent more time in body contact with adult females rather than with adult males, and with unrelated rather than related adults.

Affiliative Event Behaviours

In fig. 3.11, the number of approaches that subjects directed toward and received from adults is presented. Adult males received approaches from related adult males two times, but were not observed directing them toward related adult males in the focal animal sessions. In these two instances it was Randy who received approaches from Binky. Subjects more commonly directed approaches toward unrelated males (11 times) and

**Fig. 3.10 - Percentage of Time Adult Males Spent in
Body Contact with Related and Unrelated Adults**

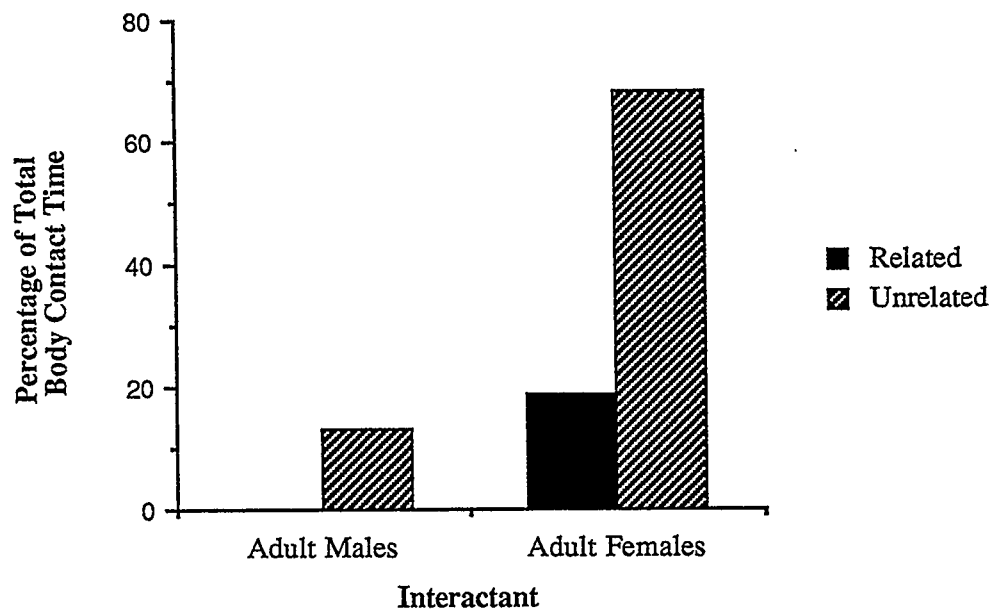
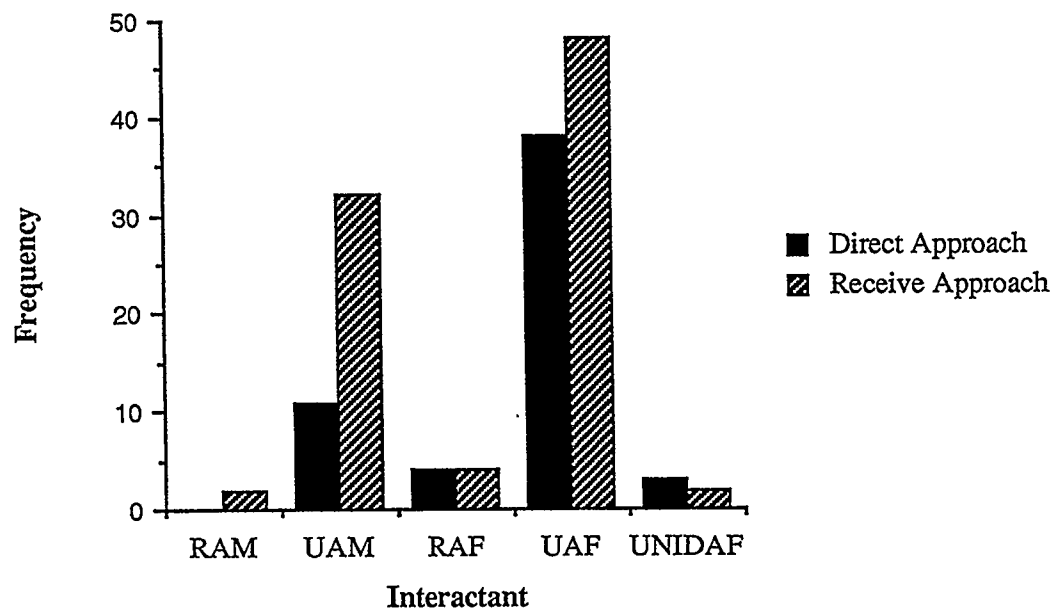


Fig. 3.11 - Frequency of Approaches Adult Males Directed toward and Received from Related and Unrelated Adults



KEY:

RAM - Related Adult Males

UAM - Unrelated Adult Males

RAF - Related Adult Females

UAF - Unrelated Adult Females

UNIDAF - Unidentified Adult Females

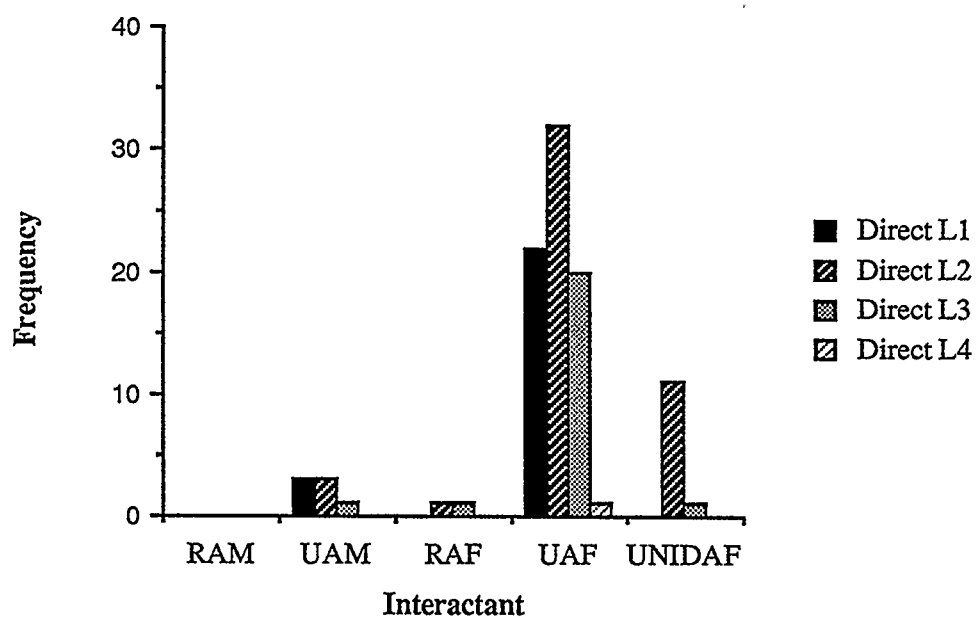
received approaches from them (32 times). Adult males directed approaches toward and received them from related adult females an equal number of times (4 times directed, 4 times received). Adult males directed approaches toward and received them from unrelated adults more than they directed them toward and received them from related ones. Lastly, subjects directed approaches toward and received them from unrelated adult females the most (38 times directed, 48 times received).

Agonistic Event Behaviours

In fig. 3.12, the frequency that subjects directed levels 1, 2, 3, and 4 of aggression toward related and unrelated adults is presented. As stated earlier, only one incidence of level 4 aggression was observed - Binky directed one score of level 4 aggression (contact aggression with observed wounding) toward an unrelated adult female. There were no other cases of level 4 aggression observed, either directed or received. Subjects never directed aggression toward related adult males. They directed levels 1 (3 times) and 2 (3 times) more often than they did level 3 (1 time) toward unrelated adult males. Subjects rarely directed aggression toward related adult females. They never directed level 1 toward them, but did direct level 2 (1 time) and level 3 (1 time) toward them. It was clear that adult males directed the most aggression toward unrelated adult females (level 1=22 times, level 2=32 times, and level 3=20 times, and level 4=1 time).

Fig. 3.13 shows the frequency of level 1, 2, and 3 aggression that adult males received from unrelated adults. No aggression was received from related adult males, but subjects received some aggression from unrelated adult males (level 1=2 times, level 2=10 times, and level 3=1 time). Subjects received very little aggression from related adult females in the form of level 1 (1 time) and level 3 (1 time), while no level 2 was received from them. A relatively great deal of aggression, mainly in the form of level 1 (25 times) was received from unrelated adult females (level 2=6 times, and level 3=6 times). Adult males directed and received more aggression from unrelated adults than they did from

Fig. 3.12 - Frequency of Directed Aggression by Adult Males toward Related and Unrelated Adults



KEY:

RAM - Related Adult Males

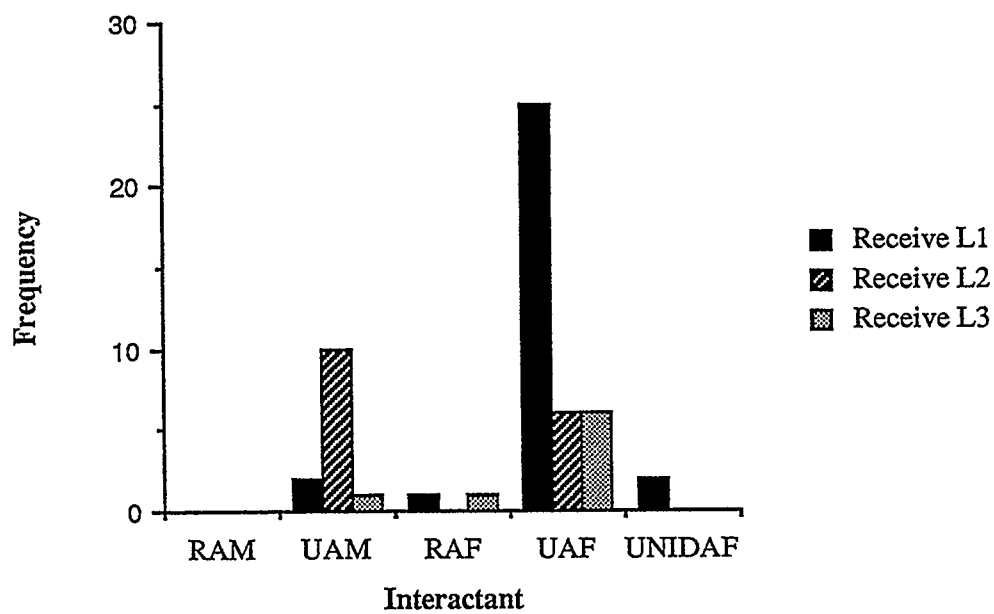
UAM - Unrelated Adult Males

RAF - Related Adult Females

UAF - Unrelated Adult Females

UNIDAF - Unidentified Adult Females

Fig. 3.13 - Frequency of Received Aggression by Adult Males from Related and Unrelated Adults



KEY:

RAM - Related Adult Males

UAM - Unrelated Adult Males

RAF - Related Adult Females

UAF - Unrelated Adult Females

UNIDAF - Unidentified Adult Females

related adults.

SUMMARY OF RESULTS

The purpose of this chapter was to describe the general state behaviours of adult males, and to explore the affiliative and agonistic nature of their interactions. An important aspect of a species' ecology is the proportion of time that members spend in different activities and the distribution of these activities throughout the day (Maruhashi, 1981). It was discovered that these males spent a large amount of time inactive (42.68%) and in feeding activity (22.32%). It was also found that the behaviour of the adult male subjects was mostly nonsocial (83.9%) in nature, while little time was spent in social activity (16.1%).

Social activity was further analyzed, and it was found that adult males received grooming for a majority of this time (62.16%). They also directed grooming (21.23%) and were found in body contact with interactants (16.58%) for a considerable amount of time. However, only a very small percentage of social time was spent in social play (0.03%). Furthermore, only one adult male was found engaging in social play (on two brief occasions).

The primary interactant of the adult males in this study are unrelated adult females. Out of all possible interactants (other age/sex classes), adult males spent the most time in social grooming with adult females. Adult males spent 9.09% of total social grooming time directing grooming toward adult females and 37.53% receiving grooming from them. Approaches were examined to determine the initiators of social interactions, and it was found that the subjects most frequently directed approaches toward adult females (45 times), and also frequently received approaches from them (34 times). Adult males received the most approaches from juveniles (68 times). Therefore, even though they directed the most approaches toward adult females, adult males received the most

approaches from juveniles. Adult males were observed in other affiliative interactions with juveniles. For instance, it is interesting that adult males spent more time in body contact with juveniles (53.21% of total body contact time) than they did with adult females (33.92%).

There was little aggression at any level in this colony during the study months. Aggression usually was quite low in intensity, and only one case of aggression with observed wounding was recorded. This was when an adult male directed one case of level 4 aggression toward an unrelated adult female. The aggression that was present most often involved adult males and adult females, and adult males and juveniles. Adult males directed aggression much more than they received it. Adult males directed the most aggression (at all levels) toward juveniles (level 1=33 times, level 2=57 times, and level 3=23 times), and also frequently directed it toward adult females (level 1=24 times, level 2=44 times, and level 3=22 times). For both juveniles and adult females, the aggression that adult males directed toward them most commonly took the form of noncontact aggression with movement (level 2). When considering received aggression, adult males most often received it from adult females (level 1=28 times, level 2=6 times, and level 3=7 times). Juveniles were found rarely to direct aggression toward adult males (level 1=5 times, level 2=4 times). Also, male-male aggression was rare (direct level 1=3 times, direct level 2=3 times, direct level 3=1 time; receive level 1=2 times, receive level 2=10 times, and receive level 3=1 time). Adult males most commonly received the mildest form of aggression - low intensity, noncontact stationary aggression.

When the sex/kinship class of only adult interactants was examined, it was found that adult males were frequently observed affiliatively interacting with unrelated adult females. Adult males spent the majority of their social grooming time receiving grooming from them (48.98%). Also, adult males spent a great deal of time in body contact (68.06% of total body contact time) with unrelated adult females. Furthermore, adult males

most frequently directed approaches toward (38 times) and received them from (48 times) unrelated adult females out of all other categories of adult interactants. Adult males spent very little time with adult relatives of either sex. They were rarely observed in social grooming activity with related adult males (received grooming=3.38%), and related adult females (directed grooming=1.54%, received grooming=4.61%). Adult male subjects were never seen in body contact with related adult males, and were seldom found in body contact with related adult females (18.70% of total body contact time). Additionally, adult males infrequently directed approaches toward and received them from related adult males (received=2 times) and related adult females (directed=4 times, received=4 times).

Generally, then, it can be concluded that adult males interacted a great deal with adult females, particularly unrelated adult females, both affiliatively and agonistically. In addition, they seem to interact frequently with juveniles. In comparison, they interacted to a lesser extent with other adult males, subadult males, and infants. Another finding worth mentioning is that adult males were the recipients of affiliative interactions more than they were the initiators. For instance, they received more grooming and approaches than they directed. However, this does not apply to aggression. Adult males directed more aggression, at all levels, than they received it. As well, they directed higher intensity (or more severe) forms of aggression than they received (they most commonly received noncontact aggression without movement).

CASE STUDIES

Ad libitum data (Altmann, 1974), or field notes, were another form of behaviour record used throughout this study to note informal observations. The purpose of this information is to illustrate only a few of the many personality traits characterizing these males, and also to demonstrate the richness of behaviour exhibited by them. Case studies will be reported on only six of the nineteen subject animals.

Ran (RAN68) is the oldest male in this colony, the last surviving Japanese-born male, and is the only surviving member of his lineage. He is the alpha male of the main troop and attained this position in early 1993, as a consequence a series of unusual events. In a period of only 5-6 months, all of the high-ranking males, including the alpha male, Rocky (#129, BE586471), disappeared (Pavelka, 1993). Some of these males were discovered dead and partially eaten by predators and scavengers. In fact, Rocky was thought to have been killed by a large cat (Pavelka, 1993). After Rocky's death, no other male tried to jockey in to the alpha male position. According to Griffin (pers. comm., 1993), the other monkeys "elected" Ran into this spot. Ran was low ranking before becoming alpha male and had to radically adjust his behaviour to fit his new position. Apparently, he has not gained confidence in his rank, and Lady Di, the alpha female, seems to be leading the main troop in troop movements. Ran can be characterized as being a very central male. Very high ranking animals, such as the alpha female and her family, were often observed in proximity to him. Furthermore, he has been seen interacting with the alpha female on several occasions. The interesting thing about Ran is that infants were often found near him. Mothers would essentially "park" their infants with Ran, let him "babysit" them, and then move off a little distance away. This was observed on numerous instances. Ran did not seem to mind their company; in fact he rarely noticed them at all. He was usually sleeping at the time. The infants rarely came into contact with him, but were usually quite close to him. Placing an infant near the alpha male would seem to be somewhat safe since no other monkey would be a potential threat.

Randy (BE596685) was a very interesting male to observe. He is only nine years old and is the second-highest ranking male in the main troop and has, as of yet, not challenged Ran for the top position (Griffin, pers. comm., 1993). Randy belongs to the highest-ranking lineage: the Bettas. His mother, Hatchet (#49, BE5966), was the alpha female of the Arashiyama West troop (before it fissioned) from 1974 until her death in

1990. Randy's sister, Lady Di (#284, BE596678), is the current alpha female in the main troop and his brother, Leon (BE596682), is the alpha male in the splinter troop. As this pattern of male dispersal breaks down, maternal kinship may be a major factor in male dominance relationships (Pavelka, 1993). Randy has combined his aggressive personality with a solid alliance system of strong kinship ties (Pavelka, 1993). Randy's presence was very obvious during feeding times. During feeding times the social situation is artificial - many monkeys congregate, and there is a high level of aggression (unlike at nonfeeding times). Randy was especially aggressive while provisioning, and would almost always chase and attack adult females and juveniles. Once feeding time was over, however, Randy was often very difficult to find. He was commonly found with the peripheral males in the main troop. He would rather quickly make his way to the periphery after feeding. He was observed in many affiliative interactions with peripheral males; for example, they would be involved in long reciprocal grooming bouts, and he was often found sitting in body contact with one or more peripheral males at a time. The only interactants who were not peripheral males that Randy was found to be engaged in affiliative interactions with were his adult female kin (particularly with his youngest sister, Spock - #49, BE596686), and one adult male kin (his nephew, Binky - BE59667784). Also, he was regularly seen in agonistic interactions with his kin (particularly his sister, Lady Di, and his youngest brother, #104 - BE596687). Randy, unlike most of the other subject animals, has not completely severed his ties to his matriline. However, these affiliative associations are restricted to his adult female siblings, while most of his other affiliative associations are with younger (usually aged 4-6) peripheral males.

Doc (MI647783) is a very low ranking male in the main troop. Doc appeared to be very aware of his surroundings and was very nervous when feeding on the chow line. He was often displaced by younger subadult males and sometimes chased off. Doc never seemed to stay in one place for a long time on the chow line because someone would

eventually come along and displace him. Doc is low ranking and is a very central and social animal. He was often observed in the company of juveniles. He was observed on numerous occasions to be interacting affiliatively with Turtleboy (BE59667892), Lady Di's one year old male offspring. Turtleboy was the only member of Di's family to be seen constantly affiliating with Doc. It was a reciprocal relationship - Turtleboy and Doc both approached one another. Doc, in several instances, was seen "holding" Turtleboy. Furthermore, while the main troop was moving outside their enclosure, Doc was seen carrying Turtleboy ventrally (Wyman, pers. comm., 1993). However, it should be mentioned that although Doc was observed to be a very social animal, he was very rarely observed to be in the company of adults of either sex. He also was never seen to interact affiliatively with subadult males. In any case, whether Doc preferred the company of juveniles, or actively sought them out (especially Turtleboy) to increase his dominance rank by nudging his way into relationships with high ranking individuals, is impossible to ascertain.

Leon is the alpha male of the splinter troop. He is Randy's maternal brother. Leon was the first and only alpha male of the splinter troop. Leon was mainly observed to be in the periphery of the splinter troop, often alone. When he was in the central part of the troop, he interacted primarily with adult males, and with adult females to a much lesser extent. He was never seen interacting with or in proximity to the alpha female, Skink (#614, MI647184). When he was in the periphery, he was usually high up a tree and appeared vigilant, scouting out the terrain, performing what Fedigan (1992) termed "lookout" behaviour. It seemed that Leon was particularly interested in, or was focused on the movement of the main troop. It appeared that the splinter troop often "adjusted" their position on the ranch according to the main troop's movements. In other words, the main troop could easily displace the splinter troop (without any aggression or even physical

contact) and the splinter troop had to "tailor" their travel according to the main troop's location.

Kujiro500 (KU677783) is a shy low ranking male in the splinter troop. Like Doc in the main troop, Kujiro500 was almost always displaced off of the chow line (in the splinter troop area). Often, low ranking adult females, subadult males and even juvenile males could easily chase him off independently. Kujiro500 was usually present in the central part of the troop during feeding period, or for the purposes of feeding. Immediately after feeding, he would often slowly make his way to a more peripheral part of the troop. Kujiro500 was often found with Horse (RO6380), a low-ranking male "friend". They were often found in grooming bouts together. Kujiro500 was never seen to be interacting affiliatively with any other individual.

Punk (BE59667580) is another low ranking male, and is a splinter troop member. He was a previous member of the main troop, but emigrated to the splinter troop during the mating season of 1992. Punk is a very social animal. Similar to Doc, Punk was frequently in the company of juveniles. He seemed to have a special relationship with one yearling juvenile female, Warteye, and was constantly found grooming her. However, unlike Doc, Punk was often observed *actively* interacting with juveniles. While Doc was constantly found with juveniles, and on occasion would be found in physical contact with them, Punk was *often* found to be grooming and in body contact with them. Another difference between Doc and Punk was that Punk, unlike Doc, was also seen interacting affiliatively with adult females, and was observed in long reciprocal grooming bouts with them.

These are only a few examples of the different characteristics displayed by six of the adult males in this study. All nineteen of the males in this study had clearly unique lifestyles and very different personalities. In all animals, especially primates, the acquisition and modification of behaviour is effected by experience during the individual life cycle. It is likely that the life-history experiences of individual males have contributed

to their preferential affiliations. The past experience of individual members of this large group may be expected to have a significant influence on their behavior (see Ehardt, 1991).

CHAPTER FOUR - RESULTS: OVERALL DIFFERENCES ACCORDING TO AGE

INTRODUCTION

A male Japanese macaque's life is characterized by group transference, in which new relationships and social positions are being continually established (Pavelka, 1993). Since wild Japanese macaque males rarely stay in a troop more than ten years (Sugiyama, 1976), this makes them more difficult to study. Most males disappear within a few years both from their natal troop and from any troop to which they later joined, and there are not sufficient data to show where they went after their disappearance. Added to this problem is the fact that estimating the ages of animals in the wild is problematic. Once skeletal maturity has been achieved, there is little in the way of predictable appearance changes (McDonald, 1988). Furthermore, at present, there are little data on how far a male travels, and how many troops a male may reach or join in his life (Sugiyama, 1976). Only a few adult male Japanese macaques survive more than 25 years and many die between 15 and 17 years of age (Masui *et. al.*, 1974). It is uncertain whether many males died in or out of a troop, and it is likely that they are less able to find food and they encounter many dangers (e.g. disease, and a high risk of predation). For these reasons, there is little known about the life history of males. This is in sharp contrast to the richly documented life histories of females who have a more uniform and stable social network.

The concept that older monkeys will be distinguishable from other adults in their social behaviour is common (McDonald, 1988). However, there is little documentation of age-related changes in adult male behaviour. In Texas, a relatively small proportion of males born in the group actually become fully adult males. The oldest males in the Arashiyama West Colony all belong to the central core of the two troops. The objective of this chapter is to investigate if variation in behaviour might be explained as a function of

variation in age of the subject animals. In this study, a cross-sectional analysis is used to approximate life-history. Since all recorded behaviour was analyzed, the complete repertoire of adult male behaviour is assessed to find changes which accompany age. The chronological age of each subject animal was treated as the independent variable in this analysis, while the dependent variables are the duration of affiliate state behaviours, the frequency of affiliate event behaviours, and the frequency of agonistic event behaviours. The total number of cases is 19 (all subject animals).

The independent variable, age, is measured at the interval level. Since the assumptions of parametric testing were not met, a nonparametric test, Spearman's rho (r_s) association, or rank correlation was utilized. The measure of association between two variables was calculated by ranking both variables and correlating their ranks (not the scores). Spearman's rho is an index of the relative strength of a relationship, and yields r_s values between -1 and + 1 (as displayed with p values in all of the tables in this chapter). In this chapter, the results of the tests performed on age and general state behaviours, age and the general categories of affiliative event behaviours, and age and the general categories of agonistic event behaviours are presented. Next, the Spearman's rho test is performed on age and more specific categories of affiliative and agonistic interactions (in relation to the age/sex class of interactant). The rank correlation is then examined according to the relatedness of adult interactants based on the same categories of affiliative and agonistic interactions. Associations are significant if they have a p value of less than $\alpha=0.05$. The general null hypothesis is that there is no significant correlation, either positive or negative, between age and the frequency or duration of any behaviour.

GENERAL STATE BEHAVIOURS

Table 4.1 displays the association between age and general state behaviours. There is no association between any of these state behaviours and a male's age. So, as a male ages, there is no change in the time he spends in various daily activity patterns.

AFFILIATIVE INTERACTIONS

In this section, the association between age and both affiliative state and affiliative event behaviours is examined. In the next three result chapters (like in the previous result chapter), for the sake of clarity, interactants are abbreviated as follows: AM (adult males), AF (adult females), SM (subadult males), JV (juveniles of both sexes), INF (infants of both sexes), RAM (related adult males), UAM (unrelated adult males), RAF (related adult females), UAF (unrelated adult females), and UNIDAF (unidentified adult females). Also, in the next three result chapters, a behaviour is listed with the interactant displayed next to it. So for example, a behaviour could be listed as "Direct Groom - UAF". This would refer to when an adult male subject directed grooming toward an unrelated adult female.

Affiliative State Behaviours

The results for tests run on age and affiliative state behaviours are presented in two tables: general categories of affiliative state behaviours are subsumed under general state behaviours (see table 4.1), while a finer break-down of affiliative state behaviours (using information about the age/sex class of interactant) are presented in a separate table (table 4.2). This format will be used in the following two results chapters. For affiliative state behaviours, there are three significant associations with age (see table 4.2). All three associations concern subadult males as interactants. There is a negative correlation between an adult male's age and the amount of time spent directing grooming toward subadult males ($r_s = -0.474$, $p = 0.040$), and there is a strong negative correlation between an adult male's

Table 4.1
Results of Spearman's Rho Test:
Age and General State Behaviours of Adult Males

Behaviour	rs value	p value
Inactive	0.324	0.175
Feed	-0.051	0.837
Out of Sight	0.074	0.765
Travel	-0.006	0.980
Other	-0.454	0.051
Self-groom	-0.239	0.324
Direct Groom	-0.159	0.515
Receive Groom	-0.140	0.567
Body Contact	0.128	0.602
Social Play	-0.220	0.930

Table 4.2
Results of Spearman's Rho Test:
Age and Affiliative State Behaviours of Adult Males

Behaviour	r_s value	p value
Direct Groom - AM	-0.091	0.711
Direct Groom - AF	0.041	0.868
Direct Groom - SM	-0.474	0.040*
Direct Groom - JV	-0.215	0.377
Receive Groom - AM	-0.454	0.051
Receive Groom - AF	0.218	0.370
Receive Groom - SM	-0.554	0.014*
Receive Groom - JV	-0.292	0.226
Body Contact - AM	0.138	0.573
Body Contact - AF	0.026	0.915
Body Contact - SM	-0.527	0.021*
Body Contact - JV	-0.135	0.582
Body Contact - INF	0.244	0.314
Social Play - JV	-0.022	0.930

* significant at $\alpha=0.05$ level

age and the amount of time spent receiving grooming from subadult males ($r_s = -0.554$, $p = -0.014$). Lastly, there is a negative correlation between his age and the amount of time an adult male spent in body contact with subadult males ($r_s = -0.527$, $p = 0.021$). Therefore, younger adult males spent more time directing grooming toward, receiving grooming from, and in body contact with subadult males than did older adult males.

Affiliative Event Behaviours

For affiliative event behaviours, the results are presented in two tables. The first table (table 4.3) illustrates the associations between age and the general categories of affiliative events, while the second larger table (table 4.4) illustrates the associations between age and finer break-down of event behaviours. In this second table, affiliative event behaviours are categorized according to the age/sex class of interactant (this format will be repeated in the following two results chapters).

There is no significant difference between males of different ages in the total number of approaches that they directed and received (see table 4.3). When approaches are broken down into age/sex classes of interactants in table 4.4, it is apparent that there are three significant rank correlations between age and affiliative event behaviours. There is a negative correlation between age and the number of directed approaches at subadult males ($r_s = -0.515$, $p = 0.024$). There is a weak positive correlation between age and the number of approaches received from adult females ($r_s = 0.461$, $p = 0.047$), and a very strong correlation between age and the number of approaches received from infants ($r_s = 0.669$, $p = 0.002$). In other words, older adult male subjects directed less approaches at subadult males, and received more approaches from adult females and infants than did younger adult males.

Table 4.3
Results of Spearman's Rho Test:
Age and General Categories of Affiliative Event Behaviours of Adult Males

Behaviour	rs value	p value
Direct Approach	0.013	0.957
Receive Approach	0.276	0.252

Table 4.4
Results of Spearman's Rho Test:
Age and Affiliative Event Behaviours of Adult Males

Behaviour	rs value	p value
Direct Approach - AM	-0.104	0.671
Direct Approach - AF	0.440	0.059
Direct Approach - SM	-0.515	0.024*
Direct Approach - JV	-0.159	0.156
Receive Approach - AM	-0.063	0.797
Receive Approach - AF	0.461	0.047*
Receive Approach - SM	-0.253	0.296
Receive Approach - JV	-0.047	0.849
Receive Approach - INF	0.669	0.002*

* significant at $\alpha=0.05$ level

AGONISTIC INTERACTIONS

The results of the Spearman's rho test conducted on age and general categories of agonistic event behaviours, and age and a finer break-down of agonistic behaviour are presented in table 4.5 and 4.6, respectively. There is only one significant association between an adult male's age and agonistic behaviour. There is a negative correlation between an adult male's age and the amount of level 2 aggression (noncontact aggression with movement) directed toward other adult males ($r_s = -0.493$, $p = 0.032$). So, younger adult males directed more noncontact aggression with movement toward other adult males, than did older adult males.

RELATEDNESS OF ADULT INTERACTANTS

In this section associations between age and behaviour are presented for related and unrelated adult interactants.

Affiliative State Behaviours

There is one correlation between age and affiliative state behaviours for related and unrelated adults (see table 4.7). There is a slightly significant (significant at the $\alpha = 0.1$ level, but not significant at the $\alpha = 0.05$ level) positive correlation between age and the amount of time spent in body contact with unrelated adult females ($r_s = 0.437$, $p = 0.061$). Older adult males spent more time in body contact with unrelated adult females than younger adult males did.

Affiliative Event Behaviours

For affiliative event behaviours and age (see table 4.8), there are two significant correlations. There is a positive correlation between age and the total amount of directed approaches toward unrelated adult females ($r_s = 0.471$, $p = 0.042$), and a positive correlation between age and the total number of received approaches from unrelated adult females ($r_s = 0.535$, $p = 0.018$). That is, older adult males directed more approaches toward and

Table 4.5

Results of Spearman's Rho Test:

Age and General Categories of Agonistic Event Behaviours of Adult Males

Behaviour	rs value	p value
Direct Level 1	0.045	0.856
Direct Level 2	0.151	0.537
Direct Level 3	-0.334	0.162
Direct Level 4	-0.152	0.532
Receive Level 1	0.144	0.555
Receive Level 2	0.383	0.106
Receive Level 3	0.052	0.833

Table 4.6
Results of Spearman's Rho Test:
Age and Agonistic Event Behaviours of Adult Males

Behaviour	r_s value	p value
Direct Level 1 - AM	-0.107	0.664
Direct Level 1 - AF	-0.214	0.379
Direct Level 1 - SM	-0.062	0.800
Direct Level 1 - JV	0.220	0.366
Direct Level 1 - INF	0.050	0.839
Direct Level 2 - AM	-0.493	0.032*
Direct Level 2 - AF	0.131	0.594
Direct Level 2 - SM	-0.306	0.202
Direct Level 2 - JV	0.207	0.395
Direct Level 2 - INF	0.348	0.144
Direct Level 3 - AM	0.065	0.791
Direct Level 3 - AF	-0.241	0.320
Direct Level 3 - SM	-0.306	0.202
Direct Level 3 - JV	-0.200	0.411
Direct Level 3 - INF	-0.022	0.930
Direct Level 4 - AF	-0.152	0.534
Receive Level 1 - AM	0.063	0.797
Receive Level 1 - AF	0.180	0.461
Receive Level 1 - SM	-0.013	0.957

Continued....

Table 4.6 Continued....

Behaviour	rs value	p value
Receive Level 1 - JV	-0.015	0.952
Receive Level 2 - AM	0.101	0.680
Receive Level 2 - AF	0.370	0.118
Receive Level 2 - SM	0.345	0.147
Receive Level 2 - JV	0.095	0.669
Receive Level 3 - AM	0.239	0.324
Receive Level 3 - AF	0.026	0.915
Receive Level 3 - SM	-0.121	0.621

* significant at $\alpha=0.05$ level

Table 4.7

Results of Spearman's Rho Test:

Age and Affiliative State Behaviours of Adult Males with Related and Unrelated Adults

Behaviour	r_s value	p value
Direct Groom - UAM	-0.091	0.711
Direct Groom - RAF	-0.341	0.513
Direct Groom - UAF	0.155	0.526
Receive Groom - RAM	-0.326	0.173
Receive Groom - UAM	-0.375	0.113
Receive Groom - RAF	-0.317	0.185
Receive Groom - UAF	0.344	0.149
Receive Groom - UNIDAF	-0.294	0.222
Body Contact - UAM	0.138	0.573
Body Contact - RAF	-0.221	0.363
Body Contact - UAF	0.437	0.061**
Body Contact - UNIDAF	-0.022	0.930

* * significant at $\alpha=0.1$ level

Table 4.8

Results of Spearman's Rho Test:

Age and Affiliative Event Behaviours of Adult Males with Related and Unrelated Adults

Behaviour	r_s value	p value
Direct Approach - UAM	-0.104	0.671
Direct Approach - RAF	-0.379	0.109
Direct Approach - UAF	0.471	0.042*
Direct Approach - UNIDAF	-0.022	0.930
Receive Approach - RAM	-0.326	0.173
Receive Approach - UAM	-0.384	0.104
Receive Approach - RAF	-0.262	0.278
Receive Approach - UAF	0.535	0.018*
Receive Approach-UNIDAF	-0.253	0.296

* significant at $\alpha=0.05$ level

received more approaches from unrelated adult females than younger adult males did.

Agonistic Event Behaviours

There is only one significant correlation between age and agonistic behaviour (see table 4.9). There is a negative correlation between age and the amount of directed level 2 aggression (noncontact aggression with movement) toward unrelated adult males ($r_s = -0.493$, $p = 0.032$). In other words, younger adult males directed more noncontact aggression (with movement) toward unrelated adult males than did older adult males.

Table 4.9

Results of Spearman's Rho Test:

Age and Agonistic Event Behaviours of Adult Males with Related and Unrelated Adults

Behaviour	r_s value	p value
Direct Level 1 - UAM	-0.107	0.664
Direct Level 1 - UAF	-0.214	0.379
Direct Level 2 - UAM	-0.493	0.032*
Direct Level 2 - RAF	-0.326	0.173
Direct Level 2 - UAF	0.182	0.455
Direct Level 2 - UNIDAF	0.088	0.720
Direct Level 3 - UAM	0.065	0.791
Direct Level 3 - RAF	-0.326	0.173
Direct Level 3 - UAF	-0.111	0.650
Direct Level 3 - UNIDAF	-0.326	0.173
Direct Level 4 - UAF	-0.152	0.534
Receive Level 1 - UAM	0.063	0.797
Receive Level 1 - RAF	-0.326	0.173
Receive Level 1 - UAF	0.289	0.230
Receive Level 1 - UNIDAF	-0.022	0.930
Receive Level 2 - UAM	0.101	0.680
Receive Level 2 - UAF	0.370	0.118
Receive Level 3 - UAM	0.239	0.324
Receive Level 3 - RAF	-0.326	0.173

Continued....

Table 4.9 Continued....

Behaviour	r_s value	p value
Receive Level 3 - UAF	0.184	0.451

* significant at $\alpha=0.05$ level

SUMMARY OF RESULTS

In this chapter, the ages of adult male subjects were analyzed in order to find out if there were correlations with behaviour. In this colony of Japanese macaques, an adult male's age had little effect on his behaviour. There were no significant differences in the general state behaviours of the subjects according to their age. It was found that the age of the subject animal had some effect on affiliative and agonistic interactions with various age/sex classes. In fact, the impact that age did have concerned interactions that adult males had with subadult males. Younger adult males were found to spend more time directing ($r_s = -0.474$, $p = 0.040$) and receiving grooming ($r_s = -0.554$, $p = 0.014$) from subadult males, directed more approaches toward subadult males ($r_s = -0.515$, $p = 0.024$), and also were in body contact with subadult males ($r_s = -0.527$, $p = 0.021$) substantially more than older adult males. There seems to be an age homophily (tendency to interact with age-mates) for this one age class of adult males. Another finding is that older adult males received more approaches from infants ($r_s = 0.669$, $p = 0.002$) and unrelated adult females ($r_s = 0.535$, $p = 0.018$) than did younger adult males. Furthermore, older adult males directed more approaches toward unrelated adult females than did younger adult males ($r_s = 0.471$, $p = 0.042$). When regarding agonistic behaviours, there was only one significant association between age and behaviour. Younger adult males directed level 2 aggression (noncontact aggression with movement) toward unrelated adult males more often than did older adult males ($r_s = -0.493$, $p = 0.032$).

CHAPTER FIVE - RESULTS: OVERALL DIFFERENCES ACCORDING TO DOMINANCE RANK

INTRODUCTION

The dominance hierarchy is best described as representing the stabilized outcome of the competition for resources (see Pavelka, 1993). The hierarchy provides all members of a social group to live in a system of rules, and allows some predictability in their highly social lives (Pavelka, 1993). The proximate benefits of high dominance rank are obvious and can be readily observed. However, this has lead many researchers to postulate functional benefits of having high rank (see Fedigan 1983; Pavelka, 1993). There are many hypotheses regarding the ecological, social, and evolutionary benefits that high rank incurs. For example, there is a general perception that social dominance is linked directly to reproductive success. However, as in many other cases, it was found that in Texas, dominance does not equal reproductive success (Fedigan, *et. al.*, 1986). As described by Fedigan, (1992), another example of how all-pervasive the effect of dominance is considered to be, regards social grooming. A common assumption exists that dominant individuals receive more grooming than subordinate individuals (Fedigan, 1992). However, this finding is not as straightforward as it may seem, and it is not expected. McKenna (1978) and Bernstein (1970) noted that social grooming is in part a social strategy which may be employed in a variety of ways (e.g. to approach the mother of a new infant, to reduce the struggles of a youngster being weaned, to court a potential sexual partner), and has no necessary relationship to dominance rank (see Fedigan, 1992). Furthermore, no evidence exists that to be groomed is somehow more desirable than to groom (Fedigan, 1992).

In Japanese macaques, there exists a linear dominance hierarchy among adult males (Norikoshi and Koyama, 1974). In the primate literature, the top-ranking male is often

referred to as the "alpha" male. The typical "alpha-male-role" includes reducing the frequency and severity of aggression in their group (de Waal, 1982), providing protection against predators, and leading group progressions (Bernstein, 1976). However, it is very difficult to document these somewhat protective behaviours in the field (van Noordwijk and van Schaik, 1988). Most troops also have a top-ranking leader female, or "alpha" female. Alpha females usually rank just below alpha males and above all other members of the troop (including the second-ranking male). Most alpha females appear to form a strong cooperative alliance with the alpha male (Fedigan, 1992).

For this study, the nineteen subject animals were categorized as either having high, medium, or low rank. The director of the site provided the rank of all of the subject animals in this study (based on the direction of agonistic and submissive signals). Of the nineteen subject animals, six were high ranking, five medium ranking, and eight low ranking. The purpose of this chapter is to determine whether differences in behaviour can be explained as a function of differences in the dominance rank of the subject animals. The dominance rank of the subject animals was treated as the independent variable in this analysis, and the dependent variable is behaviour. Rank is measured at the ordinal level.

In this chapter, the Kruskal-Wallis test was performed on dominance rank and general state behaviours, dominance rank and affiliative state behaviours, dominance rank and affiliative event behaviours, and dominance rank and agonistic event behaviours. Then this test was undertaken to find out if there were differences in social behaviour according to the relatedness of adult interactants for dominance rank and affiliative behaviour, and dominance rank and agonistic behaviour.

The Kruskal-Wallis test is a multiple-sample generalization. Since the assumptions of parametric testing were not met, the Kruskal-Wallis test, an alternative to the usual one-way analysis of variance, was employed to determine if there was a significant difference between the 3 sample medians (low, medium, and high). In the case of ties between scores

in the raw data, the p values that were adjusted for ties are displayed. Differences between the three dominance ranks are significant if they have a p value of less than $\alpha=0.05$. In each of the tables in this chapter, the high rank median, medium rank median, low rank median, test statistic (H), and p value is presented for each behaviour score. The medians displayed for general state behaviours and affiliative state behaviours are in seconds. The medians given for affiliative and agonistic event behaviours are in frequencies. The general null hypothesis is that there is no significant difference between rank and the frequency or duration of any behaviour.

GENERAL STATE BEHAVIOURS

As displayed in table 5.1, there are no differences in general state behaviours due to dominance rank. Adult males of all ranks were very similar in how they spent time in daily activity patterns.

AFFILIATIVE INTERACTIONS

Affiliative State Behaviours

There are two significant differences among the adult males based on their dominance rank and both concerned subadult males as interactants (see table 5.2). High ranking males received grooming from subadult males significantly more than did medium or low ranking males (high=146, medium=0, low=0, $p=0.026$). Also high ranking males were found in body contact with subadult males substantially more than were medium or low ranking males (high=41.5, medium=0, low=0, $p=0.026$). Therefore, high ranking adult males received more grooming from subadult males and also were in body contact more with them than were medium or low ranking adult males.

Table 5.1

Results of Kruskal-Wallis Test:

Dominance Rank and General State Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Inactive	13883.00	13678.00	12258.00	0.990	0.611
Feed	5626.000	5410.000	8596.000	2.520	0.284
Out of Sight	513.500	314.000	609.000	0.360	0.834
Travel	2401.000	2717.000	2809.000	1.120	0.571
Other	510.500	317.000	245.500	2.260	0.323
Self-groom	2160.000	1388.000	2193.000	2.210	0.331
Direct Groom	660.500	952.000	738.000	0.260	0.878
Receive Groom	2931.000	3104.000	2497.000	1.780	0.411
Body Contact	481.500	447.000	353.500	0.010	0.995
Social Play	0	0	0	1.370	0.503

Table 5.2

Results of Kruskal-Wallis Test:

Dominance Rank and Affiliative State Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Groom - AM	0	0	0	0.020	0.990
Direct Groom - AF	204.000	634.000	315.000	0.520	0.770
Direct Groom - SM	0	0	0	1.540	0.463
Direct Groom - JV	8.000	0	4.000	0.120	0.942
Receive Groom - AM	703.000	0	0	3.720	0.156
Receive Groom - AF	792.500	1716.000	1219.500	0.220	0.898
Receive Groom - SM	146.000	0	0	7.360	0.026*
Receive Groom - JV	861.000	258.000	518.500	0.130	0.938
Body Contact - AM	7.000	0	30.000	4.390	0.112
Body Contact - AF	9.500	42.500	43.500	0.780	0.677
Body Contact - SM	41.500	0	0	7.360	0.026*
Body Contact - JV	0	0	143.000	2.200	0.333
Body Contact - INF	0	0	0	0.210	0.902
Social Play - JV	0	0	0	1.370	0.503

* significant at alpha=0.05 level

Affiliative Event Behaviours

Table 5.3 shows the associations between dominance rank and the general categories of affiliative events. The dominance rank of the subjects had little influence on the total number of approaches they directed and received, and also had little impact on the finer break-down of these affiliative event behaviours (see table 5.4).

AGONISTIC INTERACTIONS

Table 5.5 presents the differences in general categories of agonistic behaviour based on the three dominance ranks. There are three differences: low ranking males directed more level 2 aggression than did medium or high ranking males (high=3.5, medium=5, low=7.5, $p=0.025$), low ranking males received more level 1 aggression than did high or medium ranking males (high=0, medium=1, low=3, $p=0.021$), and low ranking males received more level 2 aggression than did high or medium ranking males (high=0, medium=0, low=2.5, $p=0.007$). Two significant differences in behaviour due to dominance rank were found to exist when examining more specific categories of agonistic event behaviours (see table 5.6). Low ranking adult male subjects received considerably more level 1 aggression (noncontact stationary aggression) from adult females than did medium or high ranking adult male subjects (high=0, medium=1, low=2.5, $p=0.015$). Also, low ranking males received level 2 aggression (noncontact aggression with movement) more from subadult males than did medium or high ranking males (high=0, medium=0, low=0.5, $p=0.039$). In general, then, low ranking males directed (level 1) and received (levels 1 and 2) more low intensity aggression than did high or medium ranking males. More specifically, low ranking adult males received more low intensity aggression from adult females (level 1) and subadult males (level 2) than did medium or high ranking adult males.

Table 5.3

Results of Kruskal-Wallis Test:

Dominance Rank and General Categories of Affiliative Event Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Approach	4.500	5.000	4.500	0.040	0.978
Receive Approach	9.500	13.000	12.500	0.770	0.679

Table 5.4

Results of Kruskal-Wallis Test:

Dominance Rank and Affiliative Event Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Approach - AM	1.000	0	0	1.280	0.528
Direct Approach - AF	2.000	1.000	2.500	0.420	0.811
Direct Approach - SM	0	0	0	2.070	0.356
Direct Approach - JV	0.500	1.000	0	0.590	0.744
Receive Approach - AM	2.500	1.000	2.000	1.190	0.552
Receive Approach - AF	1.000	1.000	2.000	0.260	0.877
Receive Approach - SM	0	1.000	1.000	0.550	0.761
Receive Approach - JV	1.500	3.000	4.500	1.710	0.426
Receive Approach - INF	0	0	1.000	0.820	0.664

Table 5.5

Results of Kruskal-Wallis Test:

Dominance Rank and General Categories of Agonistic Event Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Level 1	4.500	4.000	4.500	0.230	0.893
Direct Level 2	3.500	5.000	7.500	7.380	0.025*
Direct Level 3	2.500	3.000	2.000	0.180	0.915
Direct Level 4	0	0	0	2.170	0.339
Receive Level 1	0	1.000	3.000	7.740	0.021*
Receive Level 2	0	0	2.500	10.020	0.007*
Receive Level 3	0	0	1.000	3.440	0.179

* significant at alpha=0.05 level

Table 5.6

Results of Kruskal-Wallis Test:

Dominance Rank and Agonistic Event Behaviours of Adult Males

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Level 1 - AM	0	0	0	1.610	0.447
Direct Level 1 - AF	1.000	1.000	0.500	0.480	0.788
Direct Level 1 - SM	0	0	0	0.230	0.891
Direct Level 1 - JV	1.500	1.000	1.500	0.010	0.994
Direct Level 1 - INF	0	0	0	0.570	0.753
Direct Level 2 - AM	0	0	0	2.800	0.247
Direct Level 2 - AF	1.000	1.000	2.000	1.300	0.522
Direct Level 2 - SM	0	0	0	1.370	0.503
Direct Level 2 - JV	1.500	4.000	4.500	4.040	0.133
Direct Level 2 - INF	0	0	0	2.800	0.247
Direct Level 3 - AM	0	0	0	2.170	0.339
Direct Level 3 - AF	1.000	1.000	1.000	0.190	0.907
Direct Level 3 - SM	0	0	0	1.370	0.503
Direct Level 3 - JV	1.000	2.000	0.500	0.840	0.657
Direct Level 3 - INF	0	0	0	1.370	0.503
Direct Level 4 - AF	0	0	0	2.170	0.339
Receive Level 1 - AM	0	0	0	2.910	0.234
Receive Level 1 - AF	0	1.000	2.500	8.490	0.015*

Continued....

Table 5.6 Continued....

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Receive Level 1 - SM	0	0	0	4.640	0.099
Receive Level 1 - JV	0	0	0	1.430	0.489
Receive Level 2 - AM	0	0	0.500	4.060	0.132
Receive Level 2 - AF	0	0	0	2.920	0.232
Receive Level 2 - SM	0	0	0.500	6.530	0.039*
Receive Level 2 - JV	0	0	0	2.910	0.234
Receive Level 3 - AM	0	0	0	1.370	0.503
Receive Level 3 - AF	0	0	0	0.940	0.624
Receive Level 3 - SM	0	0	0	2.900	0.235

* significant at alpha=0.05 level

RELATEDNESS OF ADULT INTERACTANTS

Affiliative State Behaviours

The results of the Kruskal-Wallis test for affiliative behaviour based on the three dominance ranks for related and unrelated adults is displayed in table 5.7. Adult male subjects of all ranks spent very similar amounts of time spent in affiliative state behaviours with related and unrelated adults.

Affiliative Event Behaviours

As displayed in table 5.8, there are no differences in affiliative event behaviours with related and unrelated adults based on the subject animals' dominance rank.

Agonistic Event Behaviours

According to table 5.9, there is only one considerable difference in agonistic behaviour due to the dominance rank of the subjects. Low ranking males received more level one aggression from unrelated adult females than did medium or high ranking males (high=0, medium=1, low=2, $p=0.007$).

Table 5.7

Results of Kruskal-Wallis Test :

Dominance Rank and Affiliative State Behaviours of Adult Males

with Related and Unrelated Adults

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Groom - UAM	0	0	0	0.020	0.990
Direct Groom - RAF	0	0	0	1.610	0.447
Direct Groom - UAF	204.000	0	315.000	0.140	0.931
Receive Groom - RAM	0	0	0	2.170	0.339
Receive Groom - UAM	394.000	0	0	2.520	0.284
Receive Groom - UAF	199.500	1716.000	812.000	0.510	0.774
Receive Groom - UNIDAF	0	0	0	1.510	0.470
Body Contact - UAM	7.000	0	30.000	4.390	0.112
Body Contact - RAF	0	0	0	1.540	0.463
Body Contact - UAF	9.500	32.000	41.500	0.210	0.898
Body Contact - UNIDAF	0	0	0	1.370	0.503

Table 5.8

Results of Kruskal-Wallis Test :

Dominance Rank and Affiliative Event Behaviours of Adult Males
with Related and Unrelated Adults

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Approach - UAM	1.000	0	0	1.280	0.528
Direct Approach - RAF	0	0	0	2.890	0.236
Direct Approach - UAF	1.500	1.000	2.000	0.740	0.691
Direct Approach - UNIDAF	0	0	0	1.370	0.503
Receive Approach - RAM	0	0	0	2.170	0.339
Receive Approach - UAM	2.000	1.000	2.000	0.500	0.780
Receive Approach - RAF	0	0	0	0.850	0.653
Receive Approach - UAF	0.500	1.000	1.500	0.670	0.716
Receive Approach-UNIDAF	0	0	0	0.820	0.665

Table 5.9
Results of Kruskal-Wallis Test:
Dominance Rank and Agonistic Event Behaviours of Adult Males
with Related and Unrelated Adults

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Direct Level 1 - UAM	0	0	0	1.610	0.447
Direct Level 1 - UAF	1.000	1.000	0.500	0.480	0.788
Direct Level 2 - UAM	0	0	0	2.800	0.247
Direct Level 2 - RAF	0	0	0	2.170	0.339
Direct Level 2 - UAF	1.000	1.000	1.000	0.900	0.638
Direct Level 2 - UNIDAF	0	0	0	2.900	0.235
Direct Level 3 - UAM	0	0	0	2.170	0.339
Direct Level 3 - RAF	0	0	0	2.170	0.339
Direct Level 3 - UAF	0.500	1.000	1.000	0.280	0.869
Direct Level 3 - UNIDAF	0	0	0	2.170	0.339
Direct Level 4 - UAF	0	0	0	2.170	0.339
Receive Level 1 - UAM	0	0	0	2.910	0.234
Receive Level 1 - RAF	0	0	0	2.170	0.339
Receive Level 1 - UAF	0.000	1.000	2.000	10.090	0.007*
Receive Level 1 - UNIDAF	0	0	0	1.370	0.503
Receive Level 2 - UAM	0	0	0.500	4.060	0.132
Receive Level 2 - UAF	0	0	0	2.920	0.232

Continued....

Table 5.9 Continued....

Behaviour	High Median N=6	Medium Median N=5	Low Median N=8	Test Statistic (H)	p value
Receive Level 3 - UAM	0	0	0	1.370	0.503
Receive Level 3 - RAF	0	0	0	2.170	0.339
Receive Level 3 - UAF	0	0	0	2.920	0.232

* significant at $\alpha=0.05$ level

SUMMARY OF RESULTS

In this chapter the variation in behaviour was analyzed according to whether the subject animal was high, medium, or low in dominance rank. It was found that an adult male's dominance rank had some impact on his behaviour. There were no differences in general state behaviours based on dominance rank. For affiliative state behaviours, the only significant differences in the subjects were that higher ranking adult males spent more time receiving grooming from subadult males (high=146, medium=0, low=0, $p=0.026$), and higher ranking adult males spent more time in body contact with subadult males (high=41.5, medium=0, low=0, $p=0.026$) than did medium or low ranking adult males. Also, some interesting differences were found for agonistic behaviour. When the Kruskal-Wallis Test was performed on dominance rank and agonistic event behaviours, several differences were apparent. In general, low ranking adult males received more counts of level 1 and level 2 aggression than did medium or high ranking ones (level 1: high=0, medium=1, low=3, $p=0.021$; level 2: high=0, medium=0, low=2.5, $p=0.007$). More specifically, low ranking subject animals received more level 1 aggression (noncontact stationary aggression) from adult females (high=0, medium=1, low=2.5, $p=0.039$), particularly unrelated adult females (high=0, medium=1, low=2, $p=0.007$), than did medium or high ranking subjects. Additionally, low ranking adult males received significantly more level 2 aggression (noncontact aggression with movement) than adult male subjects of other dominance ranks (high=0, medium=0, low=0.5, $p=0.039$). So, it seems that dominance rank had a significant effect on affiliative state behaviours involving subadult males as interactants. High ranking adult males received grooming from subadult males and were found to spend more time in body contact with them substantially more than did medium or low ranking adult males. Also, low ranking subjects received more low intensity aggression, particularly from unrelated adult males, than did medium or high ranking subjects.

CHAPTER SIX - RESULTS: OVERALL DIFFERENCES ACCORDING TO TROOP MEMBERSHIP

INTRODUCTION

As previously stated, two troops compose the Arashiyama West colony of Japanese macaques - the main troop and the splinter troop. The goal of this chapter is to establish whether troop membership effects adult male behaviour. Troop membership is the independent variable measured at the nominal level, and behaviour is the dependent variable. The outline of this chapter is similar to the past two chapters. The Mann-Whitney test was performed on troop membership and general state behaviours, troop membership and affiliative state behaviours, troop membership and affiliative event behaviours, and troop membership and agonistic event behaviours. Also, this test was undertaken to discover whether there were differences in social behaviour due to troop membership with related and unrelated adult interactants in affiliative and agonistic interactions.

The Mann-Whitney test, a two-sample rank test to yield differences between two population medians, was used to detect variation in behaviour between the two troops. In each of the tables in this chapter, the main troop median and splinter troop median, the test statistic (W), and p value are presented for each behaviour score. For some behaviours in this chapter, the computations could not be run because the scores were too similar (mainly because there were not enough occurrences of a given behaviour). That is, there was no variation in the data. In these cases where the test could not be run, a dash is presented in the table. The medians shown for general state behaviours and affiliative state behaviours are in seconds. The medians given for affiliative and agonistic event behaviours are in frequencies. The general null hypothesis is that there is no significant difference between troop membership and the frequency or duration of any behaviour.

GENERAL STATE BEHAVIOURS

As displayed in table 6.1, there are three significant differences in the durations of general state behaviours between main and splinter troop subject animals. Splinter troop subject animals are considerably more inactive than are main troop subject animals (main=11654, splinter=15104, $p=0.0073$). Also, main troop adult males spent more time traveling than did splinter troop adult males (main=3069, splinter=1992.5, $p=0.1266$). The third difference is that main troop adult males received more grooming than did splinter troop adult males (main=3395, splinter=2196.5, $p=0.0431$). Therefore, splinter troop adult males were more inactive, spent less time traveling, and received less grooming than did main troop adult males.

AFFILIATIVE INTERACTIONS

Affiliative State Behaviours

As stated in the previous section, the only difference in general categories of affiliative state behaviours is that main troop adult males received more grooming than splinter troop adult males. Table 6.2 shows that there were no significant differences in more specific categories of affiliative state behaviours between the main and splinter troop subject animals.

Affiliative Event Behaviours

For general categories of affiliative event behaviours (see table 6.3), there were no significant differences between subjects residing in the two troops. Only one significant difference exists in the finer break-down of affiliative event behaviours (table 6.4). Main troop subject animals received more approaches from subadult males than did splinter troop subject animals (main=1, splinter=0, $p=0.0215$).

Table 6.1

Results of Mann-Whitney Test:

Troop Membership and General State Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Inactive	11654.000	15104.000	77.000	0.0073 [*]
Feed	8688.000	5153.500	129.000	0.1266
Out of Sight	718.000	311.500	121.500	0.3635
Travel	3069.000	1992.500	146.000	0.0034 [*]
Other	267.000	358.000	98.000	0.3423
Self-groom	2028.000	2192.500	105.000	0.7102
Direct Groom	474.000	914.500	107.500	0.8365
Receive Groom	3395.000	2196.500	135.000	0.0431 [*]
Body Contact	291.000	506.000	97.000	0.3020
Social Play	-	-	-	-

* significant at alpha=0.05 level

Table 6.2

Results of Mann-Whitney Test:

Troop Membership and Affiliative State Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Groom - AM	0	0	116.000	0.5998
Direct Groom - AF	342.000	317.000	111.000	0.9666
Direct Groom - SM	-	-	-	-
Direct Groom - JV	8.000	0	112.500	0.8583
Receive Groom - AM	0	287.500	109.000	0.9644
Receive Groom - AF	137.000	581.500	123.500	0.2829
Receive Groom - SM	0	0	122.500	0.2012
Receive Groom - JV	883.000	107.000	121.000	0.3817
Body Contact - AM	0	74.500	87.000	0.0632
Body Contact - AF	31.000	145.000	101.500	0.5022
Body Contact - SM	0	0	118.500	0.3941
Body Contact - JV	13.000	125.000	102.000	0.5127
Body Contact - INF	-	-	-	-
Social Play - JV	-	-	-	-

Table 6.3

Results of Mann-Whitney Test:

Troop Membership and General Categories of Affiliative Event Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Approach	5.000	1.500	131.000	0.0880
Receive Approach	13.000	7.000	131.000	0.0895

Table 6.4

Results of Mann-Whitney Test:

Troop Membership and Affiliative Event Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Approach - AM	1.000	0	116.000	0.6128
Direct Approach - AF	1.000	1.000	118.500	0.4973
Direct Approach - SM	-	-	-	-
Direct Approach - JV	2.000	0	130.500	0.0710
Receive Approach - AM	2.000	1.500	115.000	0.7037
Receive Approach - AF	2.000	1.500	112.500	0.8646
Receive Approach - SM	1.000	0	137.000	0.0215*
Receive Approach - JV	3.000	1.500	116.000	0.6455
Receive Approach - INF	1.000	0	123.500	0.2406

* significant at alpha=0.05 level

AGONISTIC INTERACTIONS

In table 6.5, results of the Mann-Whitney test are presented for troop membership and general categories of agonistic event behaviours. While there were no differences found for these general categories, two differences were present for more specific categories (table 6.6). One difference is only slightly significant (significant at the $\alpha=0.1$ level, but not significant at the $\alpha=0.05$ level): splinter troop adult males received more level 2 aggression from adult females than did main troop adult males (main=0, splinter=0.5, $p=0.0534$). The other difference was that main troop adult males directed level 2 aggression (noncontact aggression with movement) toward adult females considerably more than did splinter troop adult males (main=2, splinter=0.5, $p=0.0033$).

RELATEDNESS OF ADULT INTERACTANTS

Affiliative State Behaviours

In table 6.7, variation in affiliative state behaviours due to troop membership, with respect to related and unrelated adult interactants, is displayed. Subjects in both troops showed similar affiliative state behaviours involving adult interactants.

Affiliative Event Behaviours

As shown in table 6.8, main troop and splinter troop adult males displayed no differences in affiliative event behaviours with adult interactants (related or unrelated).

Agonistic Event Behaviours

For agonistic event behaviours, there was one significant difference (see table 6.9). Main troop subject animals directed more level 2 aggression toward unrelated adult females than did splinter troop subject animals (main=1, splinter=0.5, $p=0.0153$).

Table 6.5

Results of Mann-Whitney Test:

Troop Membership and General Categories of Agonistic Event Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Level 1	5.000	4.000	124.500	0.2388
Direct Level 2	5.000	6.000	118.500	0.5066
Direct Level 3	3.000	2.000	120.500	0.3989
Direct Level 4	-	-	-	-
Receive Level 1	1.000	1.000	115.000	0.7026
Receive Level 2	0	0.500	106.500	0.7884
Receive Level 3	0	0.500	104.500	0.6394

Table 6.6

Results of Mann-Whitney Test:

Troop Membership and Agonistic Event Behaviours of Adult Males

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Level 1 - AM	0	0	112.500	0.7940
Direct Level 1 - AF	1.000	0	130.000	0.0812
Direct Level 1 - SM	0	0	97.000	0.1465
Direct Level 1 - JV	1.000	2.000	99.500	0.3920
Direct Level 1 - INF	0	0	112.000	0.8271
Direct Level 2 - AF	2.000	0.500	144.000	0.0033*
Direct Level 2 - SM	0	0	112.500	0.7940
Direct Level 2 - JV	2.000	3.500	98.000	0.3374
Direct Level 2 - INF	-	-	-	-
Direct Level 3 - AM	-	-	-	-
Direct Level 3 - AF	1.000	0.500	128.500	0.1156
Direct Level 3 - SM	-	-	-	-
Direct Level 3 - JV	1.000	1.000	106.500	0.7963
Direct Level 3 - INF	-	-	-	-
Direct Level 4 - AF	-	-	-	-
Receive Level 1 - AM	0	0	108.500	0.8767
Receive Level 1 - AF	1.000	0.500	120.000	0.4131
Receive Level 1 - SM	0	0	112.500	0.7940

Continued....

Table 6.6 Continued....

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Receive Level 1 - JV	0	0	102.500	0.3623
Receive Level 2 - AM	0	0	118.500	0.3934
Receive Level 2 - AF	0	0.500	91.500	0.0534**
Receive Level 2 - SM	0	0	117.000	0.4502
Receive Level 2 - JV	0	0	108.500	0.8767
Receive Level 3 - AM	-	-	-	-
Receive Level 3 - AF	0	0	104.000	0.5771
Receive Level 3 - SM	-	-	-	-

* significant at $\alpha=0.05$ level

** significant at $\alpha=0.1$ level

Table 6.7

Results of Mann-Whitney Test:

Troop Membership and Affiliative State Behaviours of Adult Males
with Related and Unrelated Adults

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Groom - UAM	0	0	116.000	0.5998
Direct Groom - RAF	-	-	-	-
Direct Groom - UAF	179.000	317.000	106.000	0.7640
Receive Groom - RAM	-	-	-	-
Receive Groom - UAM	0	287.500	105.000	0.6878
Receive Groom - RAF	0	0	110.000	1.0000
Receive Groom - UAF	1347.000	337.500	120.500	0.4016
Receive Groom - UNIDAF	-	-	-	-
Body Contact - UAM	0	74.500	87.000	0.0632
Body Contact - RAF	-	-	-	-
Body Contact - UAF	19.000	145.000	99.000	0.3859
Body Contact - UNIDAF	-	-	-	-

Table 6.8

Results of Mann-Whitney Test:

Troop Membership and Affiliative Event Behaviours of Adult Males
with Related and Unrelated Adults

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Approach - UAM	1.000	0	116.000	0.6128
Direct Approach - RAF	-	-	-	-
Direct Approach - UAF	1.000	1.000	108.500	0.9320
Receive Approach - RAM	-	-	-	-
Receive Approach - UAM	2.000	1.500	112.500	0.8650
Receive Approach - UAF	1.000	1.000	108.500	0.9324
Receive Approach-UNIDAF	-	-	-	-

Table 6.9

Results of Mann-Whitney Test:

Troop Membership and Agonistic Event Behaviours of Adult Males
with Related and Unrelated Adults

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Level 1 - UAM	0	0	112.500	0.7940

Continued....

Table 6.9 Continued....

Behaviour	Main Troop Median N=11	Splinter Troop Median N=8	Test Statistic (W)	p value
Direct Level 1 - UAF	1.000	0	130.000	0.0812
Direct Level 2 - UAM	0	0	103.000	0.3961
Direct Level 2 - RAF	-	-	-	-
Direct Level 2 - UAF	1.000	0.500	138.000	0.0153*
Direct Level 2 - UNIDAF	-	-	-	-
Direct Level 3 - UAM	-	-	-	-
Direct Level 3 - RAF	-	-	-	-
Direct Level 3 - UAF	1.000	0.500	124.500	0.2212
Direct Level 3 - UNIDAF	-	-	-	-
Direct Level 4 - UAF	-	-	-	-
Receive Level 1 - UAM	0	0	108.500	0.8767
Receive Level 1 - RAF	-	-	-	-
Receive Level 1 - UNIDAF	-	-	-	-
Receive Level 2 - UAM	0	0	118.500	0.3934
Receive Level 2 - UAF	1.000	0.500	91.500	0.0534
Receive Level 3 - UAM	-	-	-	-
Receive Level 3 - RAF	-	-	-	-
Receive Level 3 - UAF	0	0	100.500	0.3342

* significant at alpha=0.05 level

SUMMARY OF RESULTS

Troop membership had some effect on the variation of adult male behaviour in this colony of Japanese macaques. Main troop and splinter troop subject animals are quite similar in their behaviour. In reference to general state behaviours, splinter troop animals were more inactive (main=11654, splinter=15104, $p=0.0073$), spent less time traveling (main=3069, splinter=1992.5, $p=0.1266$), and received less grooming than did splinter troop subject animals (main=3395, splinter=2196.5, $p=0.0431$). There were only two other important differences between the two troops. Main troop subject animals received more approaches from subadult males than did splinter troop subjects (main=1, splinter=0, $p=0.0215$). Also, main troop subject animals directed more counts of level 2 aggression (noncontact aggression with movement) toward adult females, particularly unrelated adult females, than did splinter troop subject animals (main=1, splinter=0.5, $p=0.0153$).

CHAPTER SEVEN - DISCUSSION

GENERAL STATE BEHAVIOURS AND NATURE OF SOCIAL INTERACTIONS

General State Behaviours

In order to determine the daily activity patterns of adult males, the general state behaviours (inactive, feed, out of sight, travel, other, self-groom, direct groom, receive groom, body contact, and social play) of the subject animals were analyzed. It was found that the subject animals spent a large amount of time inactive (42.68% of their total time) and in feeding activity (22.32% of their total time). Also, the behaviour of the adult male subjects was mostly nonsocial (83.9% of all behaviour) in nature, while comparatively little time was spent in social activity (16.1% of all behaviour).

The species *M. fuscata* has been studied with respect to food habits, home range, daily range, land utilization, and/or the seasonal change in these activities (Maruhashi, 1981). According to Maruhashi (1981), the daily activity rhythm of a species can be an important index to the survival pattern of a species. However, there have been relatively few studies conducted on daily activity patterns.

Maruhashi (1981) conducted a study on the activity patterns of a wild troop of Japanese monkeys on Yakushima Island, Japan. Since the general state categories of behaviour employed in this study were similar to those used by Maruhashi, his results are compared to the results found in this study. It is important to note that Maruhashi defined adult males as males who are ten years of age and older, while adult males were defined as males who are eight years of age and older in this study. Compared to wild Japanese macaques, the subjects in this study were inactive more (study group=42.68% of total time, wild group=35.3% of total time), traveled less (study group=8.54%, wild group=17.9%), and spent more time in feeding activity (study group=22.32%, wild

group=15.9%). Also, the subject animals spent much less time in social grooming (the combined categories of directing and receiving grooming) (study group=13.42%, wild group=26.0%) and more time in self-grooming (study group=6.74%, wild group=1.7%) than did the wild adult male Japanese macaques. These differences in inactivity, traveling, and feeding could be a product of provisioning, since the subjects in this study animals do not have to travel as much and actively search for food sources as would wild animals. The difference in grooming (both social and self grooming) between the subject animals in this study and the wild animals could be explained by the fact that in Japanese macaques, the amount of time spent in grooming has been noted as having considerable intra-species variation (see Maruhashi, 1981).

While the allocation of time in general state behaviours was only examined for adult males in this study, Maruhashi (1981) also reported that different age/sex classes spend different amounts of time in their daily activity patterns. According to Clutton-Brock (1977), adult males spend proportionally less time feeding and more time resting or inactive than females or young animals in many primate species. He stated that the reason for this is that: (1) males do not incur costs of pregnancy and lactation, (2) in the majority of species, males are dominant to females and maintain priority of access to resources containing maximal food availability, and (3) they feed faster than females.

Affiliative Interactions

In comparison to other general state behaviours, adult males spent relatively little time in social activity (nonsocial=83.9% of total time, social=16.1% of total time). The majority of social time was spent receiving grooming (62.16% of total social time), while the occurrence of social play was quite rare (0.03% of total social time). The results show that the primary interactants of the adult males in this study are unrelated adult females. Of all possible interactants (other age/sex classes), adult males spent the most time in social grooming with adult females. They spent 9.09% of total social grooming time directing

grooming toward adult females and 37.53% receiving grooming from them. Also, subjects most frequently directed approaches toward adult females (total frequency=45 times), and also frequently received approaches from them (total frequency=34 times). Adult males received the most approaches from juveniles (total frequency=68 times). Although adult males directed the most approaches toward adult females, they received the most approaches from juveniles. Adult males were also observed in other affiliative interactions with juveniles. For instance, adult males spent the most time in body contact with juveniles (53.21% of total body contact time), more than they did with adult females (33.92%). Subjects comparatively interacted to a much lesser extent with other adult males, subadult males, and especially infants. In fact, they interacted the least with infants. It should be noted that adult males are the recipients of affiliative interactions more than they are the initiators. For instance, they received more grooming than they directed, and received approaches more regularly than they directed them (for all age/sex classes).

The sex/kinship class of adult interactants was examined, and it became apparent that adult males frequently interacted with unrelated adult females. Adult males spent the majority of their social grooming time receiving grooming from them (48.98% of total social grooming time with adults). Also, adult males spent a great deal of time in body contact (68.06% of total body contact time with adults) with unrelated adult females. Adult males most frequently directed approaches toward (total frequency=38 times) and received them from (total frequency=48 times) unrelated adult females. Adult males spent very little time with adult matrilineal kin of either sex. They were rarely observed in social grooming activity with related adult males (received grooming=3.38% of total social grooming time with adults), and related adult females (directed grooming=1.54%, received grooming=4.61% of total social grooming time with adults). Adult male subjects were never observed in body contact with related adult males, and were infrequently found in body contact with related adult females (18.70% of total body contact time). Lastly, adult

males rarely directed approaches toward and received them from related adult males (received - total frequency=2 times) and related adult females (directed- total frequency=4 times, received - total frequency=4 times). So it seems that when adult males did interact with kin, it was most often with adult female kin.

These findings are generally consistent with the existing data on Japanese macaque social dynamics. For instance, in her study of the same colony of Japanese macaques in the birthing season, Ehardt (1991) found that the majority of affiliation by adult males (males eight years of age and older) was with adult females. She also found that overall affiliation between adult males and all other troop members during the birth season was quite limited. Ehardt reported that in interactions, preference for kin was highly restricted and that when males did affiliate with relatives, adult female kin were the preferred age/sex class.

Juveniles were also observed interacting a great deal with adult males in this study, both affiliatively and agonistically. These close associations that adult males form with adult females and juveniles has been documented in other studies (Sade, 1972; Oki and Maeda, 1973; Mori, 1975; Takahata, 1982a). Takahata (1982a) conducted a study of the Arashiyama B Troop of Japanese macaques in Japan in several nonmating seasons. He found that adult females were the favoured grooming partner of adult males, and that juveniles were the adult males' next favoured grooming partner. Takahata suggested that this affiliation between adult males and juveniles "may be regarded as a kind of paternal care" (Takahata, 1982a). Takahata is making the assumption that these animals recognize paternal relatedness. However, research in genetic testing for paternity is just beginning and there is no indication that even the animals know their paternal relatedness to other animals (Pavelka, 1993). Takahata also stated that most grooming bouts between adult males and juveniles can be ascribed to the fact that the juvenile's mother had a peculiar proximate relation (see Chapter one) with the male.

In this study, although their interactions with juveniles were readily observed, adult males rarely interacted with infants. Infants were the initiators of all social interactions (adult males received approaches from infants, but never directed approaches at them). Also, adult males were rarely found in body contact with infants and were never found in social grooming bouts or social play with them. In fact, adult males appeared uneasy in the presence of young infants (several months of age). The mothers often were observed to quickly retrieve their infant if it ventured too close to an adult male. This finding is also consistent with published data. In her study, Ehardt (1991) found that adult males had a preferential active affiliations with adult females without neonates (especially apparent with nonkin adult females) in the birthing season. Ehardt also reported that especially when they are quite young, adult males show exaggerated avoidance and appeared startled if infants approached the male unexpectedly (Gouzoules, 1984; Ehardt, 1991). This is not unusual since males in many Old World primate species have little intensive affiliation with infants (Fedigan, 1992).

The findings of this study show that the majority of positive affiliative interactions by adult male subjects were with unrelated adult females, but affiliation between adult males and other age/sex classes (especially juveniles) was observed. Adult males favourably interacted with adult females and juveniles, though as stated earlier, their interactions with infants were limited. Also, they rarely interacted with subadult males and adult central males. This is not surprising because among rhesus macaques, adult troop males have been found to rarely exchange grooming with one another (Sade, 1972; Drickamer, 1975). However, affiliative relationships among males have been reported for some troops of macaques (Kaufman, 1967; Sugiyama, 1971; Koyama, 1974; Furuichi, 1985).

It was interesting that for all affiliative interactions with all age/sex classes, adult males were the recipients of these interactions more than they were the initiators. This is

not extraordinary, because it has been reported that adult males tend to be groomed by females more than they groom them (Oki and Maeda, 1973, Takahata, 1982a). The pattern of grooming has been reported to be differ depending on the season. Furuichi (1985) found that females tended to groom males more frequently than males groomed females in the mating season. In the nonmating season, he found that males tended to groom females more frequently than females groomed males.

This colony is unusual in that most of these adult males have extensive matriline within their troops, and normally Japanese macaque males emigrate from their natal groups as adolescents or subadults. Although there were many adult female relatives available, adult males preferentially participated in active affiliation such as grooming with nonkin adult females. This is consistent with other studies of this colony (Ehardt, 1991), the Arashiyama East Troop in Japan (Grewal, 1980; Takahata, 1982a) and with data from rhesus macaques (Missakian, 1974; Ehardt and Bernstein, 1987) that suggest dissociation from kin by maturing males.

The close social bond between females in female-bonded Old World monkey species has been readily described (see Fedigan, 1992). The findings of this study suggest that while males dissociate from their kin, they still may become well-integrated into the social structure. It can even be suggested that their relationships with adult females, who form the stable core of the group, will be a key factor in their integration (Hill, 1990). Therefore, the findings of this study indicate that social bonds exist between adult males and adult females *outside* of the mating season. In the mating season, Japanese macaques mate in the context of consort bonds (Fedigan, 1992). A consort is an exclusive sociosexual bond that forms usually between an adult male and adult female, and is present in a number of primate species, particularly species characterized by the series mounting copulatory pattern (see Fedigan, 1992, Pavelka, 1993). A mating pair enters this

prolonged intense relationship that is characterized by mutual proximity, traveling, eating, agonistic support, and may last from several hours to a several weeks (Pavelka, 1993).

There is also evidence that affiliative relationships between males and females exist outside of the mating season (see Takahata, 1982a; Smuts, 1985). Although this study did not examine individual relationships between adult males and adult females, the occurrence of affiliative relationships between adult males and anestrus females is clear. A number of studies of macaques and baboons have noted the occurrence of such affiliative relationships (see Hill, 1990). Among the Japanese macaques in the Arashiyama East colony in Japan, several affiliative relationships lasted for as long as ten years (Takahata, 1982a). The existence of such nonsexual relationships have been proposed to have many advantages for both individuals involved. It has been suggested that this relationship between an adult male and adult female may increase the likelihood of mating in some cases, but there seems to be no apparent effect on the quality of subsequent consortships (see Hill, 1990). Hill (1990) has stated that other advantages of this affiliative nonsexual relationship (for females) may be male protection of females, females benefit from potential support of the male, protection of the female's immature offspring, and preferential access to resources due to the relation a female has with a male. The evidence for apparent benefits of these relationships to the participants are inconclusive, but in any case, there may be long-term benefits that were not detected.

Agonistic Interactions

During the study months, there was little aggression at any level in this colony. In fact the aggression that was present was commonly quite low in intensity. That is, most aggression involving adult males took the form of visual and vocal threats, lunges, charges, and chases. Only one case of aggression with observed wounding was recorded. This happened when an adult male directed one instance of level 4 aggression toward an unrelated adult female. The recorded aggression commonly occurred between adult males

and adult females, and between adult males and juveniles. Generally, adult males directed aggression, at all levels, much more than they received it.

Most of the aggression that adult males directed was toward juveniles (level 1=33 times, level 2=57 times, and level 3=23 times). They also frequently directed it toward adult females (level 1=24 times, level 2=44 times, and level 3=22 times). The aggression that adult males directed toward juveniles and adult females usually took the form of noncontact aggression with movement (level 2). Adult males very rarely directed aggression toward infants, and clearly received no aggression from them. In fact, adult males most often received aggression from adult females (level 1=28 times, level 2=6 times, and level 3=7 times). While juveniles were the most common recipient of adult male aggression, they were found rarely to direct aggression toward adult males (level 1=5 times, level 2=4 times). Also, male-male aggression was rare (direct level 1=3 times, direct level 2=3 times, direct level 3=1 time; receive level 1=2 times, receive level 2=10 times, and receive level 3=1 time). Not only did adult males direct more aggression than they received, they directed higher intensity (or more severe) forms of aggression than they received. Adult males most commonly received the mildest form of aggression (low intensity, noncontact stationary aggression) from all age/sex classes.

The results of this study show that adult males rarely direct aggression toward infants (and never received any aggression from them). This is consistent with what has been reported for most nonhuman primate species, where except in cases of infanticide, young infants neither perform aggression nor receive it from other group members (Walters and Seyfarth, 1987). Also, the adult male Japanese macaques in this colony show a non-agonistic relationship with other adult males. In the nonmating season, it can be concluded that there is a relatively small proportion of agonistic behaviour involving adult males. Furuichi (1985) stated that in the nonmating season, the infrequent occurrence of agonistic interactions between adult males contrasts sharply with their behaviour in the mating

season. He also noted that the suppression of inter-male aggression in the nonmating season may be one of the factors which encourage males to choose to reside in the troop throughout the year. Furuichi suggested that aggression between individuals is mainly restrained by the inhibition of the subordinate, and relatively larger social distances are maintained between individuals.

The affiliative relationships that are formed between adult males and adult females are coupled with a relatively low incidence of low-intensity aggression. A related finding noted by Cheney and Seyfarth (1990) was that aggression among relatives is quite common in most primate species. It is understandable that since adult males spend a great deal of time with adult females, they also come into conflict with them the most. The tendency of high levels of affiliation being combined with instances of conflict is similar to what is described for female-female kin interactions (Pavelka, 1993).

This relatively peaceful nonaggressive picture of the nonmating season is supported by the existing research. The nonmating season in macaque species contrasts sharply with the mating season. The mating season is characterized by a unique repertoire of behaviours (for example, the behaviours involved in the four stages of female courtship of males) and physiological changes (for example, the Japanese macaques in the study colony get redder faces and/or perineum) exhibited by both males and females (Pavelka, 1993). In Japanese macaques, the most obvious behavioural change in the animals during the mating season is suggested to be the dramatic increase in the frequency with which males chase females (Enomoto, 1981). It has been reported for macaque species that during the mating season, males often act aggressively toward females (Kurland, 1977: *M. fuscata*; Eaton, 1974; Drickamer, 1975: *M. mulatta*; Teas *et. al.*, 1982). Additionally, male attacks on females have in some instances resulted in serious wounding (Carpenter, 1942; Enomoto, 1981). In fact, wounds and injuries, particularly in females, increase noticeably during the mating season (Pavelka, 1993). Furthermore, an increase of male aggression toward females in

the mating season has been reported in several nonhuman primate species (see Smuts and Smuts, 1992).

VARIATION IN ADULT MALE BEHAVIOUR

Several variables - a male's age, dominance rank and troop membership - were examined to determine whether they influence a male's behaviour. Age, dominance rank and troop membership were not expected to have an independent effect on the behaviour of the subjects. Each of these variables will be discussed in turn.

Variation due to Age

The ages of adult male subjects were analyzed to establish if there were any significant correlations with behaviour. It can be concluded that in this colony of Japanese macaques, an adult male's age had some effect on his behaviour. There were no significant differences in the general state behaviours of the subjects according to their age. It has been suggested that with increasing age, males were less often involved in social interactions (van Noordwijk and van Schaik, 1988). However, in this study it was found that the age of the subject animal had little effect on affiliative and agonistic interactions with various age/sex classes. The influence that age did have on behaviour concerned interactions that adult males had with subadult males. Younger adult males were found to spend more time directing ($r_s = -0.474$, $p = 0.040$) and receiving grooming ($r_s = -0.554$, $p = 0.014$) from subadult males, directed approaches more toward subadult males ($r_s = -0.515$, $p = 0.024$), and also were in body contact with subadult males substantially more than older adult males ($r_s = -0.527$, $p = 0.021$). Another finding is that older adult males received more approaches from infants ($r_s = 0.669$, $p = 0.002$) and unrelated adult females ($r_s = 0.535$, $p = 0.018$) than did younger adult males.

There was only one significant association between age and agonistic behaviour. Younger adult males directed level 2 aggression (noncontact aggression with movement)

toward unrelated adult males more often than did older adult males ($r_s = -0.493$, $p = 0.032$). Although several other correlations concerning older adult males existed, the majority of significant correlations between age and behaviour involved young adult males. In other words, age had a greater impact on the behaviour of young, rather than older adult males.

There is an age homophily (tendency to interact with age-mates) for this class of younger adult males. Younger males interacted the most with subadult males (males aged 5-7 years of age). This is not surprising because males starting as early as 2 or 3 years of age play and spend time with age mates as they grow older (Sugiyama, 1976). The other interesting finding was that older males were approached by infants more than younger ones were. It has been reported in free-ranging Japanese macaque groups that associations between infants and adult males involved mainly older, higher-ranking males (Itani, 1959; Hiraiwa, 1981).

Variation due to Dominance Rank

The dominance ranks of individuals were examined to determine if they caused any variation in behaviour. In this study, it was found that an adult male's dominance rank had very little effect on his behaviour. In this study, higher ranking adult males received more grooming than males of lesser rank. Adult males who were higher ranking spent more time receiving grooming from subadult males (high=146, medium=0, low=0, $p = 0.026$), and higher ranking adult males spent more time in body contact with subadult males than did medium or low ranking adult males (high=41.5, medium=0, low=0, $p = 0.026$). Some interesting differences were found for agonistic behaviour as well. In general, low ranking adult males received more level 1 and level 2 aggression than did medium or high ranking ones (level 1: high=0, medium=1, low=3, $p = 0.021$; level 2: high=0, medium=0, low=2.5, $p = 0.007$). In particular, low ranking subject animals received significantly more level 1 aggression (noncontact stationary aggression) from adult females (high=0, medium=1, low=2.5, $p = 0.039$), particularly unrelated adult females (high=0, medium=1,

low=2, $p=0.007$), than did medium or high ranking subjects. Also, low ranking adult males received substantially more level 2 aggression (noncontact aggression with movement) than adult male subjects of other dominance ranks (high=0, medium=0, low=0.5, $p=0.039$).

Similar to age, dominance rank had the most impact on interactions involving subadult males. High ranking males received more grooming and were found in body contact more with subadult males than males of lower rank. Thus, young high ranking males affiliate a great deal with subadult males. Also lower ranking adult males received more low intensity aggression from unrelated adult females and subadult males than higher ranking adult males. It is understandable that any lower ranking individual would be an easy target for aggression from other age/sex classes.

It should be noted that dominance is a very complex multidimensional concept. It influences access to resources - animals having the priority of access to desired resources are described as dominant, while those that are displaced from desired resources are described as subordinate (Pavelka, 1993). Although dominance did not impact the behaviours measured in this study, dominance relationships are a major part of the daily lives of these group-living animals. There are very real manifestations of dominance rank differentials in social life (Pavelka, Gillespie, and Griffin, 1991). For instance, it has been proposed that social skills (Bernstein, 1976) and the ability to form coalitions and alliances (Fedigan, 1982) are important factors of dominance rank (see Pavelka, Gillespie, and Griffin, 1991).

Variation due to Troop Membership

Troop membership had very little influence on the variation of adult male behaviour in this colony of Japanese macaques. Main troop and splinter troop subject animals are quite similar in the behaviours measured in this study. However, troop membership was correlated with some variation in general state behaviours: splinter troop animals were more

inactive (main=11654, splinter=15104, $p=0.0073$), spent less time traveling (main=3069, splinter=1992.5, $p=0.1266$), and received less grooming than did main troop subject animals (main=3395, splinter=2196.5, $p=0.0431$). Only two other significant differences between the two troops were apparent. Main troop subject animals received more approaches from subadult males than did splinter troop subjects (main=1, splinter=0, $p=0.0215$). Also, main troop subject animals directed more counts of level 2 aggression (noncontact aggression with movement) toward adult females, particularly unrelated adult females, than did splinter troop subject animals (main=1, splinter=0.5, $p=0.0153$).

The males of the two troops showed little difference in social behaviour. This is interesting since the two troops differ in their size and members. The internal make-up of the splinter troop is consistent with the normal organization of Japanese macaque society (Pavelka, 1993). The splinter troop, like the main troop, is comprised of related females and unrelated males. Yet the splinter troop is much smaller than the main troop. It contains approximately 80 individuals, while the main troop consists of over 500 individuals. Also, the extensive matrilineal lines represented in the main troop are not present in the splinter troop. This is because the splinter troop fissioned from the main troop in 1989, and is not as established as the main troop. Also, proportionately, there are more adult males in the splinter troop than there are in the main troop (the decline in male troop members with age is much more rapid than that of females) (Sugiyama, 1976). In fact from casual observations made, it appeared that splinter troop adult males displayed more adult male-adult male grooming. However, this difference was not found in the quantitative data.

COMMENT ON INTEGRATION OF QUALITATIVE AND QUANTITATIVE DATA

Through casual observation and through discussions with the director of the site, it was thought that splinter troop adult males spent more time in social grooming than did main troop adult males (see above). In fact, it was thought that splinter troop adult males also spent more time in social grooming activity with juveniles. But, as previously stated, the findings proved to be counterintuitive. Furthermore, the quantitative data revealed that splinter troop subject animals received less grooming than did main troop subject animals (main=3395, splinter=2196.5, $p=0.0431$). Other findings derived from the quantitative data are illustrated and substantiated in the qualitative data. Several such findings are discussed below.

The quantitative data showed that the adult males in this study preferentially interacted with unrelated adult female kin. It was also found that it is the females who are the main initiators of these interactions - adult females approach and groom adult males more than adult males approach or groom them. With the exception of Ran, who was born in Japan, all of the adult males are natal males. It is suggested that adult males break the associations with their kin regardless of whether they remain in their natal group or not. During this study, several subject animals were seen regularly affiliatively interacting with a particular unrelated adult female. For example, Kamster (KU657082) was seen commonly to interact with a small young adult female nicknamed Fiona (#32, MA58637489). Kamster and Fiona may be considered to be "friends" - they were consistently found in proximity of one another and were also often found affiliatively interacting with one another. Fiona has a female infant, and on one occasion, Fiona, her infant, and Kamster were seen together in a bush. Fiona was grooming Kamster while he was lying on his back. Meanwhile, Fiona's infant (several months of age) was climbing all over Kamster's stomach. Kamster was quite tolerant of the infant and looked quite relaxed, but Fiona was

cautious and seemed nervous by the situation. While grooming Kamster, she would intermittently glance at her infant. This grooming bout ended when Kamster gave Fiona a facial threat (perhaps for her infants prolonged interaction with him), This was followed by Fiona defensively screaming at Kamster and then quickly retrieving her infant and leaving the area. This was the only recorded incidence of an adult male coming into physical contact with an infant. It is interesting that Fiona was the one initiating the relationship with Kamster. She was always following him, approaching him, and grooming him, yet he was never seen reciprocating any of these behaviours. However, it is important to note that Kamster has been observed approaching and grooming other adult females.

Obe's (MI6484) niece, Skink (#614, MI647184) is the alpha female of the splinter troop. Obe was occasionally seen interacting with Skink, and has been observed to be very protective of Skunk (MI64718491), Skink's juvenile male son. Skunk has been known to carefully pick fights with monkeys and humans whenever his great-uncle Obe is within range (Pavelka, 1993). In this study, Obe was observed affiliatively interacting with Skunk on several occasions. Although it was not possible in this study (since all juveniles were not distinguishable to the observer), it would be interesting to determine whether adult males show a tendency to interact with related juveniles, similar to this example.

It was stated in an earlier section of this thesis that Randy was often found interacting with his female kin. However, he was not the only male seen to socialize with family. Three other males were observed to interact with female kin. These interactions were brief, and were infrequent. Also, the only adult female kin that these males interacted with were their sisters. All three of these males were seen in social grooming activity with their sisters: Bouncer (MA646981) with his sister Finch (#697, MA646984), Dexter (DE6584) with his sisters Art (#811, DE6586) and Dee Dee (#603, DE6583), and Barclay (BE556585) with his sisters Sashie (#933, BE586586) and Skitzzy (#33, BE586577). In

reference to interactions between adult males and kin, it has been suggested that degree of relatedness may be of significance (Ehardt, 1991). Therefore, what affiliative interactions these males do have with kin are restricted and limited, since the affiliative interactions characteristically involve their sisters.

LIMITATIONS AND PRACTICAL CONSIDERATIONS OF STUDY

There are several limitations of this study. First, this study was cross-sectional in nature. Information on the behavioural development through changes that occur as an individual matures was missed because this study was short-term. Also, this study, like other observational research, required the development of research tactics that are particularly suited to its needs (Altmann, 1974). The availability of subject animals during fieldwork is a real concern. In this study, adult male subjects were chosen according to their availability and visibility. This introduces a sampling bias since the sample of subject adult males used was not representative of all of the adult males in the colony (the sample did not include those males that were difficult to find and follow), and were chosen according to an arbitrary criterion (availability). This study was relatively short in duration, and the primary objective was to maximize the information collected. Therefore, adult males that were present in the troop on a day-to-day basis were chosen. However, the intention of this study was to only describe the sample of subject animals, and was not to generalize to any other population. Reliability is another concern. Since the observer did not conduct tests of reliability (within-observer reliability) at regular intervals during the course of the study, the repeatability and consistency of the results could not be ascertained (Martin and Bateson, 1993). Lastly, because many tests were run in this study, the results may be prone to Type 1 Error. The p values are provided for each test result, so it is left up to the reader to make their own adjustments using the Bonferroni procedure.

CONCLUSION

In female-bonded Old World monkey species, males disperse from their natal group. Males do not live their lives in only one social group, so new relationships have to be continually established, and they "do not have the automatic bonds of kinship to structure their social networks" (Pavelka, 1993). It is known that for Japanese macaques, the enduring relationships of maternal kin hold their society together. For females, these relationships guide almost all aspects of social behaviour (Pavelka, 1993). Males, on the other hand, break their matrifocal bonds, and lead a life of group transference. Therefore, the life course patterns of males and females are very different. Since they have a uniform and stable life course, the lives of females in female-bonded Old world monkey societies are well understood.

In contrast, the lives of males in these bisexual groups outside of the mating season are not as well delineated because they are more difficult to study (see Chapter one). Males normally transfer from groups several times in their life and sometimes do not join another group immediately (Sugiyama, 1976). Making this situation more problematic is the fact that it is extremely difficult to study males who disappear from a troop. Thus, partly because of the fluid nature of their lifestyle, there is a lack of studies on adult male intragroup behaviour in female-bonded Old World monkey societies.

The purpose of this study was to explore and document adult male behaviour in Japanese macaques in the nonmating season. In this colony of Japanese macaques, the nonmating season is characterized by affiliative relations between adult males and adult females, and by a low incidence of aggression (compared to the mating season). Though the adult males in this study had extensive matrilineal ties in their resident troop, their daily lives are not organized around female kin. While the kinship bonds among females remain strong throughout their lives, there was a tendency for the adult males in this study to interact preferentially with unrelated adult females. It can be suggested that breaking

associations with maternal kin may be characteristic of an adult male's life, regardless of whether he leaves his natal group or not (Grewal, 1980). So adult males may stay tied to the social group through their interactions with unrelated adult females. However, in this study, it was found that adult males were not the primary initiators of interactions. So it is the unrelated adult females who initiate the integration of adult males into the social structure.

This study contributes to what is known about patterns of adult male social dynamics. With future studies, it would be important to ascertain whether adult males associate with certain kinship groups of adult females. If they do, with how many kinship groups do they interact? Do they associate equally with these kinship groups, or do they show preferences? Also, do they interact with the same kinship groups in the nonmating and mating seasons? Do their relationships with particular kinship groups endure, or are they just temporary? How do their relationships with kin differ qualitatively from those with non-kin? This study shows that there is a significant degree of association between adult males and juveniles. It would be interesting to determine if these juveniles were the offspring of the unrelated females with whom they interacted. It is only now that we are gaining an insight into the diverse and continually changing lives of adult males in female-bonded Old World monkey societies, and with further research their place in the social group can be better understood.

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