

**Social organisation, ecology and reproduction in the Sanje
mangabey (*Cercocebus sanjei*) in the Udzungwa Mountains
National Park, Tanzania**

A thesis submitted in partial fulfilment of the requirements for the degree of

Master of Science in Conservation Biology

at

Victoria University of Wellington

By

Kuruthumu Ally Mwamende

School of Biological Sciences
Victoria University of Wellington

New Zealand

2009

Acknowledgments

This study was funded by the New Zealand Aid for International Development (NZAID). Additional funding for field work was provided by School of biological sciences, Victoria University of Wellington (a research grant to Prof. Alan Dixon), and the Karori Wildlife Sanctuary (part of grant no. 24459/Award 1401 to Dr. Murray Williams). I would like to thank my supervisors Prof. Alan Dixon and Dr. Wayne Linklater, for their support in developing and shaping ideas for this project, before and during field and for their constructive editing during thesis writing. My supervisors also have encouraged and reassured me when I most needed it. I extend special thanks to Prof. Alan Dixon, my primary supervisor, for many useful advices such to ‘watch out-as things can get a little overwhelming’, for being a friend, and who, in his own way demanded my best. For all of this I extend my deepest thanks.

For permission to work in the study area, I thank Tanzania National Parks Authority (TANAPA). The staffs of the Udzungwa Mountains National Park are thanked for their support, and help during fieldwork, especially Mr Matata Mushi, Chief Warden-in-charge, Joachim Tesha, Warden for protection, and Joram Mponjoli, Park Ecologist. Fieldwork would have not been possible without much logistical assistance of rangers from the Udzungwa Mountains National Park.

Various people have contributed both knowingly and unknowingly to my study, and to all I owe a great debt. Thanks to my friends for comments on drafts of the thesis, including Alfian A. Rija and Lisa Bryant, Alfian also helped with data entry. Most data were collected by myself, between December 2007 and June 2008 with the help my assistants unless it stated otherwise. Throughout the entire 6.5 months of fieldwork, I was assisted by Ally Mhambo. Fridolin Mselewa, Sebastian Mvelege and Pius Mwenda provided valuable assistance in collecting ranging behaviour and feeding data. Mselewa, Mwenda and Mvelege also showed me the animal’s most used trails to make sure I don’t spend hours finding a way out in tangled vegetations; without their help the work of following the mangabeys would have been much harder and arduous task. Ruben Mwakisoma is thanked for help in tree identification in the field. In addition, Enock Peter and Eliatosha Mnguu assisted to monitor thermometer and rainfall gauge, arranged field supplies, and cook for us while working in the field. I am very thankful to all of these assistants.

I thank Mr Suleiman Haji of the National Herbarium of Tanzania (NHT) at the University of Dar es salaam for botanical expertise in plant identification. Several experts are thanked for statistical input, as indicated separately in the main chapters, including Nokuthaba Sibanda and Matthew Langen. Thanks also to Stephen Hartley for assistance with GIS and Cameron Jack for help in computer logistics. I also thank Patricia Stein for providing enough working space, and to Marry Murray for making sure we are 'comfortable' during writing phase. Alfian Rija, Fiona Hodge, Lisa Bryant, Mark Heath, Shruti Patel, Heather Murray and Chris Gibbons are thanked for their company, friendship and providing me with stimulating atmosphere and comfortable office. Special thanks to Prof. Dixon and family for their friendship, occasional visit invitations to their house and for making me feel at home in New Zealand. To Dr. Murray Williams, for his advices, and who pushed for funding and arranged travel for me to attend a conference to obtain the most needed experience, for reassurance and for being an interrogator at times. For all this, I extend my deepest thanks.

I also thank the staff at Udzungwa Ecological Monitoring Centre (UEMC) for comfortable accommodation in Mang'ula, and permission to store equipment 'for free' while working in the field. The UEMC's house attendants Shabani and Leonard are thanked for their help and hospitality, especially Leonard who kept the house clean, making it a comfortable place to stay after weekly trips from the forest. Thanks to researchers Drs. Andrew Marshall and Francesco Rovero, Trevor Jones, and Andrew Bowkett working in Udzungwa, for their support, and for sharing the forest work experience. Special thanks to Dr. Andrew Marshall, who introduced me, and for being an inspiration for me to study primates. Last but not least, I thank my husband, my family and friends, for their continued support in numerous ways, including my long time away from home, for their love when I was sick, and for friendship throughout my endeavour despite some of them not fully understanding 'just what drove me to study 'Nyani'.

Finally, to Udzungwa 'Ngolaga' those endangered primates, for tolerating me to study their lives. Without their cooperation, this study would not have been feasible.

Abstract

Understanding of the biology of threatened species is central to effective planning for sustainable management of wildlife. The Sanje mangabey, *Cercocebus sanjei* of Udzungwa Mountains National Park in Tanzania is under pressure from increasing human hunting, and habitat loss threatens its long-term survival. This thesis endeavoured to document the socio-biological and ecological aspects of this little-known species in a small habituated group of 62 individuals within the Mwanihana forest in Udzungwa Mountains National Park.

I studied the social organisation, size and age-sex composition of one group by following and monitoring of the Sanje mangabeys over a six-month period. I also investigated the spatial-temporal interactions and associations between age and sex classes within a group. I assessed the Sanje mangabey's ranging and movement patterns and monitored its reproductive behaviour by examining female sexual skin swellings and relationships between sexual swellings and sexual behaviour. Further, I investigated the species feeding habits and influences of seasonal parameters (rainfall and temperature) upon reproduction, feeding ecology and behaviour of this species.

The Sanje mangabey social organisation is structured in a hierarchy characterised by dominance according to the sex and age of individuals. The study group was composed of individuals of all sexes and age classes; newborn babies, juveniles, sub adults and adults, males and females. Adult males were generally dominant over females and males of lower age. Males showed more agonistic behaviours to juveniles than did females and there were stable linear dominance hierarchies among individuals across the sexes (Landau's dominance index, $h' = 0.92$, $p = 0.0281$) and a high directional consistency index, $DC = 0.91$) for both sexes. The linearity indices' h' were 0.84, $P = 0.041$, $DC = 0.94$ and 0.93, $P = 0.0382$, $DC = 0.94$) for males and females, respectively. Individuals spent about 8% on average of day grooming each other and the rate of grooming differed across and within sexes and age classes. There was a significant relationship between duration of the initiator's first grooming episode and subsequent reciprocation by the receiver in all age classes ($P < 0.05$). The independent effects of total grooming duration of the initiator also showed a significant difference and predicted total grooming duration of the recipient ($P =$

0.0001). However, there was no evidence for grooming to be directed towards higher ranking Sanje mangabeys. The Sanje mangabey's home range was 301 hectares and exhibited a mean daily range of 1760 metres within the Mwanihana forest. The range and movement patterns of this species differed significantly between seasons of the year. During the dry season (no rain) the group covered larger distances ($P = 0.001$) between forest patches and moved significantly faster ($P = 0.001$) than during wet (rain) season.

The Sanje mangabey is omnivorous, feeding on plant material, invertebrates and vertebrates such as lizards. There were marked influences of temperature and rainfall on the feeding patterns. Mangabeys utilised the arboreal layer (>16m high) during cool and wet periods and were observed feeding mostly on the ground resources during hot and dry periods. The reproductive potential and social behaviour of the Sanje mangabey, however, did not vary with the different seasons of the year.

Sanje mangabeys have a mean swelling cycle length of 32.1 ± 2.4 days. Individual females showed differences in swelling duration ($F = 12.43$, $P = 0.043$) and no evidence of group variation in cycle length ($H = 30.2$, $DF = 6$, $P < 0.05$) was seen. Maximum swelling lasted for 4.4 ± 0.9 days on average and detumescence was 14.7 ± 3.9 days. The mean menses length was 3 ± 0.2 days ($n = 3$). Most cycling females, showed days with regular swellings of both sizes. The gestation length averaged 173 days and the interval between birth and resumption of the swelling cycle was observed to be 184 days. The sexual skin swellings appear to be sexually attractive signals of female reproductive condition. Although mating occurred in all stages of the female cycle, a peak was observed during maximum swelling size and breakdown. These findings illustrate the utility of sex swellings as signals used by males to determine reproductive condition.

Key words: Social organization, associations, ranging, dominance, sexual skin swellings, sexual behaviour, social behaviour, reproduction, *Cercocebus sanjei*, Mwanihana, Udzungwa Mountains National Park.

CONTENTS

Acknowledgements.....	
Abstract.....	
Chapter 1:	
Introduction.....	14
Social systems and social organisation.....	14
Taxonomy and Phylogeny.....	17
The Sanje Mangabey- What is known.....	18
Issues at stake.....	20
Study site.....	22
Eastern Arc Mountains.....	22
Udzungwa Mountains.....	23
Study group.....	25
Chapter Outlines and Objectives.....	26
Chapter 2: Social organisation.....	26
Chapter 3: Sanje mangabey feeding ecology and seasonal parameters.....	27
Chapter 4: Sexual behaviour and female reproductive biology.....	27
Chapter 5: Summary of findings and conservation context.....	28
Chapter 2: Social organisation, group size, age and sex composition, and ranging behaviour.....	
Abstract.....	29
Introduction.....	31
Group size and composition.....	31
Population density.....	32
Ranging behaviour.....	33
Social dominance.....	35
Grooming.....	36
Male-infant affiliations and allomothering.....	38
Methods.....	38
Study site.....	38
Study group.....	39

Group size and composition.....	39
Population density.....	41
Ranging behaviour.....	43
Spatial organisation.....	44
Focal animal sampling.....	44
Behavioural observations.....	45
Data analysis.....	46
Group size and population density.....	46
Ranging behaviour.....	47
Dominance relationships and competition.....	49
Nearest neighbour.....	50
Affiliative relationships.....	50
Results.....	51
Group size and composition.....	51
Population density.....	53
Detection probability, encounter rate and cluster sizes of mangabeys.....	54
Ranging behaviour.....	55
Daily path length, patterns of movement and seasonal variation.....	55
Home range.....	56
Variations among methods and between seasons, and core area use.....	57
Agonistic behaviour and social dominance.....	58
Summary of agonistic behaviour.....	58
Dominance.....	62
Linearity and directional consistency in dominance.....	63
Spatial/ affiliative relationships.....	65
Grooming.....	66
Grooming rates among age-sex classes.....	67
Rank distance among adults and grooming.....	68
Time matching within reciprocated grooming bouts.....	68
Male and female-infant relationships (infant carrying, attractiveness of infants and allomothering).....	69
Allomothering and male mounting success.....	70
Discussion.....	71
Group size and age-sex composition.....	71

Seasonality.....	72
Population density.....	73
Ranging.....	74
Dominance.....	77
Affiliative relationships.....	78
Grooming.....	78
Allomothering, infant carrying attractiveness of infants.....	81
Appendix 1. Ethogram: Activity categories and behaviour definition.....	83
 Chapter 3: Habitat, feeding ecology and seasonal parameters.....	86
Abstract.....	86
Introduction.....	87
Feeding ecology.....	87
Wet and dry seasons.....	88
Methods.....	89
Study group and site.....	89
Feeding observations.....	89
Habitat sampling.....	90
Plant Identification.....	91
Climatic patterns.....	91
Data analysis.....	92
Diet selectivity.....	92
Habitat use, food tree density and abundance.....	93
Climatic data.....	93
Results.....	93
Feeding behaviour.....	93
Food tree density.....	98
Patterns of rainfall: Wet and dry seasons.....	99
Temperature.....	100
Discussion.....	101
Seasonality and feeding behavior.....	103
Climatic patterns.....	103
Chapter 4: Sexual behaviour and reproductive status.....	104

Abstract.....	104
Introduction.....	105
Methods.....	108
Study group.....	109
Female Sexual skin swellings.....	109
Female reproductive status and the menstrual cycle.....	109
Pregnancy and lactation.....	111
Ovulation and duration of swelling cycle (cycle length).....	111
Patterns of births, infants in the group and breeding season.....	112
Sexual Behaviour.....	113
Data analysis.....	114
Results.....	116
Morphology of sex skin /appearance of the perineum.....	116
Cycle length and other reproductive parameters.....	118
Pregnant and lactating females.....	122
Swelling changes during late pregnancy and lactation.....	126
Sexual behaviour.....	126
Mounts and female reproductive cycle.....	127
Male mates during swelling maximum size.....	132
Copulation calls.....	134
Copulation calls and male dominance.....	136
Reproductive/breeding seasonality.....	137
Discussion.....	138
Sex skin morphology and reproductive cycle.....	138
Menstruation and cycle phases.....	139
Irregular cycles.....	140
Gestation period, lactational amenorrhoea and post-conception swelling.....	141
Sexual behaviour during menstrual cycle and theory of sex skin functions.....	143
Copulation calls and male dominance.....	144
Breeding seasonality.....	144
Conclusion.....	145
Appendix 1.....	146

Chapter 5: Summary of findings and conservation context.....	147
Social organisation, Group size, age and sex composition.....	147
Ranging behaviour.....	148
Social relationships.....	149
Feeding ecology: Diet and food selectivity.....	151
Female reproductive biology and sexual behaviour.....	152
Conservation concerns which impact the Sanje mangabey population.....	154
References.....	156

LIST OF TABLES AND FIGURES

TABLES

Table 2.1. Total age and sex composition of Njokamoni group of mangabeys.....	
Table 2.2. Model performance and mangabey density estimate selection statistics. A robust model is shown with an asterisk (*).....	
Table 2.3. Mangabeys encounter rate (mangabeys/ km ²), cluster size, population density and density of clusters during one year samples for 3 transects in Mwanihana.....	
Table 2.4. Total aggression with (fleeing) matrix for adult and sub adult male and females. Adult and sub adult males (first 7 in the row and column) and adult and sub adult female are shown in the following row and column. Aggression initiators are given by row individuals and receivers by column individuals.....	
Table 2.5. Frequency of total aggression without fleeing. Receivers are given by row individuals and initiators by column individuals.....	
Table 2.6. Dominance matrix for adult and two sub-adults males.....	
Table 2.7. Dominance matrix for adult and two sub-adults females.....	
Table 2.8. Scaled ranks, rank order and rank categories for 10 adult and two sub adult females.....	
Table 2.9. Scaled ranks, rank order and rank categories for 5 adult and two sub adult males.....	
Table 2.10. Summary of individual follows.....	
Table 2.11. Summary of grooming bouts.....	
Table 2.12. Rates of grooming (seconds per hour), between adult females.....	
Table 2.13. Rates of grooming (seconds per hour), between adult males.....	

Table 3.1. Plant species consumed by Sanje mangabey in December 2007 to June 2008.....	
Table 4.1. Female identification name, code, and number of cycles analysed (cycles N=33; cycling females N=7).....	
Table 4.2. Duration of tumescent, maximum and detumescence swelling phase for each female's individual cycle.....	
Table 4.3. Reproductive parameters in wild Sanje mangabey.....	
Table 4.4. Irregular cycles and their possible correlates.....	
Table 4.5. Numbers of mounts with intromission initiated by males (in red) and in response to female invitations (in black).....	
Table 4.6. Intromission mounts, mounts with ejaculation, intromission thrust and intromission duration of males with 7 female in relation to their ranks.....	
Table 4.7. Total number of male partners during maximum swelling size for each female cycle.....	
Table 4.8. Total copulation calls (black) and intromissions (in red) in relation to male mates.....	
Table 4.9. Inter-species comparison of reproductive cycle characteristics.....	

FIGURES

Fig. 1.1. Photographs of adult <i>Cercocebus sanjei</i> (a) male (b) female.....	
Fig. 1.2. Map (a) Eastern Arc forests in Tanzania and Kenya (b) Eastern Afromontane forests (in red).....	
Fig. 1.3. Udzungwa Mountains National Park showing location of the study site (Mwanihana forest) and distribution of Sanje Mangabeys across forest fragments in which they occur. No Sanje mangabey sightings have been recorded in the circled area.....	
Fig. 2.1. Map of the Udzungwa Mountains showing Mwanihana and other forest blocks (in black) and the National Park (in grey).....	
Fig. 2.2a. Histogram of perpendicular distances showing detection probability.....	
Fig. 2.2b. Frequency histogram of truncated perpendicular distance distances.....	
Fig. 2.3. Mean age and sex composition of Njokamoni mangabeys as of December 13 2007 to 24th June 2008.....	
Fig. 2.4. Relationship between mean distances travelled and amount of rainfall.....	
Fig. 2.5. A sample of output polygons from Calhome, generated on Excel using sample data set showing 95% utilization distributions for both Minimum Convex	

Polygon, MCP (top) and Adaptive Kernel, ADK (below) methods used to calculate home ranges. Figures on the left refer to the dry season. The dry and wet season ranges are shown on the right. The grid size for both polygons is 500m.....

Fig. 2.6. Adaptive Kernel output all points polygon showing 4 distinct core area of the home range used by Njokamoni group. Grid size = 500m.....

Fig. 2.7. Total aggression by different classes of the Njokamoni group. Note: M = Males (5 adult & 2 sub adult males), F = Females (10 adults and 2 sub adults), J = Juveniles (4 large juveniles & 4 small juveniles) and I = Infants (3 infants).....

Fig. 2.8. Association among Sanje mangabey age-sex classes, Simple rati association index was used to calculate associations between adult females and males (F & M), sub adults females and males (S), and infants (I) frequencies of the total observation time between individuals that were nearest neighbours.....

Figure 2.9. Rates of grooming (sec/hour) among age-sex classes. M: Adult males (n = 5), F: Adult female (n = 10), S: adults (n = 4), J: Juveniles (n = 8) and I: Clinging infants (n = 3).....

Fig. 2.10. Log total recipient grooming time and the initiator: There was significant relationship between the grooming time of initiator and that of recipient ($P < 0.0001$).....

Fig. 2. 11. For 5 adult males and 2 sexually reproductive sub adult males, there was a strong, positive, but non significant relationship (Pearson's $r = 0.7$, $p = 0.09$) between total allomothering performed and the number of mounts accepted by all 7 cycling females.....

Fig. 3.1. Other food items consumed by Sanje mangabey.....

Fig. 3.2. Percentage time feeding on each food item (a, Leaves; b, reproductive parts; c, invertebrates and fungi; and d, shoots and stems).....

Fig. 3.3. Rainfall patterns for Mwanihana forest in July 2007 to June 2008.....

Fig. 3.2. Mean monthly temperature in Mwanihana forest from July 2007 to June 2008.....

Fig. 4.1 Diagram showing the morphology of Sanje mangabey sexual swelling at full size (+3).....

Fig. 4.2. Photograph of a wild Sanje mangabey sex skin showing swelling stages: (a) Small (+1) (b) Medium (+2) (c) Maximum (+3) and (d) Detumescence (-2).....

Fig. 4.3. Ten individual females swelling profiles during the entire study period (178 days) for 3 lactating females KMH, KL, KM and 6 cycling females, CT, BMS, SN, MDK,MWK,MT and BMK.....

Fig 4.4. Male Sanje mangabey copulatory behaviour.....

Fig. 4.5. Mean number of presentations (top), male's inspection of sex skin (middle) and copulations (bottom) during small (+1), medium (+2), maximum (+3) and detumescence (-2 & -1) stage.....

Fig.4.6. Changes in swelling size morphology and sexual interactions of female BMK with male AMr - rank 1 (o), AMb –rank 3 (*) and AMk –rank 4 (+). Symbols show ejaculatory mounts (in red) and attempted mounts (in green).....

Fig. 4.7. Relationship between ejaculatory mounts and stage of skin swelling, top (a)) mean total ejaculatory mount in all stages, (b) bottom, Ejaculatory mounts per cycle stage and per phase per day.....

Fig. 4.8. Individual female copulation calls in relation to swelling stages.....

Fig. 4.9. Relationship between copulation calls and swelling stage for all 7 females....
.....

Fig. 4.10. Copulation calls given by female Sanje mangabey during and immediately after mating with different males are significantly related to male dominance rank ($P=0.0012$).....

1. INTRODUCTION

Social systems and social organisation

The diversity of primate social systems have been compared by the differences in spacing, grouping, mating patterns and the variability in patterns of social relationships (Clutton-Brock, 1974; Clutton-Brock & Harvey, 1976; 1977; Crook & Gartlan, 1966; Kappeler & van Schaik, 2002; van Schaik, 1983; van Schaik & van Hooff, 1983; Wrangham, 1987). Less is known, however, about social diversity within many species (Sterck, 1999). A society can be defined as a network of relationships between members of a social unit. Kappeler & van Schaik (2002) define a social system or society as a set of conspecific animals that interact regularly with each other, and explain social organisation as a term describing the size, sexual composition and spatio-temporal cohesions of a society. Social organisation also describes how animals treat conspecifics and non conspecifics, and how activities are coordinated in a particular social unit.

The Papionini (baboons, mandrills and mangabeys) is a diverse group belonging to the family Cercopithecidae (Kappeler & van Schaik, 2002). They inhabit a wide range of habitats, from arid regions to evergreen tropical rainforests, with some species able to utilize both environments or adapt to areas where only forest fragments remain (Chalmers, 1968; Chapman *et al.*, 2005; Freeland, 1980; Olupot *et al.*, 1994; Olupot *et al.*, 1997; Onderdonk & Chapman, 2000; Struhsaker, 1997; Wasser, 1993; Wiczkowski, 2005b). Habitat diversity among populations of African papionins is almost as great as interspecific differences. Most African Papionins are either semi-terrestrial or terrestrial.

Mangabeys occur in both continuous evergreen, swamp forests and in areas where only patches of forest remain, from Gabon in West Africa to eastern Africa (Chalmers, 1968; Mc Graw & Fleagle, 2006). Mandrills are found only in a few equatorial West-central African rainforests (Mc Graw & Fleagle, 2006). Baboons occur in non-overlapping geographical ranges of sub-Saharan Africa (Campbell *et al.*,

2007; Groves, 2006). Baboon ranges, however, are often connected, leading to interbreeding between species (Brain, 1990; Elton, 2007; Jolly, 2007).

Mangabeys, baboons and mandrills share many features of their anatomy and physiology, but they are behaviourally diverse which makes them an excellent group in which to study primate social systems (Groves, 2001; Hill, 1969; 1970; 1974; Jolly, 2007; Maestriperi, 1998; Mc Graw & Fleagle, 2006). Despite some clear differences in their social behaviour, African Papionins share many features in their ecology. All African Papionins are opportunistic omnivores, capable of living on whatever vegetable or animal foodstuffs available. They all coordinate their foraging activities within their social groups (Fraser & Plowman, 2007), usually sleep in one site and often form larger temporary associations at a favoured foraging or sleeping site (Bolwig, 1978; Jolly, 2007). The various species, however, possess different dietary and foraging tactics, which are reflected in adaptations of their masticatory and digestive systems (Chalmers, 1968; Daegling & Mc Graw, 2007; Hoshino, 1985; Mc Graw & Fleagle, 2006).

In most groups of African Papionins, females remain in their natal group and males emigrate to another group before sexual maturity and may migrate again during adulthood (Alberts & Altmann, 1995). Patterns of association in African Papionins comprise a network of relationships, some transient, others permanent. For example, mothers and the female offspring often interact to adulthood, resulting in a cluster of related females or matriline. Because males migrate, kin-based interactions among males are rare (Alberts, 1999; Altmann, 1979; Altmann *et al.*, 1996; Charpentier *et al.*, 2004; 2007; Kappeler & van Schaik, 2002; Reynolds, 1968).

The relationship between males and females of reproductive age is categorised as either consortship or friendship. The former involves interactions and temporary mating associations between an adult male and female (Jolly, 2007). Friendship involves close, long-term, relaxed and hedonic relationships between an adult male and one or more females and their immature offspring (Smuts, 1985). When the association of partners is coincident, harems are formed, this is apparent in groups of Hamadryas (*Papio hamadryas*) and Guinea baboons (*P. papio*). Social behaviour and social relationships requires understanding social roles and system of communication.

The relative amount of adult males and females has been used as a criterion for distinguishing group-living species (Kappeler, 2000). Presence of females determines presence of males in multimale-multifemale groups (Altmann, 1990; de Ruiter & Geffen, 1998; Wrangham, 1980). The temporal overlap of female receptive periods has predicted the number of males in such groups after controlling for female number (Nunn, 1999b). Kappeler (2000) has also used variations in group cohesion to provide finer characteristics of groups with multiple males and females. Group members can either be relatively cohesive or exhibit temporal variation in group cohesion e.g. in fission-fusion groups (Strier, 1992).

Habitat loss and degradation due to anthropogenic influences has direct impacts on natural movement patterns, limiting the amount of space available for animal use and species distribution (Brain, 1990; Burgess *et al.*, 2007a; Struhsaker, 1997). Resource use and climatic changes also influence the ranging behaviour of primates, and these effects may be pronounced if the animals live in a previously disturbed forest or where the preferred resources are uncommon in that environment. Primates living in threatened habitats may respond to changes in ecological conditions in different ways (Marshall, 2007; Struhsaker, 1997). For example, as a strategy to increase their foraging efficiency, they may travel to non-forest habitats (Freeland, 1980; Wieczkowski, 2005b), and due to scramble competition they may deplete certain forest patches. They can also increase levels of aggression or reduce foraging group sizes (Buzzard, 2006; Isbell, 1991; Onderdonk & Chapman, 2000; Snaith & Chapman, 2005).

Another aspect of Papionin societies is social dominance. Social dominance is an asymmetrical power-based relationship that is maintained by force or threat (Bernstein, 1981). Dominant individuals are capable of displacing others from resources that are desired by all (e.g. mating opportunities, favoured sleeping places or food). A decision to fight or retreat is based on having learned the outcomes of previous encounters with the opponent (Bernstein, 1966; 1981; 2007; Bernstein *et al.*, 1983). An escalation of conflicts in a group selects for priority-of-access behaviours (based on dominance) required to resolve the conflicts without costs of overt

aggression (Bernstein, 1966; 1981; 2007; Bernstein *et al.*, 1983). Hierarchies are therefore important to limit injury and conflict.

Awareness of the dominance-defined system is expressed by non-hostile and vigilance or 'attention structure' behaviours (Chance, 1967). For example, low ranking animals spend time and energy monitoring whereabouts of dominants. Generally, adults are dominant over juveniles and sub-adult and adult males are dominant over females. The offspring may acquire positions in dominance hierarchy adjacent to that of their mothers, and win dominance interactions in the group that they would otherwise lose. It is thought that juveniles achieve and maintain high status through formation of coalitionary support with their female parent, ultimately reducing the effect of competition (Chapais, 1988a; 1988b; Chapais *et al.*, 1991; Harcourt, 1992). Juveniles may also form coalitions with powerful peers e.g. the offspring of high-ranking females (Cheney, 1977).

Taxonomy and Phylogeny

An effort to describe behavioural evolution and socioecological theory also requires understanding the phylogenetic relationships of the species concerned. Various authorities have produced important works on the taxonomy, distribution and zoogeography of the Papionini (Barnicot & Hewett-Emmett, 1972; Colyn *et al.*, 1991; Cronin & Sarich, 1976; Disotell, 2000; Elton, 2007; Hill, 1969; 1970; 1974; Kingdon, 1997). Mangabeys have attracted particular interest among taxonomists (Groves, 1978; 2006; Grubb *et al.*, 2003). Osteologically, mangabeys are members of the baboon-macaque group (Groves, 1996; 2001; Hill, 1974; Pocock, 1925). Based on cranial measurements, mangabeys have been separated into two groups that are accorded generic status: *Cercocebus* containing the semi-terrestrial species, and *Lophocebus* comprising the arboreal species (Groves, 1978; 2001). Molecular reviews by Barnicot & Hewett-Emmett (1972) Disotell (2000) placed *Lophocebus*, *Papio* and *Theropithecus* sister taxa of the *Cercocebus* and *Mandrillus* clade. Terrestrial mangabeys are thus considered to be closely related to *Mandrillus* (Mandrills and drills) than they are to arboreal mangabeys; the former sharing a common foraging regime characterised by hard object foods (Hoshino, 1985; Mc Graw & Fleagle, 2006).

Morphological similarities among many species are, however, not reflected in their macromolecules (e.g. mitochondrial DNA and serum protein). The mangabey situation is a good example of a morphological phenomenon that involved apparent misplacement of two species, *C. albigena* and *C. aterrimus* among the Old World monkeys. New sources of information have therefore been applied to resolve long-standing or unsuspected taxonomic controversies. Molecular data provide an important and independent source of phylogenetic information (Disotell, 2000). Subsequently, primate systematists have constantly been revising primate groups e.g. (Groves, 2001; 2004; Grubb *et al.*, 2003).

The Sanje mangabey was described by Homewood & Rogers in (1981) and classified as a subspecies of the Tana River mangabey (*C. galeritus sanjei*). In 1996 Groves showed that this mangabey was validly named *C. galeritus sanjei*. However, considering macromolecular (DNA, serum protein and allozymes) and craniometric evidence as well as external morphology, this mangabey has been classified at the species level (Groves, 2001). Presently, 4 species of *Cercocebus* are recognised (Groves, 2001; 2005); the Tana River crested mangabey (*C. galeritus* Peters, 1879), Sanje crested mangabey (*C. sanjei* Mittermeier, 1986), agile mangabey (*C. agilis* Milne-Edwards, 1886) and Red-capped mangabey (*C. torquatus* Kerr, 1792). While Grubb *et al.* (2003) stress the need for a careful genetic-behavioural revision; Groves (2001; 2005) recognises 3 species of *Lophocebus*, the Grey-cheeked mangabey (*L. albigena* Gray, 1850), Black mangabey (*L. aterrimus* Oudemans, 1890) and Apdenbonschi or Southern black mangabey (*L. opdenboschi* Schouteden, 1944). Also, there is a newly discovered species of *Lophocebus*, the highland mangabey (*L. kipunji*) from the forests of south eastern Tanzania (Jones *et al.*, 2005). This taxonomic arrangement will be followed throughout this thesis.

The Sanje Mangabey- What is known?

The Sanje mangabey (Figure 1.1) is a semi-terrestrial, forest- living primate that is restricted to the Udzungwa forests of the Eastern Arc Mountains in Tanzania. Like most other mangabeys, they occur in riverine forest; presumably a refuge habitat to avoid competition with baboons and aggressive guenons (Kingdon, 1997). Sanje mangabeys occur in two populations which are separated by roads, residences, farms

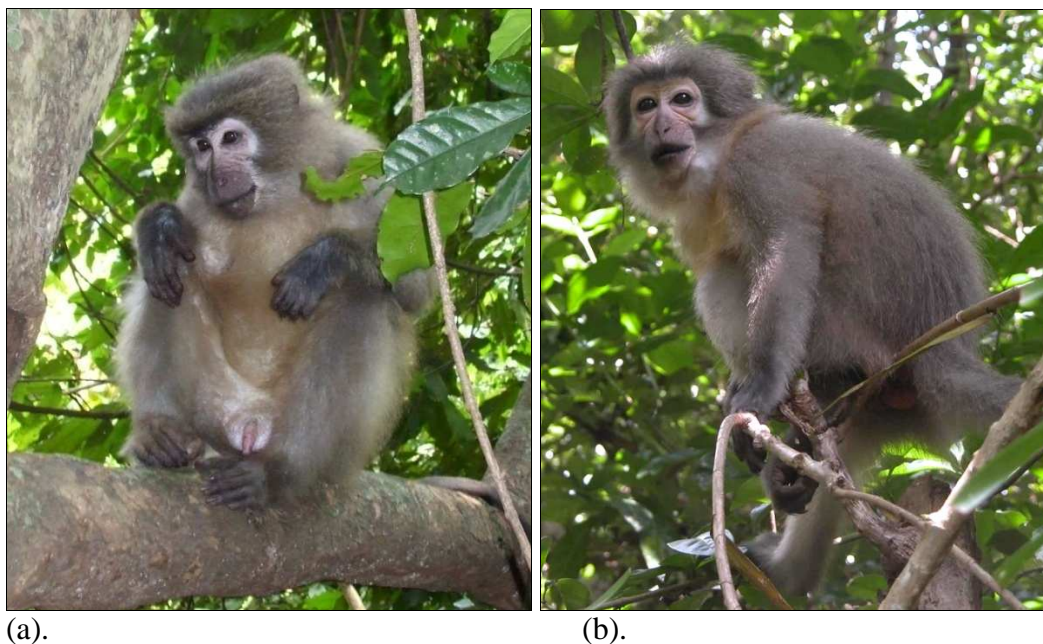
and fire maintained grasslands (Ehardt *et al.*, 2005). Not much information exists regarding *C. sanjei* in the wild and there are none in captivity.

The conservation status of the species shows slow decline in some areas of Mwanihana forest where they were abundant in the past. Although considered relatively poorly known by the International Union for Conservation of Nature and Natural Resources (IUCN), *Cercocebus sanjei* has been listed as endangered (Ehardt *et al.*, 2008). The endangered status is based on the small extent of its distribution and fragmented population. A substantial proportion of the population resides in the Udzungwa scarp forest where protection is limited and there are ongoing threats resulting in decline in habitat and numbers of mature individuals. Across its range, the Sanje mangabey is threatened by habitat loss and degradation due to agriculture, infrastructure development, fires, wood extraction and hunting (Ehardt *et al.*, 2008; Ehardt *et al.*, 2005; Marshall & Wrangham, 2007; Rovero *et al.*, 2006).

Male and female Sanje mangabeys differ in their external morphology. Adult males have more lavish coats, pronounced crests, manes, relatively greater facial length and larger canine teeth than females (Daegling & Mc Graw, 2007; Deputte, 1992; Leigh *et al.*, 2005; Mc Graw & Fleagle, 2006). This species, like many other mammals is sexually dimorphic in body size, the male being the larger sex (Anderson, 1994; Clutton-Brock *et al.*, 1977; Darwin, 1871; Plavcan, 2001). The body mass of male and female Sanje mangabeys is approximately 10.3kg and 5.8kg respectively (Homewood & Rodgers, 1981; Jolly, 2007).

Sanje mangabeys are more dimorphic than are species of *Lophocebus*, but less dimorphic than baboons (Altmann *et al.*, 1981; Jolly, 2007), or mandrills where males are much larger than females. They also differ in hair patterns, and in their extraordinary coloured faces and hindquarters (Dixon, 1998; Setchell & Dixon, 2001a; 2001b; 2002; Setchell *et al.*, 2001). Male Sanje mangabeys display loud vocalisations known as the ‘whoop gobble’ calls. The call communicates intergroup location and may function as spacing signals. Sex differences in the vocalisations of some primates are associated with sexual dimorphism in the vocal tract (Dixon, 1998). Sexually dimorphic traits in primates may have a significant function in mating

systems and group social interaction (Dixon, 1998). There is a need, therefore, to understand the evolutionary and phylogenetic background of such traits.



(a). (b).
 Fig 1.1. Photographs of adult *Cercocebus sanjei* (a) male (b) female

Issues at stake

Because of concerns about disturbance in the Udzungwa and Eastern Arc mountains, previous published studies have focused on documenting the presence, distribution density and habitat quality of this species. These studies provide preliminary ecological information (Ehardt *et al.*, 2005; Rovero *et al.*, 2006). Population viability is often predicted by several, interrelated factors such as group sizes, composition and fluidity, specific diet (type, diversity, flexibility), degree of terrestriality, range size, degree of interspecific competition (niche separation and overlap in keystone resources) and dispersal ability (Fimbel, 1994; Johns & Skorupa, 1987; Marshall, 2007; Marshall *et al.*, 2005; Onderdonk & Chapman, 2000; Thomas, 1991; Tutin, 1999; Tutin *et al.*, 1997; Wilson & Johns, 1982). However, much of this critically important information is not available for the Sanje mangabey.

Estimates of group size and density in Mwanihana have been attempted by various researchers. There are thought to be 0.3 to 0.6 groups per km², with a mean of 10.2 individuals per group. Thus, it is thought that there are 900 mangabeys in the 177km² Mwanihana forest (Dinesen *et al.*, 2001; Ehardt *et al.*, 2005; Wasser, 1993). These

estimates however largely based on very limited information. Ehardt *et al.* (2005) also point out that no basic information exists concerning Sanje mangabey group structure and demography. Group size and age-sex composition estimates are important as far as population viability assessments for conservation decision-making are concerned.

Aspects of social organization such as proximity or how long individuals spend time together are important components as well because social relationships between individual Sanje mangabeys are not known nor how the whole group interacts. Additionally, intraspecific group interactions and responses to one another, especially under conditions of resource variability have never been documented. Dominance, degree of interspecific competition, expression, avoidance and control of aggression in Sanje mangabeys are also worth investigating, since they function to limit injury and conflicts.

Sanje mangabey range size, daily ranging behaviour and range use is unknown. Previous work on another group in the Mwanihana forest indicates that its home range overlapped that of other two groups, and included >200ha of a very diverse habitat (Ehardt *et al.*, 2005). Dietary characteristics, such as composition, diversity and flexibility are also not understood. We do not know what habitats are utilized or the age-sex relationships during feeding. Available information suggests that this species spends approximately 51% of their time foraging on the ground (Ehardt, 2001). However, it is not known how much they are dependent on certain forest layers, or their ability to use secondary forests for resources.

Finally reproductive information, such as frequency and duration of menstrual cycles, sex skin swelling and sexual behaviour of male and female mangabeys, important for understanding their mating systems is entirely lacking.

Overall, for this species, there is little information on its demography, socioecology, reproductive behaviour or the parameters of the forests where they live in. This study was carried out in order to obtain some of these critical data by addressing the following objectives:

1. To examine the social organisation, size and age-sex composition of a social group of *C. sanjei*.
2. To document female sexual skin morphology and examine temporal relationships between sexual swellings and sexual behaviour.
3. To assess and update Sanje mangabey range and movement patterns.
4. Assess spatio-temporal interactions and association between age/sex classes within the group.
5. To collect data on feeding ecology and determine the influence of seasonal parameters on ecology, reproduction and behaviour.
6. To provide new information about an endangered species in a poorly explored area within an international biodiversity hotspot.
7. To make suggestions for conservation management.

Study Site

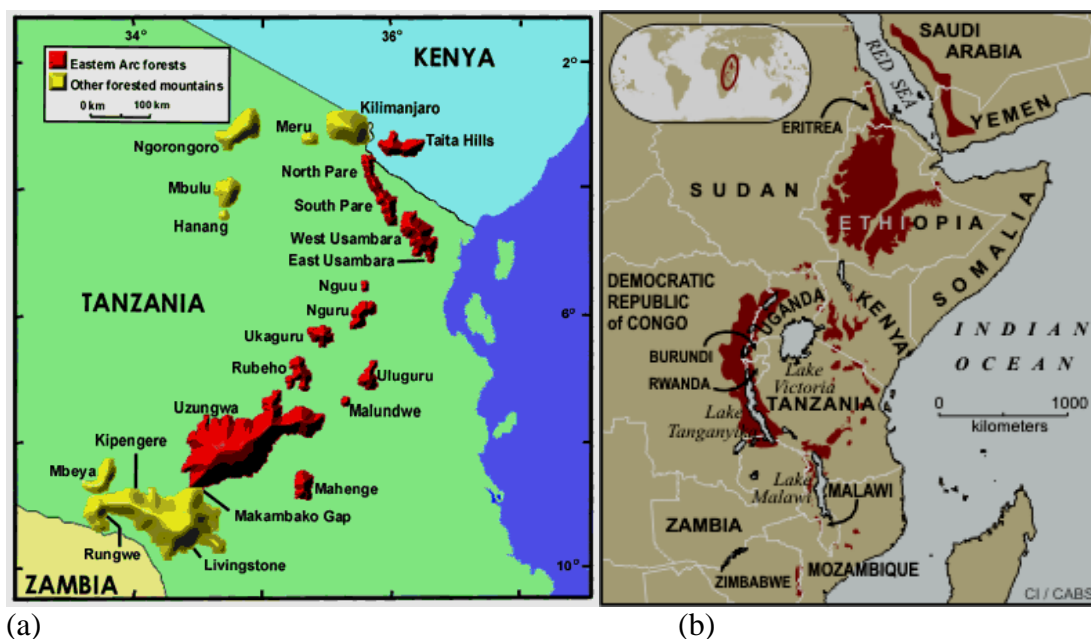
Eastern Arc Mountains

This study was conducted in the Udzungwa Mountains which constitute the largest block of the Eastern Arc Mountains (Figure 1.2a). The Eastern Arc Mountains (EAM), which extend from south-eastern Kenya to southern Tanzania, are well known for their conservation value. They are one of the world's most important areas for the conservation of biodiversity due to the high number of endemic plant species per unit area (Myers *et al.*, 2000). The mountains are an important source of hydroelectric power in Tanzania, and contribute significantly to ecotourism, which represents more than 6% of the country's economy (WTO, 2006). The Eastern Arc Mountains of Tanzania are thought to be worth US\$ 620 million to the Tanzanian economy (Burgess *et al.*, 2007b).

The Eastern Arc Mountains are now recognised as part of the large Eastern Afromontane hotspot (Figure 1.2b). The Eastern Afromontane hotspot encompasses several widely scattered, but biogeographically similar mountain ranges in eastern Africa, from Saudi Arabia and Yemen in the north to Zimbabwe in the south (<http://www.biodiversityhotspots.org>). This hotspot also includes the Neocene volcanoes of Kenya and the Tanzanian Highlands (e.g., Mt Kilimanjaro, Mt Meru, Mt Kenya and Mt Elgon). The flora of the Eastern Afro-montane hotspot shows much uniformity and continuity; its composition changing with increasing altitude (Lovett,

1996; Lovett *et al.*, 2006). The most widespread tree genus is *Podocarpus*. A zone of bamboo is found between 2,000 and 3,000 meters altitude and a *Hagenia* forest zone up to 3,600 meters. At the highest elevations, such as on Mt. Kilimanjaro and Mt. Kenya, Afro-alpine vegetation characterized by the presence of giant senecios (*Dendrosenecio* sp.), lobelias and *Helichrysum* scrub occurs (<http://www.biodiversityhotspots.org>).

The EAM are subject to high human pressure due to increasing populations, making it one of the areas most susceptible to future species loss (Baillie *et al.*, 2004). A high proportion of the remaining forest in the Eastern Arc is degraded. However, the overall extent of degradation remains unclear (Burgess *et al.*, 2007a; Marshall, 2007). The majority of Eastern arc forests are legally protected. However, like most tropical forests (Asner *et al.*, 2005), increasing forest degradation as a result of inadequate management capacity, limited funds, climatic impacts and increasing human pressure is likely.



(a) (b)
Fig. 1.2. Map (a) Eastern Arc forests in Tanzania and Kenya (b) Eastern Afromontane forests (in red). Source: (a) <http://www.easternarc.org> (2002) (b) <http://www.biodiversityhotspots.org> (2007)

Udzungwa Mountains

The Udzungwa Mountains (also known as the Udzungwas) [7°46'S, 36°43'E] have a habitat that is quite variable between its fragments. The forest is surrounded by woodland and bushy grassland in some areas. The Udzungwa mountains have the

largest primary closed-canopy forest of any area in the Eastern Arc (Burgess *et al.*, 2007b; Marshall, 2007), with *Papyrus* and *Carex* dominating its wetlands. The area is home to many rare and restricted-range species including the Sanje mangabey. It also harbours 102 vertebrate and 36 tree species that are endemic or near endemic to the Eastern Arc (Burgess *et al.*, 2007b). Despite its biological diversity and high levels of endemism, the Udzungwa Park is less researched compared to other Parks such as Serengeti (where most tourism is conducted). Ongoing studies of primates, duikers, reptiles and vegetation in the Udzungwa Mountains (including the results presented in this thesis) are only now beginning to reveal information about the biology, structural and microhabitat details that are important for conserving biodiversity (Marshall, 2007; Struhsaker *et al.*, 2004).

This study was conducted in a small area of the Mwanihana forest (177km², Dinesen *et al.*, 2001) in the north-eastern part of the 1,990km² Udzungwa Mountains National Park (7°46'S, 36°51'E) (Figure 2). Mwanihana includes 106 km² of closed canopy forest, and its elevation ranges from 300 to 2300 m above sea level (a.s.l.) (Lovett, 1996; Lovett *et al.*, 2006; Marshall, 2007). Its proximity to Park headquarters enhances its potential for protection and the conservation of rare and endemic species that occur in the Udzungwa Mountains. The mean annual temperature measured at 300 m a.s.l. ranges from 24 °C to 28 °C (UMNP data, 1998) and the mean annual rainfall is 2000 mm (average for 1998-1999). The endangered Sanje crested mangabey only occurs in two forests (Udzungwa Scarp and Mwanihana; Figure 1.3) with the largest population in Mwanihana. Prior to habituation of mangabey groups for research purposes, the mangabey population inhabiting this forest was poorly studied.

The forest in Mwanihana can be classified as 'tropical moist forest' (Whitmore, 1990). The habitat at lower altitudes is mostly comprised of dry deciduous forest of *Brachystegia* spp. (Leguminosae), *Dalbergia melanoxylon* (Papilionoideae), *Diplorhincus condylocarpon* (Apocynaceae), *Uapaca mitida* (Euphorbiaceae), and *Combretum* spp. (Combretaceae), semideciduous forest of moderate to old-growth (transitional) forest of *Sorindeia madagascariensis* (Anacardiaceae), *Combretum* spp. (Combretaceae) *Ricinodendron heudelotii* (Euphorbiaceae), *Ficus* spp. (Moraceae), and *Trema orientalis* (Ulmaceae), and evergreen old-growth montane forest of

Podocarpus spp., *Prunus* and *Hagenia* with other common species such as *Parinari excelsa* (Chrysobalanaceae), *Macaranga* spp. (Euphorbiaceae), *Erythrophloeum suaveolens* (Leguminosae), *Synsepalum cerasiferum* (Sapotaceae), *Sorindeia madagascariensis* (Anacardiaceae), and *Parkia filicoidea* (Leguminosae) (Ehardt *et al.*, 2005; Lovett *et al.*, 2006; Marshall, 2007; Rovero *et al.*, 2006).

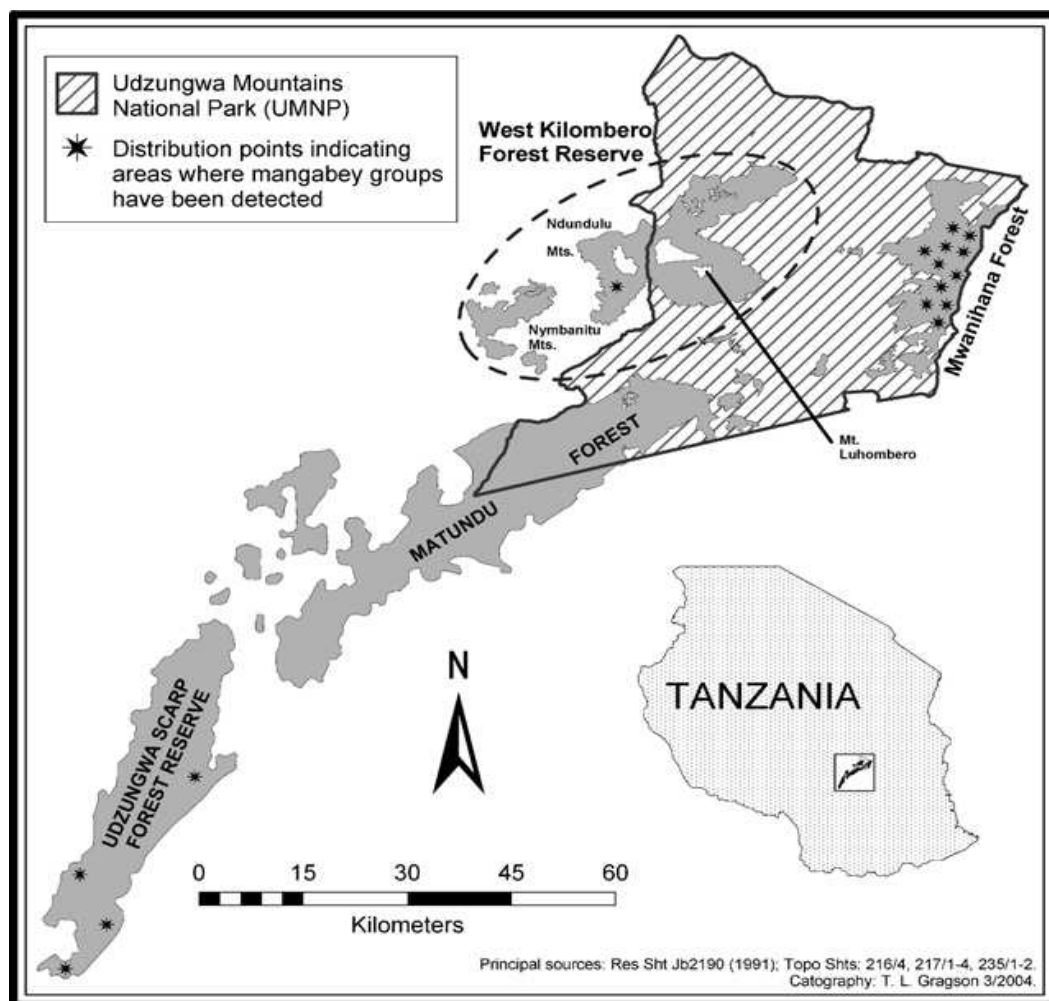


Fig. 1.3. Udzungwa Mountains National Park showing location of the study site (Mwanihana forest) and distribution of Sanje Mangabeys across forest fragments in which they occur. No Sanje mangabey sightings have been recorded in the circled area. Map adapted from Ehardt *et al.* (2005).

Study group

One habituated group was selected for this study because there was the potential to easily observe its composition, spatio-temporal organization and sociosexual behaviour. Habituation of the free ranging group allowed close observation of animals to within 5 metres. There are two groups of habituated mangabeys in the Udzungwa

mountains National Park. I studied the Njokamoni group. The group had been habituated and observed for various lengths of time since annexation of the Park in 1998. Between mid-2000 and late 2005, the size of this mangabey group increased from 32 to 49 animals (Jones *et al.*, 2006). The group spends most of its time near the Njokamoni River, from 300 to 1300m (a.s.l.) Social groups of monkeys are cohesive, permitting detailed analysis of group sizes of this species (Marshall *et al.*, 2005). The conspicuous nature of this semi-terrestrial monkey makes it possible to undertake detailed investigations of their behaviour and ecology.

There are seven other primate species in the study area: the IUCN vulnerable Udzungwa red colobus (*Piliocolobus gordonorum*), range-restricted Angolan black and white colobus (*Colobus angolensis palliatus*), Sykes monkey (*Cercopithecus mitis*), yellow baboon (*Papio cynocephalus cynocephalus*) and vervet monkey (*Chlorocebus aethiops*). Others are forest dwelling galagos such as the Udzungwa or forest galago (*Galagoides zanzibaricus* syn. *G. udzungwensis*) and mountain dwarf galago (*Galagoides urinus*).

Chapter Outlines and Objectives

The research is presented as a series of chapters (2 to 5), partly in the style of scientific papers. Each chapter can be understood independently from the rest, while contributing to the specified aims of the thesis as explained in the chapter outlines below. This format has been selected over a more traditional thesis format to facilitate subsequent publication of the research. The four main chapters discuss general aspects of social organisation and reproduction in Sanje mangabey. Chapter 2 presents information on social organisation, ranging behaviour and assessment of the influence of seasonal parameters on different aspects of social organisation. Data on habitat and feeding ecology are presented in Chapter 3. Female reproductive biology and patterns of sexual behaviour are covered in chapter 4. A discussion of all chapters will be presented in Chapter 5 in order to bring all of the findings together and to present overall conclusions, suggestions for future research and for conservation management.

Chapter 2: Social organisation

This chapter presents broad representation of mangabey social organisation, including an analysis of group structure, range and social interactions of the Sanje mangabey in the Mwanihana forest. This includes an analysis of the relationship between mangabey abundance and social group size, an assessment of the size, and age and sex composition of groups in order to determine population density and distribution and an examination of the movement patterns and home range of the habituated group. This chapter also informs current knowledge of the Sanje mangabey's spatial organization and interactions among the age and sex classes. Finally, the chapter updates published population estimates for the Sanje mangabey (Dinesen *et al.*, 2001; Wasser, 1993).

Chapter 3: Sanje mangabey feeding ecology and seasonal parameters

In Chapter 3 I present an analysis of mangabey feeding ecology and vegetation composition in relation to foraging behaviour. The chapter aims to examine Sanje mangabey food utilized to assess the diet type, diversity, flexibility and feeding behaviour. Two sets of data on mangabey feeding ecology are analysed: (1) dietary composition and diversity among the various age-sex classes and (2) relationships between available food, food selection and ability to use different forest patches (e.g. secondary forest). Chapter 3 also assesses how temperature and rainfall influences feeding. While this chapter is useful for assessment of feeding behaviour and vegetation composition, it also provides habitat measures relating to Sanje mangabey ranging behaviour (As covered in Chapter 2). Finally; it also includes temperature and rainfall measurements to examine their influence on behaviour and ecology.

Chapter 4: Sexual behaviour and female reproductive biology

It is thought that females of various Old World monkey species use sexual skin swellings as signals to advertise their fertility and attract the interest of potential mates (Dixon, 1983; 1998; Nunn, 1999a). There is currently no information on menstrual cycles, sexual skin morphology or patterns of sexual behaviour in the Sanje mangabey. Therefore, chapter 4 examines the temporal relationships between sexual skin swellings and sexual behaviour. It also documents the morphological changes in swellings in different reproductive states and measures changes in sexual behaviour during various swelling phases. In addition, it provides a comparison of swelling morphology and reproductive parameters with that of closely related species, in order

to examine relationships between *Cercocebus* and other clades. This chapter also addresses the broader issue of the evolution of sexual skin swellings in female Old World monkeys, using the Sanje mangabey as a test case.

Chapter 5: General discussion

This final chapter brings all of the findings together and presents overall conclusions, suggestions for future research and conservation management. The discussion also places the findings in context with previous studies in the Udzungwa Mountains and elsewhere, in order to draw conclusions about this mangabey's social organisation, ecology, reproductive behaviour, and conservation prospects for the Udzungwa ecosystem.

2. SOCIAL ORGANISATION, GROUP SIZE, AGE AND SEX COMPOSITION, AND RANGING BEHAVIOUR

Abstract

There is little information about Sanje mangabey social organisation, group size, population density, social relationships, dominance, grooming and ranging behaviour. In this study, observations and counts of group size and age-sex composition were conducted daily, and means were computed for a 6 months period. Previous researchers in the Udzungwas have used the line transect method to estimate Sanje mangabey population abundance. These studies, however, devoted little attention to the interpretation of line transect data and the need to include both group and solitary individuals in the analyses. I present Sanje mangabey population density and abundance estimates performed in DISTANCE, using counts collected from three transects. Further, I studied ranging patterns to determine home range size and how wet and dry seasons might affect ranging behaviour. UTM coordinates were collected via GPS from the group centre every 20 min during all-day follows. Estimates of home range size were performed in CALHOME. Behaviour data were collected using scan and focal animal sampling to investigate social dominance, spatial associations and grooming.

The results suggest that this group contains 62 individuals. Although it was not possible to assess the influence of seasons on group composition, the general trend shows there are small increases in the number of individuals during the wet season. This may be due to absence of subgrouping and a low level of inter-group competition, as a result of high food abundance during this period. The current estimate of population density is 1.24 mangabeys per hectare and the Mwanihana population is estimated to be 689 individuals. This result shows that the population of this endangered primate is decreasing, calling for appropriate conservation measures to address the causes of its declines. The total home range size was 301 ha and the mean day range 1760 m. Movements and ranging patterns varied markedly during the wet and dry seasons. On days when the group visited distant forest patches (drier days), the mangabeys travelled significantly further ($P < 0.001$), significantly faster

($P < 0.001$) via the most direct routes, and with fewer stops compared to days when they visited closer patches (wet days). The days they travelled further also increased the home range size from 173.7 ha to 343.4 ha. These results indicate that rainfall has important effects upon range use and home range size in the Sanje mangabey.

Studies of agonistic behaviour showed that male Sanje mangabeys spend more of their daily time involved in aggressive acts than do females. Aggression and responses to aggressive acts were quite variable among age classes; with more chases and scares from adults to juveniles than for sub adults, who were mostly physically attacked. For both sexes there are stable linear dominance hierarchies among individuals (Landau's dominance index, $h' = 0.92$, $P = 0.0281$) and a high directional consistency index, $DC = 0.91$). The linearity index, h' for males was 0.84, $P = 0.041$, and $DC = 0.94$. For females, the linearity index, h' was 0.93, $P = 0.0382$ and $DC = 0.94$). The agonistic rank order had strong predictive value for other social behaviours. This result suggests that the frequency and direction of agonistic interactions in Sanje mangabeys are reliable indicators of dominance. Comparisons across age and sex classes showed that individuals differed in frequencies of association. Results for group association indicate that females associate more with females and their young than with any other group members. Males associated with sub adult females a little more than with adult females.

The group spent 8% each day grooming each other. Females groomed males at a rate of 6.64 sec/hour, female groomed females at a rate of 0.05sec/hour, male-male (0.04sec/hour). Sub adults groomed males at a rate of 6.36sec/hour, female- infant rate was 5.27 sec/hour and female-juvenile rate was 5.23 sec/hour. There was a significant relationship between duration of the initiator's first grooming episode and subsequent reciprocation by the receiver in all age classes ($P < 0.05$). The independent effects of total grooming duration of the initiator showed a significant difference and predicted total grooming duration of the recipient ($P < 0.0001$). There was non-significant tendency for grooming to be directed towards higher ranking monkeys. These results from behavioural and ranging patterns provide the first empirical measures on Sanje mangabey social organization.

Key words: social organization, group size, population density, dominance, grooming.

Introduction

There has been a shift in studies of primate socioecology, from consideration of individual spatial relationships, to a focus upon group social interactions within particular ecological contexts (Alberts & Altmann, 1995; Bernstein, 1966; 1981; Charpentier *et al.*, 2004; Clutton-Brock, 1974; Crook & Gartlan, 1966; Henzi & Barrett, 1999; Wrangham, 1980). The patterns and nature of social interactions give understanding of particular social relationships between individuals (Hinde, 1976). Variations among relationships may be brought about by the frequency, nature and intensity of affiliative, affiliative and agonistic interactions. Social relationships, interactions and association patterns have not been adequately studied in mangabeys. These aspects of social systems and their functional significance are important for understanding the selection pressures responsible for adaptive change in social structure and the evolution of primate societies. Knowledge of behaviour and ecology is crucial to the understanding of mangabey social organisation.

Group size and composition

Diversity of primate groups with respect to size, sex ratio and temporal stability has been extensively reviewed (Kappeler & van Schaik, 2002; van Schaik & van Hooff, 1983). The number of adult females divided by the number of adult males is used to define the sociogenic sex ratio in a group. Variation in group size is one of the important aspects of diversity in social organization of group-living species.

Several factors have been correlated with group sizes. First, increased costs of travel and foraging due to within-group feeding competition set the upper size limit (van Schaik, 1983). Group size and resource distribution affect each individual's access to food, which, for females, affects their reproductive success (van Noordwijk & van Schaik, 1999; Wrangham, 1980). Another factor that determines variations in group size and favours group living is predation risk. Group-living primates of Africa are largely affected by presence of natural predators, particularly the African crowned-hawk eagle, *Stephanoaetus coronatus* (Brown, 1971; Brown *et al.*, 1982; Ehardt *et al.*, 2005). Other predators are leopards (*Panthera pardus*) and snakes. According to van Schaik (1983), van Schaik & van Hooff (1983) and Dunbar (1988), terrestrial

monkeys reduce the risk of predation by living in big groups. Aggression against predators in multi-male groups is mostly undertaken by adult males (Shultz, 2001). Upon attack by an eagle, monkeys either scream and escape (Cordeiro, 1992; Shultz, 2001) or attack in response (Gautier-Hion & Tutin, 1988; Jones *et al.*, 2006). Finally it is necessary to consider infanticides by males (Hrdy, 1979). Due to its direct effect upon juvenile sex ratio, infanticide may provide a selective force that reduces group size under certain conditions (Steenbeek & van Schaik, 2001; Struhsaker *et al.*, 2004).

There are also mechanisms that regulate group size. The proximate size regulating mechanisms are birth and death rates. Immigration and emigrations may also affect group size and composition. These, however, are largely constrained by intrinsic sex bias in most species (Alberts & Altmann, 1995; Altmann *et al.*, 1985; Brain, 1990; Chalmers, 1968). Sexual bias in residency may also have a consequence for the genetic structure of groups (Altmann *et al.*, 1996) and species breeding patterns (Clutton-Brock, 1989; Moore & Ali, 1984; Packer, 1985).

Between mid 2000 and 2005, group size for the Njokamoni Sanje mangabeys varied between 32 and 49 animals (Jones *et al.*, 2006). However, present exact numbers of adults, juveniles and infants are not known. Habituated mangabey groups provide an ideal sample with which to investigate demographic changes and the ecological correlates of group size. No basic information exists for the Sanje mangabey demographic variation or group sizes and age-sex composition (Ehardt *et al.*, 2005). From a conservation perspective, such data are vitally important in determining habitat requirements and potential management of this endangered species.

Population density

Systematic information on the demography and population density of Sanje mangabey is limited (Dinesen *et al.*, 2001; Marshall, 2007; Marshall *et al.*, 2005; Rovero *et al.*, 2006; Wasser, 1993). In these studies, estimates of population abundance were obtained using line transect methods. Although Sanje mangabeys live in groups, it is very hard to sight many groups along the transect and because, solitary adult males and sub adults often occur, these methods probably underestimate mangabey numbers. Line transect sampling has been used to estimate population density for a variety of vertebrates e.g. reptiles and amphibians (Greenberg, 2001; Rand, 1964),

birds (Dinesen *et al.*, 2001; Kuitunen *et al.*, 1998; Newmark, 1991) and large mammals (Kahurananga, 1981; Melton, 1983; Plumptre, 2000). The use of similar techniques to estimate population density of sighted and heard mangabey groups and individuals will contribute significant knowledge to efforts to provide exact measures of mangabey abundance. The aim of this study was to determine group size and composition of a habituated Njokamoni group and of mangabey population density in the Mwanihana forest.

Ranging behaviour

Day range refers to distance moved by an animal in a 24-hr period. An area occupied or travelled by a group to meet its nutritional requirements is a home range. Studies of home range sizes have predominantly focused on assessing influences of increased number of individuals or available food and intra-group competition on range size (Fashing *et al.*, 2007; Isbell, 1991; Olupot *et al.*, 1994; Olupot *et al.*, 1997; Olupot & Waser, 2001). Population density has been negatively correlated with home range size; for example, a larger home range size is associated with fewer intra-group encounters due to lower population density (Butynski, 1990; Ostro *et al.*, 1999). This relationship is complex, because low population density together with low food availability favours larger home ranges (Clutton-Brock & Harvey, 1977). The relationship between food and home range size depends on patterns of distribution of food as well. Low food availability reduces per capita feeding efficiency (Isbell, 1991). Increased feeding competition in groups of frugivores that feed on clumped resources will result in increased daily distances travelled (Chapman *et al.*, 2002; Isbell, 1991; Isbell *et al.*, 1998). Sanje mangabeys, like the closely-related Tana River mangabey feed on fruits and seeds of different species that are distributed in clusters.

Demographic and ecological factors such as group size, feeding competition, predation, forest size, and rainfall can influence home range size. For forest primates, home range size is constrained by the sizes of forest fragments e.g. in *Cercocebus galericus* (Homewood, 1976; Kinnaird, 1990a) and rainfall e.g. *C. albigena* (Freeland, 1980). For instance, it has been shown that *Colobus guereza* and *Macaca silenus* living in forest fragments encompass smaller home ranges than conspecifics living in continuous forests (Onderdonk & Chapman, 2000). Home range may also increase if forest area increases e.g. *Lophocebus albigena jonstonii* (Olupot *et al.*, 1994).

For most of the forest mangabeys, little is known about their ranging patterns. Habituated mangabey groups are thus an ideal sample to investigate ranging behaviour and its ecological correlates, such as relationship between group size, daily distance and range size. Home range has never been thoroughly studied in Sanje mangabeys. Here I investigate home range and effect of seasons on the ranging behaviour of the Sanje mangabey.

A home range of approximately 200 ha for one group overlapping with 2 other groups was reported by Ehardt *et al.* (2005). My observations of the Njokamoni group suggest that it has increased its range. The animals were observed to visit areas they had not previously been recorded in since habituation and behavioural observations began in 1995. Also, throughout the study, the group has been showing high frequencies of aggression during feeding, moving shorter distances during rainy than on dry days. Little is known of what drives Sanje mangabeys to move to certain areas more often than others, or whether their movement is seasonal. It is also not known if they spend most of their time in certain favoured areas of their range (i.e. core areas) where there is high abundance and even distribution of food. Such information is thus crucial to understanding the animals, biology and needs. It is thus important for management and conservation purposes (Chapman *et al.*, 2002; Ostro *et al.*, 1999; Tutin, 1999).

I intended to investigate ranging behaviour and ecological factors associated with Sanje mangabey. I hypothesised that the home range, compared to the overlapping range of another habituated group, is increasing due to greater daily distances travelled and associated with expanding group size. Daily ranging might be affected by several factors (predicted) e.g. group size, decrease in fruit biomass, density of preferred food trees in the existing range, or a decrease in number of trees per individual mangabey. Increased feeding competition requires a larger home range, and this predicts greater daily travelled distances. Sanje mangabeys use loud vocalisations ('whoop gobbles') as a spacing mechanism between groups (defined in Appendix 1). I predicted that this group's range might not be constrained by the proximity of neighbouring groups. Also, since the group was observed to visit non-

forest habitats, I predicted that ranging is not constrained by extent of forest cover or fruit biomass.

Social dominance

Dominance relationships of terrestrial mangabeys have been studied in captive groups e.g. (Bernstein, 1971; 1976; Ehardt, 1988a; 1988b; Gust, 1994b; 1995; Gust & Gordon, 1991a; 1994). Little is known, however, about hierarchies and dominance relationships in groups of mangabeys in their natural environment. Group size may limit resource availability, leading to competitive social interactions. Competition may be divided into contest and scramble components (van Schaik & van Noordwijk, 1988). According to Range & Noë (2002) scramble competition, unlike contest competition, does not lead to direct conflict; it thus requires no conflict resolution mechanisms such as subordinate behaviours towards certain individuals. When some individuals can systematically exclude others from a preferred or scarce resource, contest competition occurs. Success in contest competition depends on dominance rank: lower ranking individuals may have less access to 'high quality' resources (van Noordwijk & van Schaik, 1987; 1999). Competition may also result in more peripheral positions for low-ranked group members (Busse, 1984; van Noordwijk & van Schaik, 1987). Scramble competition occurs when food patches are very small and spread out or when large patches feed multiple individuals simultaneously. Success during scramble competitive interactions depends on group size, with larger groups facing stronger within-group competition, but perhaps less contest competition (van Noordwijk & van Schaik, 1999). Hierarchy formation is affected by the type of competition present in a particular species. For example, captive female sooty mangabeys form a linear hierarchy typical of species exhibiting strong contest competition, but do not express other behaviours expected for such species (Range & Noë, 2002).

Dominance among adult primates can be expressed in terms of the distance between animals' respective dominance rank and the 'gradient' (or steepness) of the dominance hierarchy (Bernstein, 1966). The slope of the dominance gradient determines the rank distance required to produce power differential between highest and lowest ranking (de Vries *et al.*, 2006; Henzi & Barrett, 1999). As a strategy to gain more fitness to overcome unfavourable asymmetry in fighting ability, individuals

may form alliances. Sharing of resources and maintenance of alliances between partners is affected by kinship: with more positive relationships occurring between closely related than between distantly related or unrelated individuals (Dunbur, 1988; Hamilton, 1964a). Previous studies on terrestrial mangabeys in captivity found no particular bonds between females (Ehardt, 1988a), no sign of support for kin, or kin increasing their ranks in the dominance hierarchy (Gust & Gordon, 1994).

Dominance hierarchies among same-sex adults are relatively linear. However, two or more individuals may form a coalition to displace an animal that could dominate each of them individually (Bernstein, 2007). A preliminary study on wild *Cercocebus galeritus* (Gust & Gordon, 1991b) suggested that a stable dominance rank order occurs between females and that rank reversals may occur between males. Stable dominance rank order was found in another terrestrial mangabey, *C. torquatus atys* (Bernstein, 1976). There has been no study on dominance in *Cercocebus sanjei*. This thesis addresses the following questions: Can Sanje mangabeys be ranked in a linear dominance hierarchy? Does rank correlate with reproductive or mating success? I predicted that 1). High-ranking individuals receive less aggressive encounters than low ranking during feeding, once dominance relationships are established. 2). Higher-ranking males will have higher rates of access to females (details for this will be discussed in chapter 4).

Grooming

Competitive interactions and higher rates of aggression (e.g. within multi male-multi female groups) may result in the development of coalitions or alliances. In female-bonded groups, social grooming has been suggested to act as a mechanism for formation of coalitions. Grooming allows females to alleviate the negative effects of ecological competition upon their reproductive success (Dunbur, 1988; Harcourt, 1992; van Schaik, 1989; Watts, 2000b). Social grooming also acts as a means by which conspecifics ensure direct intrinsic benefits (e.g. parasite removal) and support from other individuals in the group (Henzi & Barrett, 1999). Grooming exchange may facilitate aid and tolerance (Watts, 2000a; 2000b), or strengthen long-term social bonds (Defler, 1978). Grooming can thus be both payoff currency or exchanged for its 'value equivalent'. Conversely, grooming has been found to cleave groups along individually advantageous lines (Seyfarth, 1977; 1980).

For females, there is evidence suggesting that grooming may increase tolerance and reduced aggression from dominant animals (Barrett *et al.*, 2002; Chancellor & Isbell, 2009; Fairbanks, 1980; Perry, 1996; Silk, 1982; Ventura *et al.*, 2006; Watts, 2000b). Grooming can also be exchanged for increased access to scarce resources such as food or water (de Waal, 1997; Gumert & Ho, 2008; Ventura *et al.*, 2006; Weisbard & Goy, 1976), or lenience around infants (Gumert, 2007; Muroyama, 1994). These kinds of interactions are typically dyadic in nature (Henzi & Barrett, 1999).

Grooming is a time-consuming activity that can occupy up to 20% of each day (Henzi & Barrett, 1999). Understanding grooming interactions in Sanje mangabeys is therefore important, since grooming may have great biological significance as far as their socioecology is concerned. This behaviour in groups of Sanje mangabey has never been studied. I hypothesised that female Sanje mangabeys exchange grooming as a ‘commodity’. The patterning of grooming interactions was predicted as follows: animals exchange grooming for equal amounts of grooming time and immediate reciprocation (to avoid being cheated) by grooming partners (Defler, 1978; Watts, 2000a). To balance the trade, partners should time-match grooming contributions within a reciprocated bout, regardless of aggression or competition, resulting in a positive correlation between amounts of time spent grooming by each partner. However, dominance differentials need be considered. A dominant individual may only invest the time needed to initiate sustained bouts of grooming, resulting in less consistent time-matching between partners (Chancellor & Isbell, 2009; Watts, 2000b).

Ehardt (1988a) found no particular bonds between female Sooty mangabeys. It might be expected that kinship does not influence grooming patterns in Sanje mangabeys because, in the absence of familiarity, affinity based interactions are small in most other monkeys except for *Macaca* spp., *Papio* spp. and *Cercopithecus aethiops* (Chapais *et al.*, 1991; Charpentier *et al.*, 2007; Reynolds, 1968; van Schaik, 1989; Wrangham, 1980). I also studied how dominance rank influences patterns of grooming and interchange. The hypothesis was that dominant individuals might receive more grooming from low ranking individuals, leading to similar amounts of reciprocation among dyads. Following Seyfarth (1977), it was predicted that dominant individuals would be more attractive as grooming partners because they

could offer better coalitionary support, and that low-ranking individuals would compete for grooming access to higher-ranking partners.

Male-infant affiliations and allomothering

Traditionally, it has been thought that males in multi-male primate groups provide relatively little direct care to infants (Smuts & Gubernick, 1992). Perhaps, because of low confidence of paternity, males contribute less to rearing the young (Struhsaker, 1997; Struhsaker *et al.*, 2004; van Schaik & Paul, 1996). Some members of the tribe Papionini, such as baboons exhibit intense affiliative interactions between adult males and infants e.g. (Buchan *et al.*, 2003; Busse & Hamilton III, 1981; Wallis, 1983). Studies of male-infant relations are scant in mangabeys, and little attention has been given to the intensity and form of male care patterns in the previously mentioned studies. The importance and intensity of male infant care may relate to affiliations between the male and the infant's mother, and the presence of conspicuous signs of ovulation in females (Dixon, 1998; Maestripieri, 1998). It is not known whether females enforce male care by preferring infant-caring males as mating partners or whether breeding males carry infants to avoid aggression i.e. agonistic buffering as in Barbary macaques; (Whiten & Rumsey, 1973) or whether males only care for infants that are supposedly theirs. I decided to collect data on male involvement in infant care. The goals were to characterise the patterns, form and intensity of male infant care in Sanje mangabeys, and to use the data to test the hypothesis that male care for infants is a strategy to increase mating opportunities.

Methods

Study site

Studies were conducted in the Mwanihana forest (7°50'12.01''S, 36°49'28.47''E) Udzungwa mountains (Fig. 2.1). The east-facing Mwanihana escarpment (177km², Dinesen *et al.*, 2001) harbours more than 60% of the mangabey population (Ehardt *et al.*, 2005). The other population of this species occurs in the Udzungwa Scarp forest. The focus area of this study was the forest (up to 1700m altitude) between Sanje village (7°47'00.00''S, 36°54'00.00''E) and Park headquarters (7°50'15.50''S, 36°52'76.80''E) inhabited by the Njokamoni group of mangabeys. Three existing transects (Sanje, Mwanihana and Campsite 3) were also used to gain access to the animals. The study area has one main camp site (Njokamoni camp) which was used as

a base for research activities, with one additional temporary camp along the Mwanihana trail.

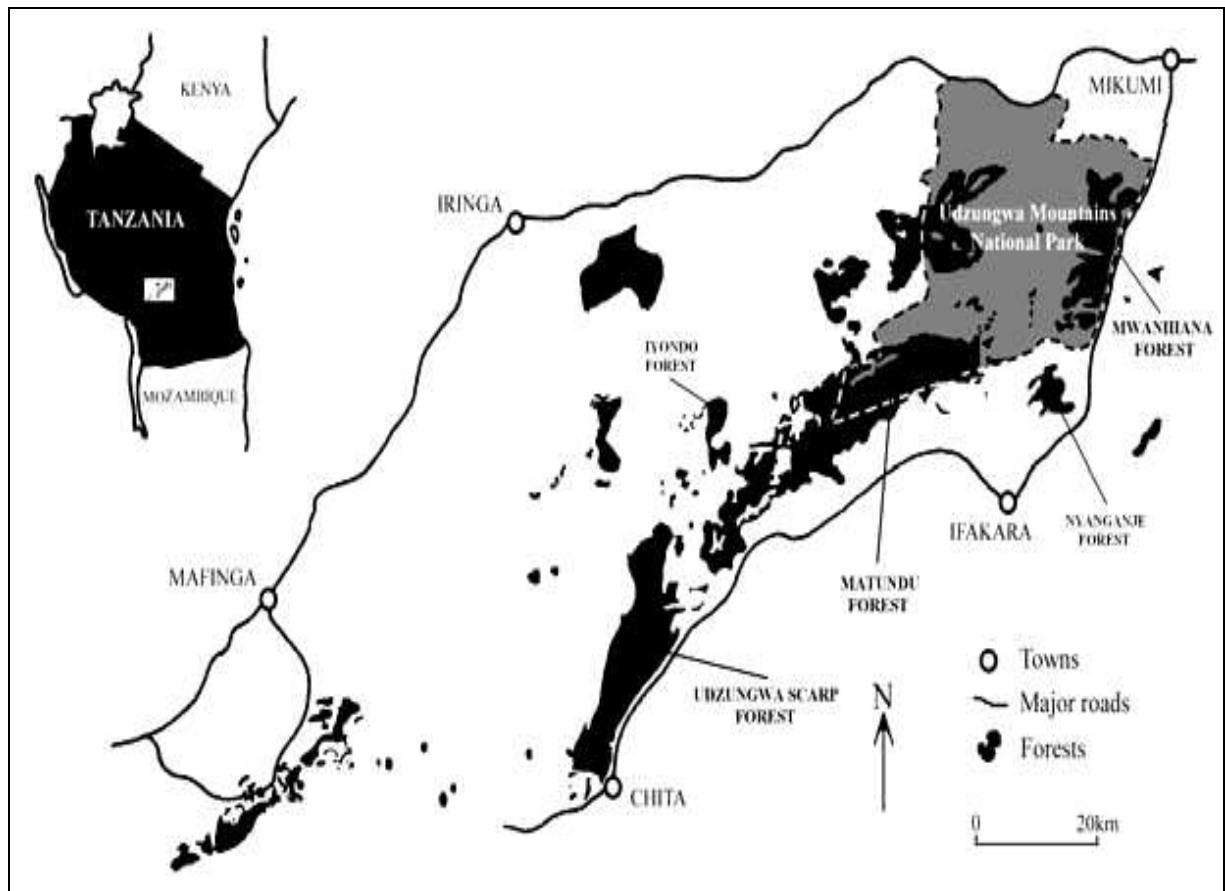


Fig. 2.1. Map of the Udzungwa Mountains showing Mwanihana and other forest blocks (in black) and the National Park (in grey). Adapted from Marshall *et al.* (2005).

Study group

Data were collected on one group of mangabeys. Another habituated group and approximately 16 other non-habituated groups exist in this area (Ehardt *et al.*, 2005; Lovett & Wasser, 1993). The study group was estimated to consist of 49 animals in 2005 (Jones *et al.*, 2006) but at the start of this study no precise information on group size, age and sex composition, social organisation, or ranging behaviour was available. Data on social organisation and ranging behaviour was collected for the Njokamoni group, and the presence of other groups that shared the study group's home range was recorded as result of visual or vocal contacts.

Group size and composition

The Njokamoni mangabey group was located at its sleeping site and was followed on foot from 6:30am to 6pm. Observations on composition and demographic changes of the group were made once a day, 21 days a month between December 2007 and May 2008. Group counts were made by walking around the group in the direction of animal travel. Total group counts were performed and the sex/age classes were scored. It was not always possible to count all individuals accurately. A count was considered as being complete based on its quality (group passing over a trail, through a break, across a river/stream or when the whole group was resting) and agreement with previous and subsequent counts. Replicates of counts over the course of 23 weeks enabled me to arrive at an accurate assessment of group size and composition. A mean complete group count throughout the study was calculated (n= 148 days). Sanje mangabey mean group counts were not available from other studies for comparison. Group size counts of neighbouring groups were collected were considered incomplete due to the non-docile nature of these non-habituated mangabeys. Hence they were not used for comparison.

Sex and age of class were estimated for each individual. Age class was determined based on the size of the animal, and on whether individuals showed particular behaviours (Agetsuma, 2001; Stanford, 1995). Sex was determined using visible genitalia or secondary sexually dimorphic traits typical of all primate species (e.g. male's face being darker than female's). I used 5 categories of age class (for each sex) namely; adult male (AM), adult female (AF), sub adult male (SAM), sub adult female (SAF), large juvenile male (LJM), large juvenile female (LJF), small juvenile male (SJM), small juvenile female (SJF) and infants (male and female). The age-sex classes were defined as follows;

1. Adult male (AM): maximum body size, large canines. Testes fully descended and prominent sometimes emit distinctive 'loud calls'.
2. Adult female (AF): maximum body size and more slender in size than AM. Chest slightly less covered with hair, sexual skin present, nipple's often elongated and red. Often seen carrying infants if lactating.
3. Sub-adult male (SAM): sexually mature male but yet to attain maximum body size. Testes descended but not prominent.

4. Sub-adult female (SAF): sexually mature female, yet to attain maximum body size, sex skin swelling often beginning at this age.
5. Large juvenile male (LJM): medium body size, sexually immature males that were occasionally dependent on their mothers.
6. Large juvenile female (LJF): medium body size, sexually immature females, occasionally dependent on their parents.
7. Small juveniles male (SJM): small in size, sexually immature males that were dependent on parents for resources, seldom clinging ventrally to mother or suckling.
8. Small juvenile female (SJF): small in size, sexually immature females that seldom cling to their mother's bellies for suckling or for aid to acquire resources.
9. Infants (male and female): smallest in size, suckling, and very much dependent on mothers for food and physical contact.

Population density

Censuses were conducted of group sizes and age-sex compositions of the other mangabey groups in the area using Line Transect Distance Sampling (LTDS) procedures (Buckland *et al.*, 1993). LTDS methods are based on animal-to-observer (sighting) and transect-to-animal (perpendicular) distances (Whitesides *et al.*, 1988). I used the perpendicular distance method to estimate population density in Mwanihana. The LTDS technique was selected due to its extensive use in primate studies (Chapman *et al.*, 1988; (Marshall *et al.*, 2005; Mitani *et al.*, 2000; Rovero *et al.*, 2006; Whitesides *et al.*, 1988).

For accurate density estimation, critical assumptions of LTDS need to be met. The LTDS technique depends upon detection (i.e. detection function for a line =1) and counting of animals on one or both sides of a survey path. It is also assumed that no animal moves in response to observers prior to detection. Lastly, the method requires that all measurements are recorded accurately. Despite its many assumptions and requirements, LTDS remains the most practical method for estimating forest primate population densities (Struhsaker, 1997).

Because of terrain and habitat conditions in the Mwanihana forest, a walking survey was performed. Line transects were traversed once a month. Three existing transects (Sanje, Mwanihana and Campsites 3) were used. These transects, due to their layout, ensured that a maximum survey area was covered. The transects were 4km long and had signs every 50m marking the distances along the line of survey. Transects were walked at 1km/hr; allowing intervals of 30-60 seconds to stop and scan the forest. All transects were walked between 6:30am and 11:30am. I also ensured that transects were not used by other researchers or crossed by people before we used them. Transect studies were not conducted during periods of heavy rain. Because different species can be observed and surveyed simultaneously along line transects, I also collected data on four other monkeys, the Iringa red colobus, Angolan black and white colobus, yellow baboon and Sykes monkey.

The time of each encounter, species, record type (visual, auditory), the number of animals or groups (size) and age and sex composition of the group was recorded. Points along the transect at each animal sighting were noted and three variables were measured relative to the position of animals;

- (i) Sighting distance (DO): the distance at an inclined angel from observers to the point where the first animal was spotted. Estimated using a Nikon range finder (range 500 m) and occasionally by eye.
- (ii) Sighting angle (θ , = direction to the left or right or the angle subtended relative to the line of traverse and the animal or a group); measured using a compass bearing.
- (iii) Perpendicular distances (position) from the line transect to the point where animals are positioned (in relation to the closest 50 m mark, centre of the cluster and the sighting angle). Calculated by multiplying the animal-observer distance (DO) by the sin of sighting angle θ . Perpendicular distance was used to model detection function in DISTANCE.

A mark was made on the transect at the point at which the first animal was seen; this acted a reference point from which the above measurements were made. Groups were considered as separate when they were >10m apart. The observer moved up and down

the transect to collect more information e.g. the area occupied by the animals. I also recorded some behavioural details (e.g. activity, reaction upon seeing observer) and noted any association observed between species. Transect survey data for the six month prior to commencement of this study were available from Park records and these were utilized to estimate density and population sizes. It has been noted that different observers can vary when estimating sighting distances (Mitani *et al.*, 2000). Consistency among observers is necessary for accurate population estimates. These data were collected by the same personnel (trained in doing line transects) who assisted me in this research.

Ranging behaviour

The position of the habituated group was mapped using the Geographical Positioning System (GPS) to sample daily movements, range size and use. To obtain adequate data for estimation of home range, I collected data from 0700-1800hr, for 6 days, 3 times per month from Dec 2007 to June 2008. In order to estimate the home range of *Cercocebus galeritus*, Homewood (1976) collected a different set of data 5 days per month for 7 months. Kinnaird (1990a) collected data on *C. galeritus* 3 days per month for 15 months.

A Garmin GPS 60 was used to mark positions of the Njokamoni mangabey group. A position was accepted if at least 3 satellites (but usually 5) were captured to triangulate the position. In areas of high stem and leaf cover, the GPS was counterbalanced so that positions could be obtained when the observer was in clear view of the sky. The position of the centre of the group was recorded every 20 minutes. The group centre was estimated as the centre of a polygon drawn to include all animals in view at that moment. The Universal Transverse Mercator (UTM) was calculated for all the 20 minute points. I also estimated group dispersal distance or spread from the centre at the start of every 20 min-focal samples. Dispersal distance was estimated at least twice per hour as a diameter of the circle (in metres) that would encompass all group members in sight. This was done in order to collect data on possible subgroup formation. Three local assistants were trained to estimate group spread. A high degree of reliability was found between the assistant's estimates and actual measurements (measured with a measuring tape) Spearman's $\rho = 0.97$, $P < 0.0001$, $N=18$ per assistant). The total time a given 100m^2 of forest was occupied

during foraging/feeding was also recorded. I tested the distribution of 20 m distance travelled in dryer and wet days against Poisson distribution to determine if the use of forest is random. These measures provided estimates of mangabey day range, patterns of movement and their ranging behaviour during the wet and dry season months.

Spatial organisation

Focal animal sampling

Focal animal sampling was used to quantify mangabey spatial organisation and relationships in the habituated study group. Focal animal sampling refers to a sampling method in which all occurrences of specified interactions of an individual are recorded during each sample period. A record was made of length of each sample period, and for each sample individual, the amount of time during the sample that it is actually in view (Altmann, 1974). A nearest neighbour technique was employed, based on distances between the focal animal and adjacent individuals. A stratified sample of 20 individuals of various sex and age classes was chosen. Focal individuals were selected at random, or by fixed rotation between age and sex classes (similar to the focal individual) whenever the random focal animal was unavailable. On most of observation days, each focal animal was not sampled more than twice, and in few occasions some individuals were followed 3 times a day. Focal samples lasted for 20 minutes, with at least 120 minutes between consecutive samples of the same individual.

Two types of food patches were defined; 1) Areas of up to 5 m diameter on the forest floor containing mushrooms or termites (*Macrotermes* spp.) and 2) Circular patches of fruits and seeds of 5m radius, around trunks of food trees. The distance between the focal individual and its nearest neighbours that were within 5 metres radius of the food patch was estimated once each for all 20 minute focal samples. The estimated distances were then recorded on a pre-designed check sheet and later converted to defined 3 point scale. The scale was defined as;

1. Very close: any distance between 0 metres to 1.5m from nearest individual to focal animal.
2. Close: distance of 1.6m to 3.0m between focal animal and the adjacent individual.
3. Far: distances between 3.1m to 5m between nearest animal and the focal

individual.

The focal animal's nearest neighbours inside the boundaries of 5 m radius were recorded as 'inside', and if they were 'outside', only their numbers were recorded. Between 900 and 1706 minutes of data collections were obtained for per individual. A total of 710.8 hours of focal follows of 25 individuals were collected (mean 684 ± 51 hours per individual). Data were collected by myself and two field assistants at 6 day intervals, 6 days each, three times per month.

Behavioural observations

Behavioural data were recorded for all members of the group by following the monkeys as they moved throughout the day. Data were collected for at least 10 hours for 6 consecutive days, 3 times a month, giving a total of 18 days with a total recording time of 1140 hours. Scan sampling (Altmann, 1974) at 5 minute intervals was used to record the group's social behaviour. Each scan lasted for 20 minutes. For each minute, the social interactions and activities of all individuals were scanned and recorded using data sheet. Four types of behaviour were assessed: agonistic, affiliative, proximity and self-directed. These were defined as follows;

1. Agonistic behaviours: This category included aggressive and submissive behaviours such as lunges, crouches, chases, bites and screams.
2. Affiliative: These are non-hostile, socially motivated behaviours. This category included activities such as grooming, contact grunts, lip smacks, playing and huddles.
3. Proximity: This category included approaches, avoids, supplant, rides, individual follows, and passes between animals.
4. Self directed: Locomotor activity which is motivated by and/or involves the movement of one or more conspecifics. In this category I recorded scratches, self grooming, body shakes, nose wiping and yawns.

Definitions of behavioural patterns recorded are provided in Appendix 1. Sexual behaviour was also recorded during the same sample (see chapter 4). Whenever a group or part of the group was under observation during scans, I recorded the social behaviours between dyads for the 20 individually identified animals and any other unidentified individuals. Immigration and disappearances of individuals were noted

whenever possible. The time engaged in activities in each of these behaviour categories was generated from all scans. Overall, the data set consisted of 1110 hour of group's scan follows. The measurements of relationships between individuals provided a representation of the group's overall social structure. Using records of rainfall and temperature for the whole period spent in the field, behavioural variations in wet and dry seasons were quantified.

Data analysis

Group size and population density

Mean group sizes and age-sex compositions of the Njokamoni habituated group were computed using EXCEL. The mean numbers for each age-sex class were calculated. The program, DISTANCE-version 5.2 (Thomas *et al.*, 2006) was used to analyse data for estimation of population density. In LTDS, all the animals present are not expected to be visible. It is assumed that probability of detection is 1 for animals on transect, and decreases away from the transect line. The models in DISTANCE corrects for 'missed' sightings of animals by constructing different detection functions from observations and using a likelihood and Akaike Information Criterion, AIC, to chose the detection function that best fits the pattern observed.

The width sampled for line transect is the perpendicular distance from the centre of survey trail to the extreme of effective detection on both sides of transect (Whitesides *et al.*, 1988). Strip width can be estimated from both animal-observer distance methods. Sample widths estimated from observer-to-animal distances assume that number of sightings of animals beyond the effective distance equals the number of missed sightings at nearer distances (Defler & Pintor, 1985; Freese *et al.*, 1982; Rovero *et al.*, 2006). Parametric and non- parametric models suggested by most recent studies assume a decrease in probability of detecting animals at increasing distances from the transect line (Anderson *et al.*, 1979; Buckland *et al.*, 1993; Buckland *et al.*, 2001; Marshall, 2007). For perpendicular methods, detection probability is an important parameter for estimation of strip width. In DISTANCE, animal detection probability, $g(x)$ is represented by fitting detection function, which replaces fixed sample-width estimates in calculations of population density in the observer-to-animal methods. The models in DISTANCE allows for calculation of effective strip width of a line which are used to estimate population density.

Population density estimates of animals were calculated in DISTANCE from total number of mangabey groups and solitary individuals observed.

Prior to analysis, data testing was performed to assess whether the assumptions for this method were met in the field, by plotting the frequency of sighting distances (histogram and scatter plot) to examine any violations of the assumption that no animals moves in response to observer prior detections (Buckland *et al.*, 2001). There were minimal outliers for mangabey data. Outliers reduce the precision of model fit. Therefore, I right-truncated distances to eliminate outliers and allow for suitable width for model fitting in DISTANCE. Right truncation was done at 50 m. Figure 2.2. a,b shows different shapes of the detection function for mangabey distance data.

Three detection function models (uniform, hazard-rate and half-normal) were used in DISTANCE for analysis and compared to determine the best model suitable for estimation of density. The models used three adjustments namely: simple polynomial, cosine and hermite polynomial. The best fitting model for the data was selected by comparing the relative fit of these functions using the AIC values (Buckland *et al.*, 1993; Buckland *et al.*, 2001). The best density estimator was the one with the smallest AIC. I also estimated mangabey encounter rate (number of individuals or groups per square kilometre, expected cluster size, density of cluster, and the overall density and abundance of mangabeys in the area. For final analysis, I used hazard rate and half normal-key model functions.

Ranging behaviour

Daily distance travelled was calculated as a sum of daily distances between each 20 minute GPS points. For each 6-day sample, a mean daily distance (mean of daily values for each of the 6 days) then per month was calculated, and an average daily range was obtained. These data were used to compare daily distances travelled by this group and that of another habituated group (calculated using a different method). The minimum convex polygon method (MCP) was used to describe mangabey occupation of the area. In this method, the outermost sets of data points representing animal locations are connected to form a polygon.

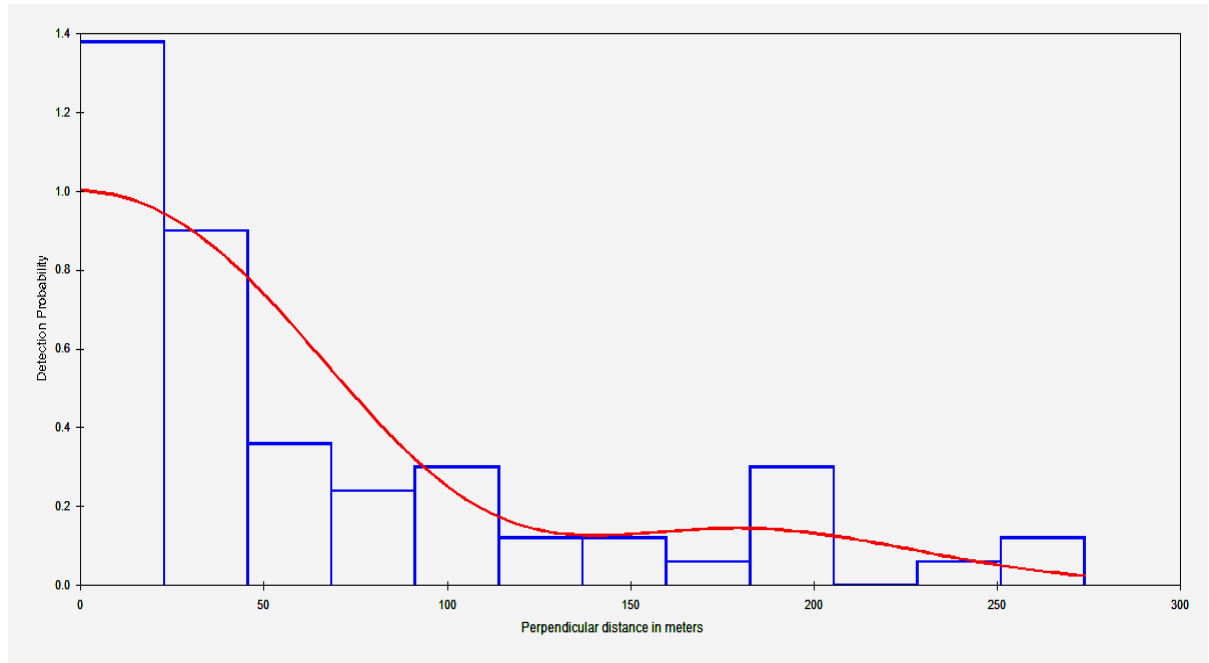


Fig. 2. 2a. Histogram of perpendicular distances showing detection probability

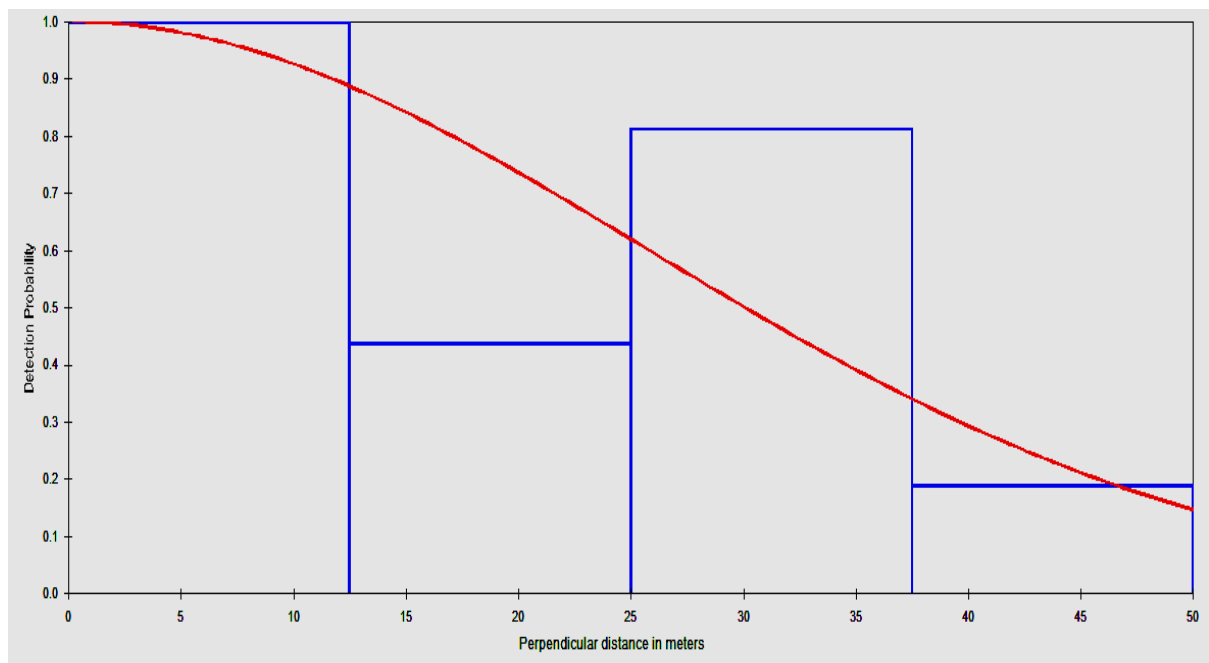


Fig. 2.2b. Frequency histogram of truncated perpendicular distance distances

CALHOME (CALfoni HOME ranges- an animal movement program) (Kie *et al.*, 1996) was used to calculate home range. A polygon was constructed, to include all GPS points marked from daily animal follows over the whole data collection period. The points needed to calculate home range (written in CALHOME) were later imported to the Geographical Information System Arc view 3.3. The positions

(recorded every 20 minutes) were plotted on the GIS generated map to provide an objective measure of daily and monthly range. The total distance travelled per day was calculated using GIS measuring tools and the maximum area used by the group was obtained. For purposes of providing a method comparison, Adaptive Kernel method (ADK) was also used to calculate home range using similar location points. Mean daily ranges were compared among seasons using one-way ANOVA.

Dominance relationships and competition

Aggressive behavioural variables were assessed as expression of dominance following van Hoof & Wensing (1987). Relative dominance ranks were defined and determined by the direction of aggressive and submissive dyadic interactions; including chases, stares, lunges, fights, bites, neck bites, hits, screams, grimaces, crouches, flee, involve third party, intervenes, confronts, avoids, and supplants. I carried out hierarchical rank order analysis using MatMan software (de Vries *et al.*, 1993). Since the behaviours analysed involved unknown relationships, I calculated the improved linearity index (h') in Matman. For a hierarchy to be strongly linear, the index of linearity should be ≥ 0.90 (Martin & Bateson, 1993). Percentage of rank reversal was also used to determine linearity. I used a scaling method developed by Batchelder & Bershard (1979) and first applied to dominance matrices by Jameson *et al.* (1999). In general, an individual's dominance rank depends on its proportion of wins and losses in agonistic interactions, and the scaled dominance scores met in dominance interactions. When a relationship between individuals was unclear, the average rank was assigned to both.

All occurrences (Altmann, 1974) data were used to determine the degree of unidirectionality of dominance relationships among individuals in any dyad and degree of linearity of the rank orders (Leinfelder *et al.*, 2001; Vervaecke *et al.*, 2000). One interaction was used to establish directionality in any dyad (i.e. pair wise encounters) using directional consistency index (DC). DC measures the frequency with which the behaviour occurred in its more frequent direction relative to total number of times the behaviour occurred (van Hooff & Wensing, 1987). The index ranges between 0 (completely bidirectional) to 1 (completely unidirectional), and it is calculated by $(H-L) / (H+L)$. H is the total number of times behaviour occurred in the direction of higher frequency and L is the total number of agonistic interactions in the direction of

lower frequency e.g. (Archie *et al.*, 2006; Murray, 2007). As a descriptive measure, the numbers of one-way relationships were counted (i.e. number of dyads in which aggression was shown in one direction only, irrespective of its frequency within the dyad).

Competition rates were estimated on the basis of aggression: i.e. the aggression rate, defined as the number of agonistic behaviours (stares, lunges, chases, fights, bites, neck bites, hits, screams, grimaces, crouches, flee, involve third party, intervenes and confronts,) per hour. I used the Wilcoxon Matched Pairs Test to determine whether or not aggression rates were dependent on distance of the location of neighbour inside the 5m radius patch.

Nearest neighbour

A simple ratio association index (Cairns & Schwager, 1987) was used to calculate the association indices, using the number of minutes two individuals were nearest neighbours, divided by the sum of the number of minutes each was observed without the other and the number of minutes they were neighbours. Association indices could vary from 1 (nearest neighbours all the time) to 0 (never nearest neighbours). Grooming samples from instantaneous scans were compared with association samples. I used paired t- tests to examine if there is any difference between close associates and grooming partners.

Affiliative relationships

For each focal female-female dyad, hourly rates of interaction were calculated by dividing the number of total interactions between A and B by the sum of total observation time (hours) that A and B were observed (Range & Noë, 2002). In addition, I tested whether rank distance affected affiliative behaviour among males and females. Rank distance was defined as the number of adult individuals ranking between the two individuals concerned plus 1 (i.e. adjacently ranking individuals have a rank distance of 1). The measure was based on the constructed dominance hierarchies. The other variable was proximity, defined as the percentage of instantaneous samples spent as nearest neighbours during scan sample observations. The last variable was grooming duration, defined as the percentage of instantaneous

samples spent grooming during scan sample observations. One dyadic matrix for each of these variables was created for female-female and male-male interactions

Male-infant affiliations form and pattern frequencies were summarised for each male. The data were later correlated with mating data to examine relationships of infant caring males and their mating opportunities. Grooming data were grouped into bouts (defined as a continuous period of grooming involving the same 2 individuals). The duration of grooming bouts was recorded to the nearest minute. If the identity of one of the individuals changed or grooming was suspended for more than 1 minute, I considered the bout to have ended. To make this analysis comparable to Manson et al. (2004) and Chancellor & Isbell (2009), voluntary and non voluntarily terminated bouts were not differentiated. The total amount of time spent grooming was estimated for each dyad as the proportion of all sample intervals during which grooming occurred. Minutes per hour were calculated for each female dyad. For all dyads, there were no more than 2 episodes between pairs.

The first groomer was designed as the instigator and the second individual as receiver or instigator or receiver in the second bout. All bouts for each instigator individual were extracted, and organised into clusters defined by the identity of the recipient. The arrangement provided an upper limit of $N(N-1)$ clusters for each age-sex group, (N is the number of a known age-sex group in the sample e.g. I for females, $N=12$). There could be two clusters per dyad i.e. a cluster when for example, female MWK initiated and MDK was the recipient and vice versa. I used logistic regression to test the hypothesis that duration of the first initiator's grooming episode predicts reciprocation by the recipient. The model included duration of the first grooming of the initiator, group, and the interaction between initiator and the group as fixed effect. For grooming bouts that were reciprocated, I tested the hypothesis that the time the initiator invests grooming predicts the time the recipient grooms. The model included total grooming time of initiator, age-sex class in the group and the interaction between initiator and that age-sex class in the group. Analyses for grooming data were performed using the software JMP 7 (SAS Institute Inc., Cary NC).

Results

Group size and composition

During the six month study, the Njokamoni group of mangabeys showed substantial growth. The group had 48 individuals at onset of the study (December 2007) and 62 animals at study end (June 2008), with 3 births occurring during that period. The mean size of Njokamoni mangabey group between Dec 2007 to May 2008 was 59.1 ± 0.3 individuals (n= 148 days, median =59, mode = 62), larger than previous estimates for 2000 to 2005 (Jones *et al.*, 2006). Figure 2.3 summarises monthly data for group size and age-sex composition of the group. The mean size, median (and mode) composition for each class is shown in Table 2.1. The socionomic sex ratio (i.e. number of adult females divided by the number of adult males) for Sanje mangabey is thus 2.83. There was a small, non consistent variation in numbers of individuals in the group over seasons. There was a 16 % increase in numbers of individuals seen in January as the rains progressed; a 6% decrease in February while rains increased, a 12% total increase from February till May, and then a 9% decrease in May to June.

Table 2.1. Total age and sex composition of Njokamoni group of mangabeys

Mangabey age and sex	Mean \pm SE	Median	Mode
Adult male	4.6 ± 0.1	5.0	5.0
Adult female	13.0 ± 0.2	13.0	14.0
Sub adults	16.7 ± 0.3	16.5	16.0
Large juveniles	15.1 ± 0.3	16.0	18.0
Small juveniles	5.9 ± 0.2	5.0	5.0
Infants	3.2 ± 0.1	3.0	3.0
Group size	59.1 ± 0.3	59.0	62.0

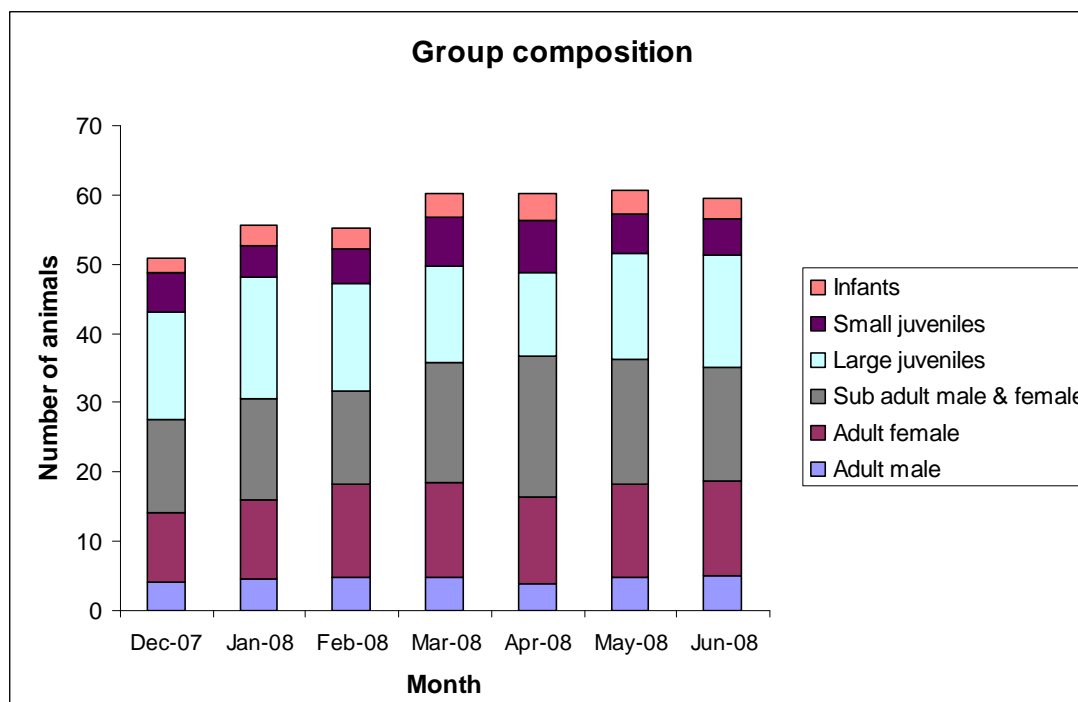


Fig. 2.3. Mean age and sex composition of Njokamoni mangabeys as of December 13 2007 to 24th June 2008.

Population density

Between June 2007 and May 2008, 51 groups of mangabeys were recorded on Sanje, Campsite 3 and Mwanihana trails. The group sizes for the Mwanihana transect ranged from 3-20 individuals, 3-10 in Campsite 3, and 5 to 17 in Sanje. Five solitary individuals were counted, and 10 groups or solitary individuals were heard along three transects during 1 year sampling (my own records, and the Park records for six months prior my study).

Table 2.2 shows performance of models and statistics used to select the best model for density estimation. AIC selects the half normal key with simple adjustment as the best model fitting the grouped data ($P = 0.001$). The population density estimate of mangabeys in the lower Mwanihana forest (300-900 m above sea level) in June 2007 to May 2008 was 1.24 ± 0.33 mangabeys per hectare (Table 2.3). This population density is smaller than that estimated by Dinesen *et al.* (2001) and that considered by Ehardt *et al.* (2005) after re-analysing Dinesen *et al.*'s (2001) and Wasser's (1993) data. The total mangabey population in Mwanihana was estimated to be 689 individuals. This estimate is slightly higher than that reported by Dinesen *et al.* (2001)

for lower Mwanihana (500 individuals) and very close to Ehardt *et al.*'s (2005) 700 individuals estimate for the whole of Mwanihana.

Table 2.2. Model performance and mangabey density estimate selection statistics. A robust model is shown with an asterisk ().*

Model (key/adjustment)	AIC	Density	LCL	UCL	CV	p-value ∞
50 m half normal/simple	*297.91	1.236	0.705	2.168	0.263	0.001
50 m hazard rate/hermite	298.31	1.521	0.879	2.634	0.252	0.001
50 m uniform/simple	298.47	1.239	0.727	2.109	0.233	0.001
100 m hazard rate/hermite	*444.85	6.753	3.500	13.032	0.337	0.008
100 Uniform/cosine	462.24	0.928	0.928	2.386	0.234	0.008
100 m half normal/cosine	463.58	1.545	0.949	2.516	0.243	0.008
hazard rate/simple	*669.03	3.998	2.203	7.256	0.307	0.013
Half normal/cosine	684.690	1.472	1.034	2.096	0.178	0.026
Uniform/cosine	685.000	1.116	0.801	1.555	0.167	0.026

AIC- Akaike's Information Criterion, UCL& UCL- density lower and upper confidence limits, CV- coefficient of variation and ∞ -Goodness of fit test.

Detection probability, encounter rate and cluster sizes of mangabeys

As per assumptions of LTDS, the probability of detecting mangabeys decreased with distance for both original and truncated distances (Fig 2.2 a & b above). The overall probability of observing mangabeys in the forest was 0.61 (df. = 38, CV= 14.4). The mean cluster size was 13.46 ± 0.51 , $n=39$, larger than the expected cluster size of 12.28 ± 0.34 (Table 2.3). No cluster size bias adjustments were made for all three transect distances. The number of mangabeys encountered per square kilometre traversed was 3.31. The estimated effective strip-50m width for the 3 transects was 30.42 ± 4.37 (the widths were not significantly different for all transects, $p = 0.06$). The density of mangabey clusters in Mwanihana was 0.55 ± 0.12 mangabeys/ha⁻¹.

Table 2.3. Mangabeys encounter rate (mangabeys/ km²), cluster size, population density and density of clusters during one year samples for 3 transects in Mwanihana.

Parameter	SE	CV	95% CI		d.f
			LCL	UCL	
Effective strip width	30.42	4.37	14.36	22.18	40.6
Mean cluster size	13.45	0.51	14.66	12.58	14.65
Expected cluster size	12.28	0.34	14.77	11.69	30.06
Encounter rate	3.31	-	16.4	1.64	6.6
Population density	1.24	0.33	26.33	0.71	2.17

Density of clusters	0.54	0.12	21.8	0.32	0.92	3
Number of mangabey encounters	51					
Among transect encounter rate comparison	$\chi^2 = 6.1$, $p = 0.05$					

Ranging behaviour

Daily path length, patterns of movement and seasonal variation

During the six months study period 1448 location points for the Njokamoni mangabey group were collected. The group travelled an average daily distance of 1760 ± 8 m (range 843-2130m) moving at an average speed of 103 m per 20 minutes (303m/hr). There was a significant deviation in distribution of distance moved in 20 m from expected Poisson distribution for both seasons ($\chi^2 = 28.9$, $P < 0.002$ and $\chi^2 = 40.8$, $P < 0.001$ during dry and wet season respectively). There was considerable variation in the daily distance travelled, mean rate of group movement and speed during rain and dryer months. The wet season in Udzungwa last from mid December to April and the dry season start in May and extend until November (details are covered in Chapter 3). There was a marked difference in distance travelled during days with rain and no rain (cut-off: no rain = 0-100 mm/ month; rain ≥ 100.1 mm/month). The 100 mm rainfall cut-off was used because, in Tanzania 87% of regions receive rainfall of less than 100 mm per month during the drier months (T.M.A, 2008).

On days (drier days, $n = 27$) during which the group visited distant forest patches while foraging, the monkeys travelled significantly further ($p < 0.001$), and significantly faster ($p < 0.001$) via the most direct routes and with fewer stops and backtracks compared to days when they visited closer food patches (rainy days, $n = 89$). This result indicates that the group spent more time in certain areas, and moved rapidly through others, in relation to weather conditions. These patterns of movements also, I believe, relate to food and food encounter rates (i.e. abundance), rates of renewal in the patches and animal's spatial memory ability during foraging- see (Brain, 1990; Buzzard, 2006; Erhart & Overdorff, 2008; Freeland, 1980; Homewood, 1976; Kinnaird, 1990a). The days the group made longer visits also increased the home range size from 173.7 ha in the rainy season to 343.4 ha in the dry season. Longer daily path lengths were associated with increased travel speeds to distant forest (i.e. patches) and then back to the regularly used portion of the home range in Njokamoni. These results reflect the importance of seasonal factors and food tree

abundance, distribution or biomass in relation to home range use by the Sanje mangabey.

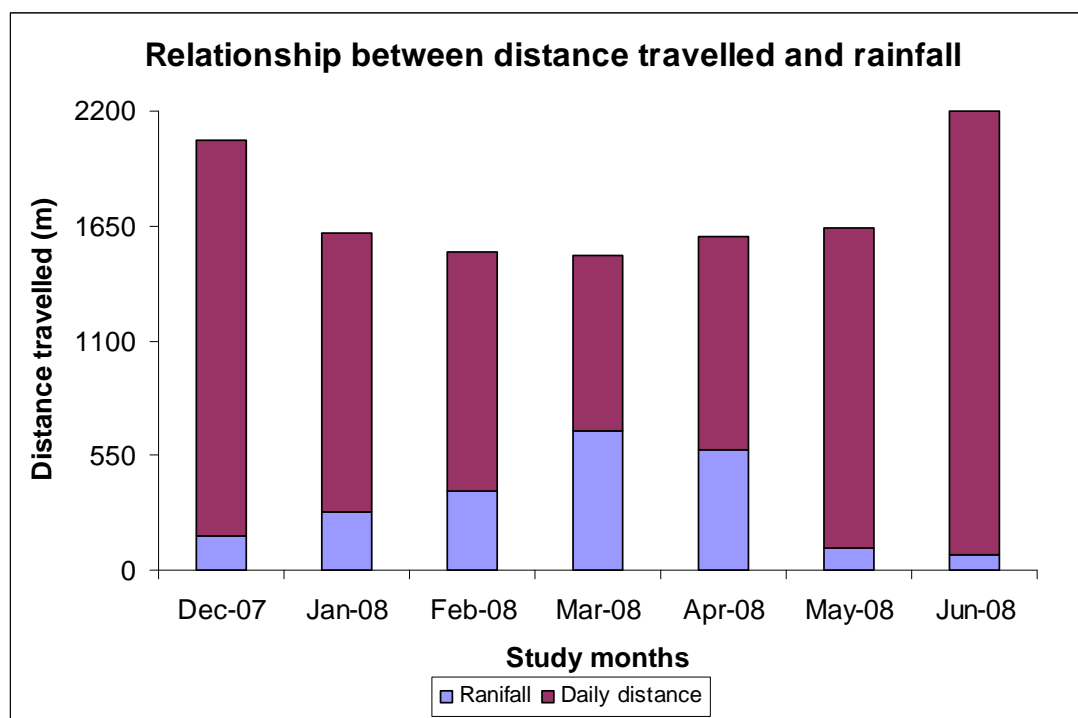


Fig. 2.4. Relationship between mean distances travelled and amount of rainfall. There was significant difference between mean monthly distance and total rainfall ($p < 0.001$).

Home range

The mean home range during the six month study calculated using Minimum Convex Polygon method was 301 ha. Using the Adaptive Kernel method, home range was 353 ha; bigger than MCP. This home range estimate is larger than home range estimates made during the past 2 years, when the group ranged entirely within the Njokamoni forests. The current home range included forests surrounding the Njokamoni camp and Sonjo. The group's home area was from Njokamoni river water intake at the forest edges to Njokamoni water fall, south of water fall to Nyati, Pimbi, Limao, Kima, Korongo *Milletia*, and MP sleeping camps. The range extends from Korongo *Milletia* to Mponjoli, Ukindu A & B, *Treculia*, and Njokamoni base camp to wooded forest at Ummy camp 1 & 2 in Sonjo around Mwanihana trail. Figure 2.5 shows the home range area for MCP and ADK calculates using 95% contour intervals.

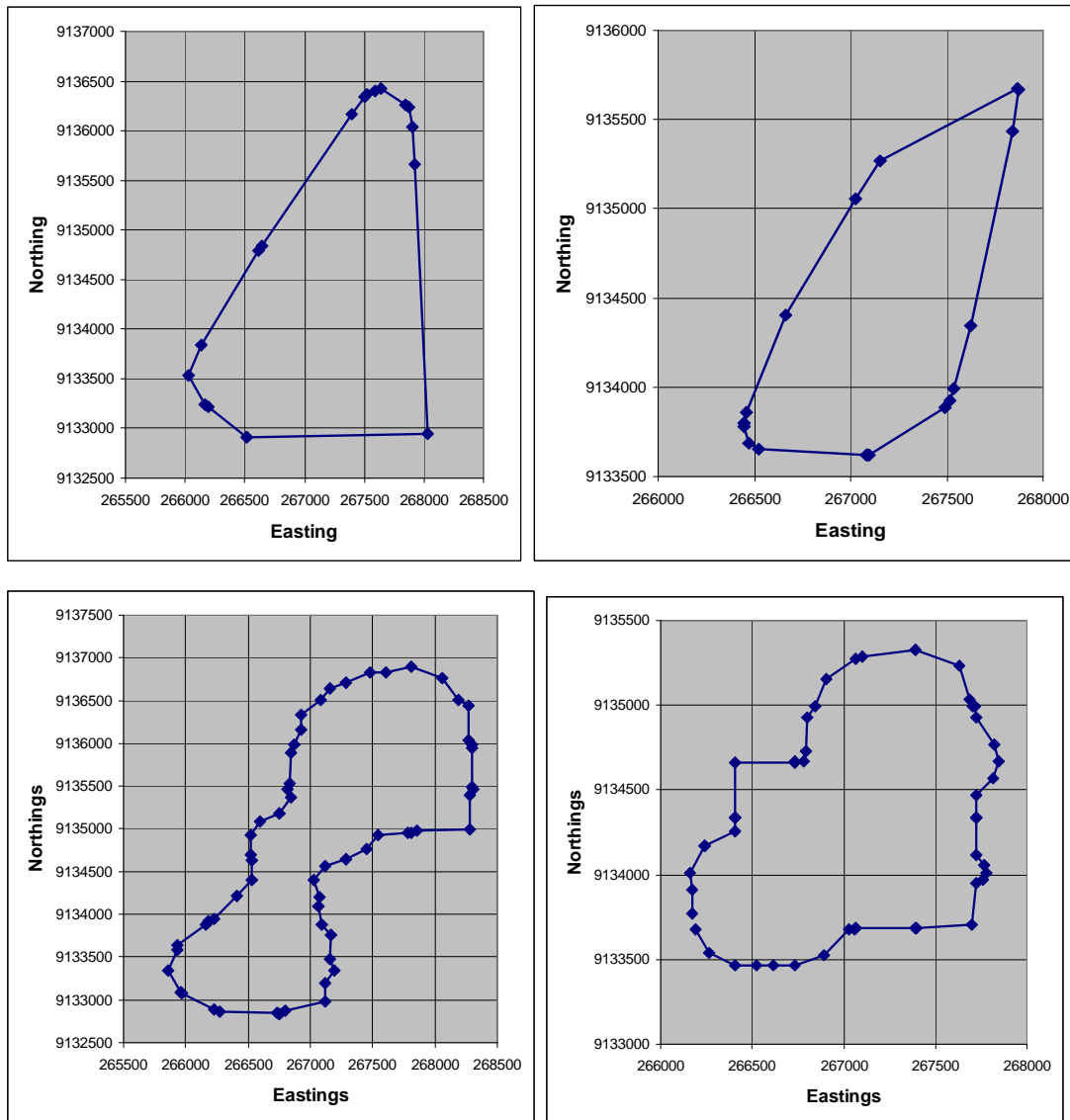


Fig 2.5. A sample of output polygons from Calhome, generated on Excel using sample data set showing 95% utilization distributions for both Minimum Convex Polygon, MCP (top) and Adaptive Kernel, ADK (below) methods used to calculate home ranges. Figures on the left refer to the dry season. The wet season ranges are shown on the right. The grid size for both polygons is 500m.

Variations among methods and between seasons, and core area use

There were variations in the home range area used by the group during dry and rain seasons (Figure 2.5). During dry periods, the MCP estimate of home range was 454.1 ha, and the ADK home range was of 449.1 ha. In the wet season, the home range estimates were 157.5 ha (MCP) and 210.6 ha (ADK). Estimates of the home ranges using the two methods were positively correlated ($r^2 > 0.76$, $P < 0.05$). However, as home range increased, variation in the sizes calculated using the two methods also increased ($F = 87.47$, $r^2 = 0.91$, $P < 0.001$). There were differences in the estimates of the home range size between the two methods ($F = 8.12$, $P < 0.005$). The results also

suggest that the Njokamoni group of Sanje mangabeys use 4 distinct core areas as part of their range (Figure 2.6). This result confirms my assumptions that the group might be ranging entirely within certain parts of forest during one season before moving, and that the animals spend ‘quality time’ in other areas, perhaps feed on rare items that might not be available in the other area (see chapter 3 for further information on this question).

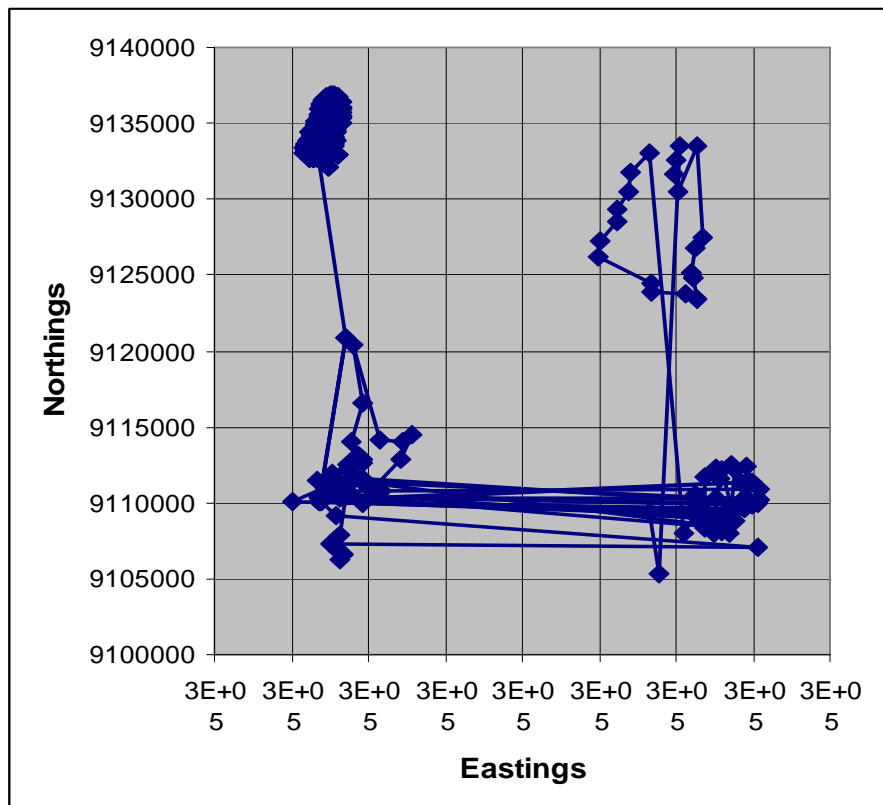


Figure 2.6. Adaptive Kernel output all points polygon showing 4 distinct core area of the home range used by Njokamoni group. Grid size = 500m.

Agonistic behaviour and social dominance

Summary of agonistic behaviour

I recorded 4768 aggressive acts during 10 hours of daily scan observations. The mean rate of aggression in the group was 79.4 episodes per day (mean rate per hour was 0.85). Adult males were involved in aggressive acts more often than any age class in this group (Figure 2.7). The rate of aggression per hour for males was 1.69. Females were involved in aggression at a rate of 0.68 per hour; male- female rate was 1.03/hr and the female-male rate was 0.88/hr. The juveniles were least involved in aggressive

acts. The rate for juveniles was 0.27/hr and the juvenile-infants rate was 0.01/hr. Males and female aggression towards juveniles was small compared to that among adults; male-juvenile rate was 0.41/hr, male-infant 0.02/hr, female-juvenile 0.33/hr and female-infant 0.02/hr. Table 4 summarizes these data on aggression which resulted in submission. The matrix of aggression without fleeing is presented in Table 5.

Aggressive acts by males more often involved chasing and biting than those of females. Adult males threaten juveniles more often (72%) than they threaten adult females (51%) or sub adult males (43%). When threatened by females, sub adult males seldom flee, but did so when threatened by males. Although the general trend was for males to be aggressive towards females, there were cases where females initiated aggressive acts towards males and won. These interactions mainly involved two females, KL and BMS (high ranking in the female rank order) and 2 low ranking males, (AMB (third in rank) and AMC (fourth in rank)). During aggressive acts, these two females were often supported by 2 other males (AMR and AMK) that were higher in rank and largest in size. The support occurred whenever defeat was likely. Table 2.4 summarizes observed aggressive interactions between identifiable individuals as initiators (row) and receivers (column individuals). The matrix of aggression which was not followed by fleeing is presented in Table 2.5. These are the data from which I determined the dominance relationships between individuals (see next section).

There were significant variations in rates of aggression between the wet and dry seasons ($P < 0.001$). During rainy season, rates of aggression were smaller (group rate per hour = 40.2) than during dry days (81.7 per hour).

Table 2.4. Total aggression with (fleeing) matrix for adult and sub adult male and females. Adult and sub adult males (first 7 in the row and column) and adult and sub adult female are shown in the following row and column. Aggression initiators are given by row individuals and receivers by column individuals.

	AMB	AMC	AMK	AMR	AMM	SAM	SAN	KL	CT	KM	BMS	MDK	SN	KMH	MWK	MT	BMK	SAFA	SIFA
AMB	X		2	0	26	8	4	2	4	0	0	0	2	0	0	0	0	2	2
AMC		0 X		0	17	6	10	6	8	0	0	6	0	4	0	2	0	0	0
AMK		2	0 X		19	4	4	2	0	0	0	0	0	0	0	0	0	0	0
AMR		15	6	8 X		6	6	14	0	0	0	0	0	2	0	0	2	0	0
AMM		0	2	12	4 X		4	4	0	2	2	0	0	0	0	0	0	0	0
SAM		36	38	38	56	8 X		63	14	8	8	5	12	10	4	8	8	6	18
SAN		22	24	26	61	14	2 X		4	0	0	6	0	0	2	6	0	2	42
KL		8	10	4	4	0	10	2 X		0	0	2	0	1	2	0	0	2	0
CT		2	8	6	4	0	2	2	6 X		0	2	2	0	0	0	0	4	6
KM		4	0	6	4	2	2	2	2	0 X		1	0	4	0	0	0	2	3
BMS		6	6	4	8	10	18	4	8	0	2 X		2	0	0	2	2	0	2
MDK		6	6	4	8	0	4	10	0	0	0	4 X		0	0	0	0	2	6
SN		4	12	4	12	0	2	2	0	2	2	2	4 X		2	2	0	0	2
KMH		6	0	2	0	6	2	4	4	2	0	0	0	0 X		0	2	2	4
MWK		6	8	8	0	2	4	6	2	0	2	4	6	3	2 X		6	2	4
MT		4	10	6	0	0	6	6	0	0	0	0	2	0	0	0 X		2	6
BMK		4	8	4	8	4	4	10	2	2	0	0	4	0	0	2	2 X		0
SAFA		8	12	8	10	4	37	37	7	0	2	14	10	2	10	8	2	16 X	
SIFA		0	4	2	2	4	26	32	6	0	2	8	2	3	2	4	2	0	40 X

Table 2.5. Frequency of total aggression without fleeing. Receivers are given by row individuals and initiators by column individuals.

Recipient of aggression (which does not flee)																			
Aggressor	AMB	AMC	AMK	AMR	AMM	SAM	SAN	KL	CT	KM	BMS	MDK	SN	KMH	MWK	MT	BMK	SAFA	SIFA
AMB	X	2	0	6	5	0	0	0	0	0	0	0	0	0	0	0	0	2	2
AMC	0	X	0	5	2	4	4	1	0	0	1	0	0	0	0	0	0	0	0
AMK	0	0	X	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AMR	3	3	2	X	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0
AMM	0	0	3	1	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAM	0	0	0	0	2	X	1	0	2	1	1	2	2	0	1	1	1	3	1
SAN	0	2	0	0	0	0	X	0	0	0	0	0	0	0	1	0	0	2	2
KL	1	2	0	0	0	0	0	X	0	0	0	0	1	0	0	0	0	0	0
CT	0	0	0	0	0	0	0	0	X	0	0	2	0	1	1	0	1	0	0
KM	0	0	0	0	0	0	0	0	0	X	1	0	0	0	0	0	0	0	0
BMS	2	1	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	2	2
MDK	0	0	0	0	0	0	1	0	0	0	0	X	0	0	0	0	2	0	2
SN	0	0	0	0	0	1	1	0	0	0	0	0	X	0	0	0	0	0	2
KMH	0	0	0	0	0	0	0	0	1	0	0	0	0	X	0	2	2	2	0
MWK	0	0	0	0	0	0	0	2	0	2	0	1	0	0	X	1	0	1	0
MT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	1	2
BMK	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	X	0	0
SAFA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	X	2
SIFA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	X

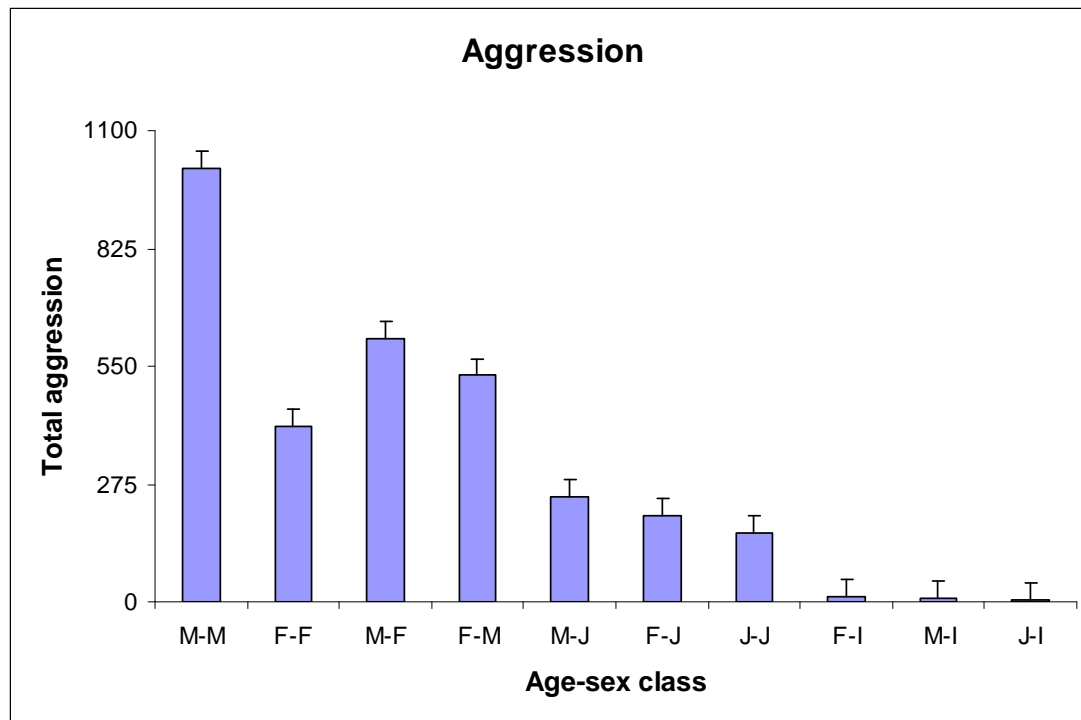


Fig. 2.7. Total aggression by different classes of the Njokamoni group.

Note: M = Males (5 adult & 2 sub adult males), F = Females (10 adults and 2 sub adults), J = Juveniles (4 large juveniles & 4 small juveniles) and I = Infants (3 infants).

Dominance

I observed 201 dominance interactions between adults and sub adult males and females from group's total 4768 agonistic interactions, during 794.3 observation hours. Dominance interactions were defined as those in which one animal was clearly aggressive and won an encounter with another, submissive individual. Forty dominance interactions were observed for males (5 adult and 2 sub-adults). Individual males won 95% of all possible dyads ($n = 42$). Dominance relations were unknown between male AMC and AMK (Table 2.6), since they were both observed to flee from one another. Male AMR was the highest ranking individual. Among the 12 females used in analyses I observed 100 dominance interactions in agonistic encounters. Only 76% of interactions in female dyads produced clear-cut winners out of 132 possible (Table 2.7). The highest ranking females was KL (lactating during 5/6 months of data collection), followed closely by BMS.

Table 2.6. Dominance matrix for adult and two sub-adults males

	AMB	AMC	AMK	AMR	AMM	SAM	SAN
AMB	X		1	0	1	1	0
AMC		0 X		0	1	1	0
AMK		1	0 X		1	0	0

AMR	0	0	0	X		0	0	0
AMM	0	0	1		1	X	0	0
SAM	1	1	1		1		1	X
SAN	1	1	1		1		0	X

Dominance matrix between adult males and 2 sub adult males; 1: indicates row individual is dominant to column individual, 0: column individual is dominant to row individual, bold printed 0: unknown relationship.

Table 2.7. Dominance matrix for adult and two sub-adults females

	KL	CT	KM	BMS	MDK	SN	KMH	MWK	MT	BMK	SAFA	SIFA
KL	X	0	0	0	0	1	0	0	0	0	0	0
CT	1	X	0	1	1	0	0	0	0	1	0	0
KM	1	0	X	0	0	1	0	0	0	1	0	0
BMS	1	0	1	X	0	0	0	0	1	0	0	0
MDK	1	0	0	1	X	0	0	0	0	1	0	0
SN	0	1	0	1	1	X	1	0	0	0	0	1
KMH	1	1	0	0	0	0	X	0	1	1	0	0
MWK	1	0	1	1	1	1	1	X	1	0	0	0
MT	0	0	0	0	1	0	0	0	X	0	1	0
BMK	0	0	0	1	0	0	0	0	0	X	0	0
SAFA	1	0	0	1	1	1	1	1	0	1	X	0
SIFA	1	0	0	1	0	0	1	1	0	0	1	X

Dominance matrix between adult females and 2 sub adult females; 1: indicates row individual is dominant to column individual, 0: column individual is dominant to row individual, bold printed 0: unknown relationship.

Linearity and directional consistency in dominance

Linearity and directionality of dominance relationships were calculated from dominance-submission interactions. Fleeing upon aggression was a good dominance measure in adult males and females since it has a high significant linearity index ($h' = 0.92$, $p = 0.0281$) and a high directional consistency index ($DC = 0.91$). For the whole group, 59% of all dyads showed unidirectional aggression. For females, the linearity index, h' was 0.93, $p = 0.0382$ and $DC = 0.94$). Among males, the linearity index was low but significant ($h' = 0.84$, $p = 0.041$). The males, however, showed a high directional consistency index, $DC = 0.94$. This result suggests that frequencies of agonistic interactions among individual Sanje mangabey are robust/formal indicators of dominance. The matrix of aggressive behaviours that was not followed by fleeing had a low and non significant index of linearity ($h' = 0.66$, $p = 0.217$), and a low directional consistency index, $DC = 0.63$ and almost 72% of dyads showed bidirectional aggression.

Given the presence of dominance interactions between females that showed unknown relationships, I tested for convergence of scaled dominance following Jameson *et al.* (1999). The scaled score converged after 24 iterations. The results for scaled dominance are presented in table 2.8. Categorical ranks were assigned to all twelve females (as high, middle and low) based on scaled scores. Rank orders are based on individual's relative number of wins and losses within all interactions as estimated in the dominance interactions. Two female dyads and one triad were assigned equal rank orders (MDK-BMK, KMH-SN, and CT-MWK-SIFA) because they showed equal scaled numbers of submissive interactions to each other. Table 2.9 summarizes dominance ranks for males. Since there were high directional consistency indices for both males and females, it seems unlikely that the higher ranking individuals would be overturned to low ranking ones. For males, one dyad was assigned equal rank because they showed similar amounts of numbers of submissive responses towards each other.

Table 8. Scaled ranks, rank order and rank categories for 10 adult and two sub adult females

Female ID	Scaled rank	Rank order	categorical rank
KL	1.973	1	High
BMS	1.824	2	High
MDK	1.705	3	Medium
BMK	1.625	3	Medium
KMH	1.251	4	Medium
SN	1.092	4	Medium
MT	0.921	5	Medium
KM	0.563	6	Medium
CT	0.191	7	Low
MWK	0.097	7	Low
SIFA	0.023	7	Low
SAFI	-0.954	8	Low

Categorical ranks are based on scaled dominance values

Table 2.9. Scaled ranks, rank order and rank categories for 5 adult and two sub adult males

Male ID	Scaled rank	Rank order	categorical rank
AMR	2.823	1	High
AMM	2.142	2	Medium
AMB	1.674	3	Medium
AMK	1.538	4	Medium
AMC	1.269	4	Low
SAN	0.917	5	Low
SAM	0.821	6	Low

Categorical ranks are based on scaled dominance values

Spatial/ affiliative relationships

I collected 1146 focal follows on 22 individuals Sanje mangabeys (table 2.10). Individuals with less than 10 follows were excluded from the analysis. During the follows, I observed 412 approaches between individuals of different sex (approach rate = 0.39 approaches/follow hour). Approaching adult and sub adult individuals often established proximity (43%) than, passing (31%), grooming/solicit grooming (12%), feed (11) or scream (3%). Approached individuals often watched (33%), leaved (21%), had no response (15%), groomed (7%), turned away (5), received grooming (5%) or feed (4). I found no significant difference between grooming partner and nearest neighbours ($P > 0.05$).

Table 2.10. Summary of individual follows.

Name	Focal follows	Follow days	Total sample d minutes	Minutes out of site
AMR	66	55	1402	18
AMB	39	28	1432	18
AMM	48	29	919	41
AMC	42	31	912	18
AMK	62	55	1402	8
SAM	74	63	1422	58
SAN	40	17	666	74
KL	92	63	1606	134
CT	55	42	1052	148
KM	69	48	1358	22
BMS	39	31	759	21
MDK	40	21	791	9
SN	48	29	919	41
KMH	40	17	666	134
MWK	36	14	716	4
MT	38	16	756	4
BMK	34	19	662	18
SAFI	71	60	1392	28
SIFA	74	53	1388	32
INFANT 1	60	42	1042	8
INFANT 2	55	48	919	21
INFANT 3	24	16	664	16

Comparisons across age and sex classes showed that individuals differed in frequencies of association. Adult females did not associate evenly with other adult females in the group. Females associate more with males and their young than with other females or any other group members (Figure 2.8). Males associated with sub adult females a little more than with adult females, and sub adults associated more with adult males than with other sub adults. The association indices can vary from 1 (nearest neighbours all the time) to 0 (never nearest neighbours). Rank distance and association was positively correlated for both males and females (Pearson's r rank distance-proximity correlation for female-female = 0.69, Male-male = 0.73, $P < 0.001$). The positive correlation between individuals' rank distance and association suggests the relative amount proximity occurs in the group based on rank order between dyads.

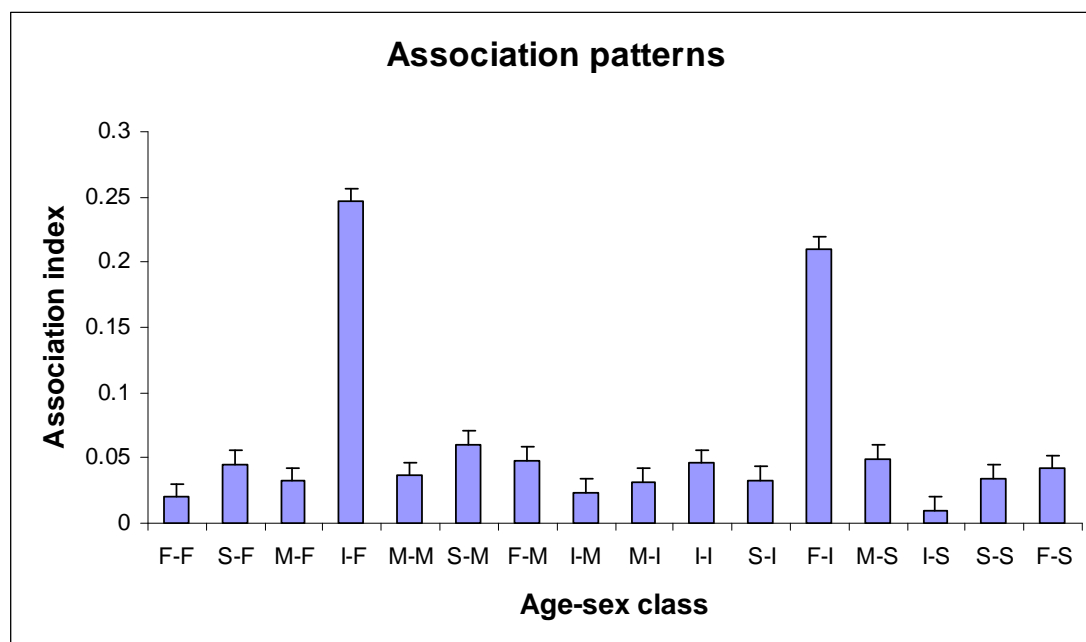


Fig.2.8. Association among Sanje mangabey age-sex classes, Simple ration association index was used to calculate associations between adult females and males (F & M), sub adults females and males (S), and infants (I) frequencies of the total observation time between individuals that were nearest neighbours.

Grooming

Between December 2007 and May 2008, the Njokamoni group spent an average of 8% of each day grooming (Table 2.11). There were 532 grooming bouts in 18 clusters in my analysis. On an average, 5.3% grooming bouts were reciprocated (range, 5-26). Adult female mangabeys reciprocated in 14% of bouts of 18 clusters, 11 (13%) had a

bout that was reciprocated at least once. There was a significant relationship between duration of initiator's first grooming episode and subsequent reciprocation by receivers in all age classes (Pearson's: $r = 0.49$, $P = 0.006$, $\chi^2 = 1.46$, $P < 0.05$).

Table 2.11. Summary of grooming bouts

	Adult Females	Adult Males	Juveniles	Group
Mean % time grooming	6.3	6.7	3.1	8.3
Mean % reciprocated bouts	14	7.6	26.2	5.3
Mean % clusters reciprocated at least once	91	51	89	72.2
Number of cluster	18			
Number of bouts	532			

Grooming rates among age-sex classes

When grooming episodes were averaged across dyads for each individual, and then averaged across individuals for each sex class, females groomed males at a rate of 6.64 sec/ hour, which is 133 times as less as females groomed females. Female groomed females at a rate of 0.05sec/hour and male-male (0.04sec/hour). Sub adults groomed males at a rate of 6.36sec/hour, female- infant rate was 5.27 sec/hour and female-juvenile rate was 5.23sec/hour (Figure 2.9). Tables 2.12 and 2.13 show grooming rates for each female-female and male-male dyad between December 2007 and June 2008.

Table 2.12. Rates of grooming (seconds per hour), between adult females

	CT	KL	KMH	MT	SN	BMS	MDK	MWK	BMK	KM
CT	X	0.3	0.8	0	0.1	0.2	0.4	0.8	0.2	0.2
KL	0.8	X	0.1	0.2	0.9	0.9	0.9	0.5	0.7	0.4
KMH	0	0.2	X	0.8	0	0.2	0	0.1	0	0.3
MT	0	0.5	0.6	X	1.1	0	0.2	0.6	0.4	0.3
SN	0.1	0.1	0.4	0.8	X	0.2	0.1	0.8	0.5	0.1
BMS	0.3	1	0.6	0.1	0.8	X	0.5	0	0.6	0
MDK	0.2	0.1	1.1	0.4	0.1	0.1	X	0.3	0.2	0
MWK	0	0.3	0.6	0	0.5	0.6	0.3	X	0.3	0.2
BMK	0.3	0.4	0.4	0.2	0.1	0.5	0	0.3	X	0.4
KM	0	0	0.5	0.1	0.1	0.2	0.2	0.1	0	X

Initiator are given by column individual and receivers by row individual

Table 2.13. Rates of grooming (seconds per hour), between adult males

	AMB	AMC	AMK	AMM	AMR	SAM	SAN
AMB	X	0.00	0.00	0.00	0.00	0.00	0.00
AMC	0.00	X	0.00	0.00	0.10	0.00	0.00
AMK	0.00	0.00	X	0.00	0.00	0.00	0.00
AMM	0.00	0.00	0.10	X	0.00	0.00	0.00

AMR	0.00	0.00	0.00	0.00	X		0.00	0.20
SAM	0.40	0.30	0.40	0.50		1.40	X	0.10
SAN	1.20	0.80	0.30	0.20		2.90	0.00	X

Initiator are given by column individual and receivers by row individual

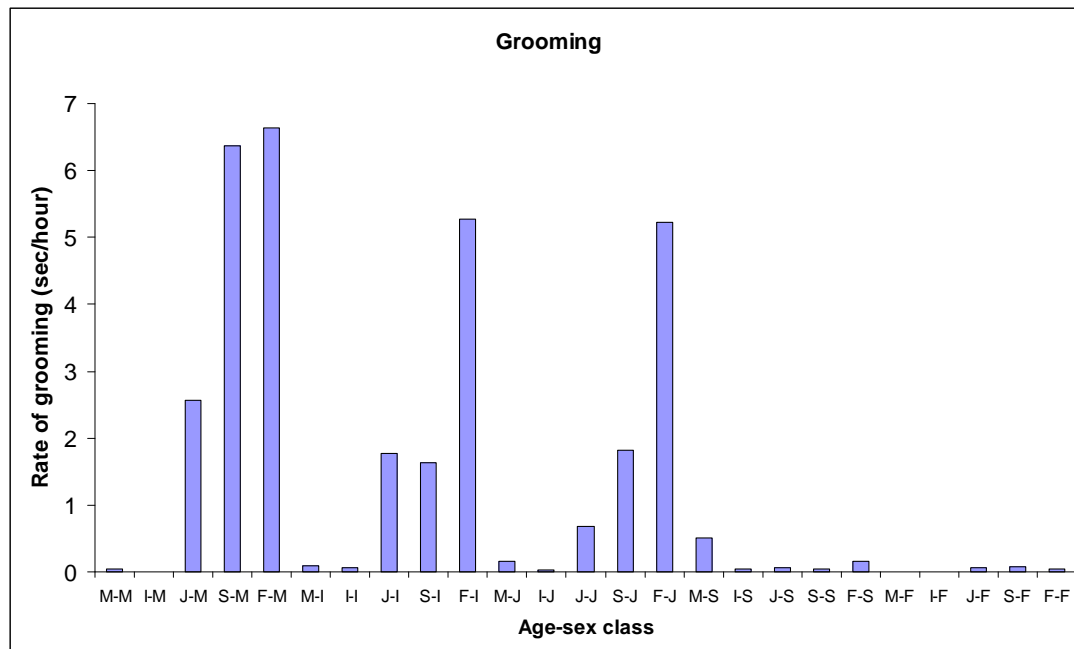


Figure 2.9. Rates of grooming (sec/hour) among age-sex classes. M: Adult males ($n = 5$), F: Adult female ($n = 10$), S: adults ($n = 4$), J: Juveniles ($n = 8$) and I: Clinging infants ($n = 3$).

2.7.2. Rank distance among adults and grooming

The grooming patterns show a tendency for grooming to be directed towards higher ranking individuals, and for adult females to groom young. The observed differences, however did not reach statistical significance. My analysis of independent effects of rank differences did not suggest that rank predicts grooming patterns ($\chi^2 = 2.83$, $p = 0.069$). However, the second ranking female, BMS, was groomed more by the highest ranking female KL rate: 0.9 sec/hr and females lower in rank, MWK (0.6 sec/hr) and BMK (0.5sec/hour) (Table 2.11). BMS reciprocated MWK's grooming for shorter durations. However, she reciprocated more of KL and BMK grooming bouts. Grooming discrepancy was thus only weakly related to the distance between ranks in these females. For males, top ranking AMR received more grooming from lower ranking sub adult males SAM and SAN. AMR was never groomed by male AMM (rank 2) or AMB (rank 3).

Time matching within reciprocated grooming bouts

Least squares analysis of covariance (ANCOVA) shows that the total time (hours) spent grooming by recipients was positively and significantly correlated with the total duration of time spent grooming by the initiators for all age classes (Fig.2.10). The independent effects of the 6 main age classes (i.e. adult female, adult male, sub adults, large juveniles, small juveniles and infants) showed that age class intercepts significantly differed from each other ($F_{5, 30} = 9.75$, $P < 0.001$). The pair wise interaction between the two predictors was not significant ($P = 0.07$), so only the main effect model is presented here. The independent effects of total grooming duration of the initiator showed significant differences from each other and predicted total grooming duration of the recipient (least square ANCOVA: $F_{1,30} = 26.1$, $P < 0.0001$). This suggests that all age and sex classes in the Njokamoni group showed time matching of their grooming behaviour.

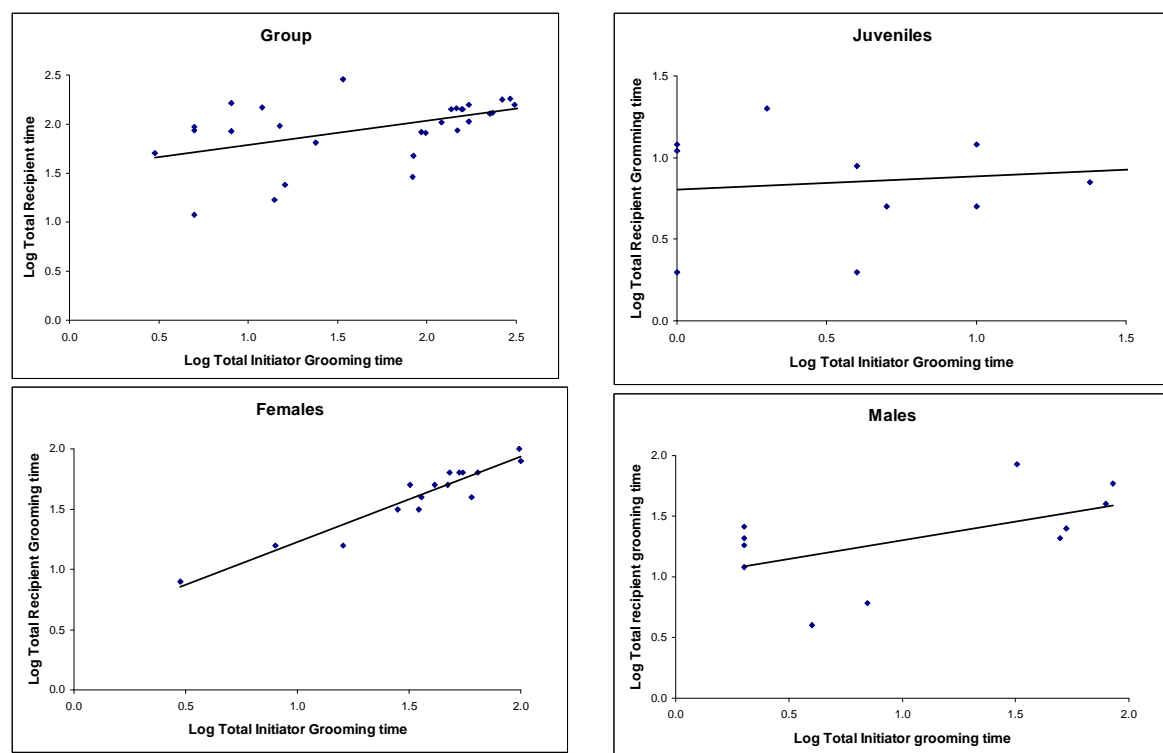


Fig.2.10. Log total recipient grooming time and the initiator: There was significant relationship between the grooming time of initiator and that of recipient ($p < 0.0001$).

Male and female-infant relationships (infant carrying, attractiveness of infants and allomothering)

Like most other mangabeys, a common infant carrying posture involves the infant clinging ventrally to its mother. For the 2 births that occurred during the data collection period, infants started playing, grasping and mouthing objects between 3 and 5 weeks of age. The two infants were able to walk, run, jump and engage in social play when they were 12 weeks old. For one infant born approximately 14 hours after the female was observed still pregnant, group members did not approach her to within 5m except for 4 adult females. Three days later, juveniles started to approach, sniffing the infant but never attempting to touch it. The mother seemed to maintain her distance from sub adult males whenever an approach was attempted.

Male Sanje mangabeys express care for infants by carrying and supporting them during agonistic interactions. Males have also been observed carrying infants in other circumstances such as when juveniles play with the infant for more than 3 minutes. In these incidences, the male would approach, snatch the infant and hand it to its mother, or seldom run away with it. The males were also observed to carry infants when mothers left them unattended and when the mother was involved in aggressive encounters ($n = 104/147$ for KL, $98/123$ for KMH, and $57/81$ for KM). This behaviour is likely to protect the infants from aggression (van Schaik & Paul, 1996). However, resident male Sanje mangabeys also selectively support offspring when the mothers are involved in agonistic disputes, by discouraging proximity or attack upon the infant.

Allomothering and male mounting success

The amount of allomothering of various female's offspring by male Sanje has shown to correlate with mounting success (Figure 2.11). For example, male AMB, who ranked second in the dominance order, allomothered infants of 3 different females more than any other males, had more of his mounts accepted by all cycling females than the higher ranking male AMR. For 7 sexually reproductive males (five adult males and 2 sub adult males), there was a strong, positive, but non significant relationship, between total allomothering performed and the number of mounts accepted by females (Pearson's $r = 0.7$, $P = 0.09$). Details of mounting and other aspects of sexual behaviour are covered in Chapter 4.

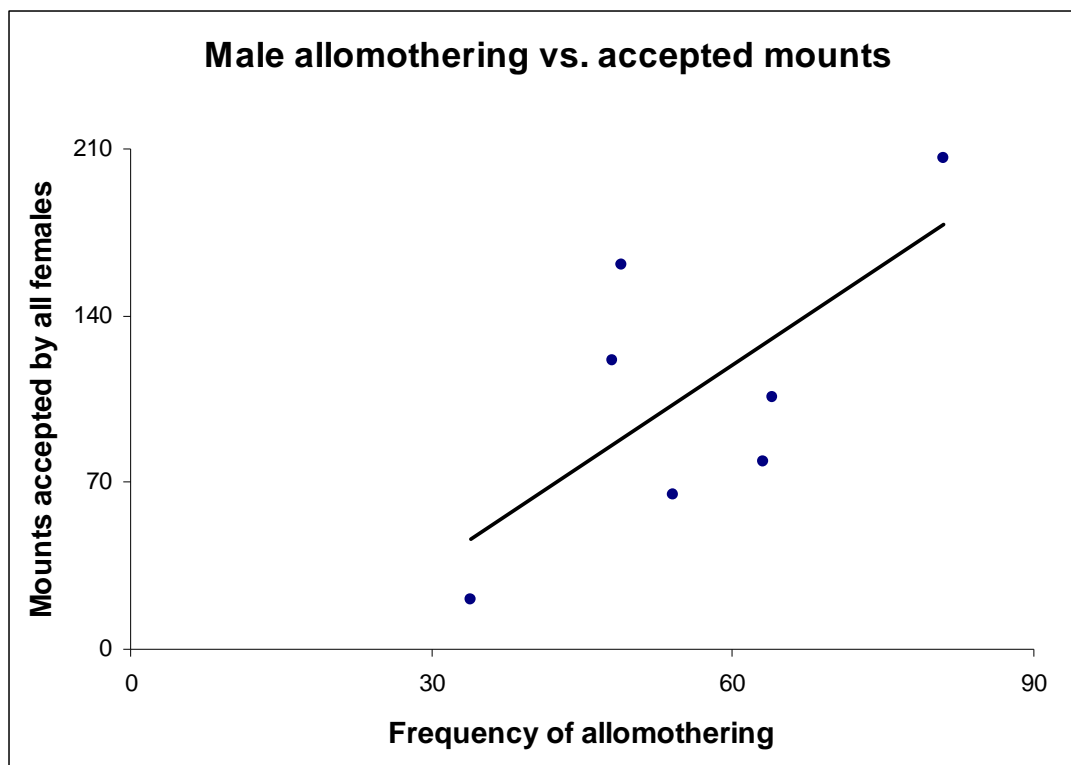


Figure 11. For 5 adult males and 2 sexually reproductive sub adult males, there was a strong, positive, but non significant relationship (Pearson's $r = 0.7$, $p = 0.09$) between total allomothering performed and the number of mounts accepted by all 7 cycling females.

Discussion

Group size and age-sex composition

The Njokamon habituated group currently has 59 individuals. This group size is larger compared to estimates for mid 2000 to 2005 (Jones *et al.*, 2006). The other 3 groups detected in the Njokamoni study area ranged from 27-51 individuals with a mean of 40. It might expected that the effects of food competition (either through group size or dominance rank) are most strongly felt in a stable or decreasing population. However, the Njokamoni group continued to grow during the study period at an average rate of 8% per 2 years as compared to 2005.

The major predators on Sanje mangabeys, African crowned eagles, leopards and pythons, were sighted occasionally throughout the study (two incidences of leopard footprints, one sighting of python and more than 20 sightings and 4 incidences of attacks by eagles). The group avoided parts of the forest where python and leopard footprints were sighted, by shifting activities (away from those areas instantly) despite

the high abundance of ripe fruits. The attacks by eagles were all sensed by the group, and fleeing were instantaneous. This group is the one in which an adult male mangabey attacked and injured an eagle, who later died from the injuries (Jones *et al.*, 2006). Large group size might thus have an advantage as regards to detection (Dunbar, 1988; van Schaik, 1983; van Schaik & van Hooff, 1983). Since the study group increased in size, and there were increased encounters with other 3 groups in the vicinity of Njokamoni forest, it is possible that the mangabey population was recovering from a reduction in the past that contributed to small group size. Therefore, the population, I suggest, should be subjected to further investigation for group sizes; current group counts are only from the Njokamoni area and no reliable counts were made before.

Seasonality: Among the births observed and reports from previous observations of Njokamoni and other groups, there is no consistent variation in the degree of birth seasonality. The three births that occurred in the group were in December and January (i.e., late dry and early wet seasons respectively). There were two other infants born in August and October 2007 (Mselewa pers. Comm.). Group sizes however, showed mild increases in the number of individuals during heavy rains in March and size started to decrease during early dry season in June (figure 3). These variations in size and composition of the Njokamoni group might have been a function of a range of factors such as seasonal food availability, migrations to and from other groups and subgroup formation. I did not assess seasonal food availability to tentatively quantify its effect on group size. However, seasonal food availability is known to affect the age and sex composition of many primate species including mangabeys (Hoshino, 1985; Isbell *et al.*, 1998; Mitani, 1989; Onderdonk & Chapman, 2000; Saj & Sicotte, 2007; van Schaik & van Noordwijk, 1988).

Males and females of other mangabeys are known to migrate to and from groups, altering their composition and size (Olupot & Waser, 2001; Wahungu, 1998; Walker *et al.*, 2004; Wiczkowski, 2005a). It is possible that the observed changes in number of individuals during rainy and drier months were due to migrations. Migrations have also been reported in baboons and other Papionins (Alberts & Altmann, 1995; Altmann *et al.*, 1985; Busse, 1984). Migrations have important effects in relation to

the breeding systems of group living species and in maintaining genetic diversity as well (Arlet *et al.*, 2009; Clutton-Brock, 1989; Moore & Ali, 1984).

Population density

Estimates of abundance and density of primate species are characteristically difficult and problematic in application, requiring assumptions that are often hard to meet (Marshall, 2007; Mitani *et al.*, 2000; Struhsaker, 1997; Whitesides *et al.*, 1988). For example, the assumptions and correction factors needed in perpendicular methods may result in many errors, most of which are unknown to the researchers (Marshall, 2007). Having recognised this, I presented an estimate of population density and abundance in Mwanihana for July 2007 to June 2008, which I believe is comparable to most other estimates for this area.

The density of the Sanje mangabey population was estimated to be 1.24 mangabeys per hectare, smaller than that estimated by Dinesen *et al.* (2001) and that considered by Ehardt *et al.* (2005). The density of mangabeys before right truncation was 3.99 mangabeys/hectare. The effective strip width (30.4) might have influenced the estimated density, which in turn gave a low estimate of density in the area. Detection probability might also have affected the estimate. Mangabey detection decreased at distances as close 25 m due to uneven topography of the study area. The mangabeys were sometimes also recorded in valleys and across ridges. Similar topographic effects were reported by Rovero *et al.* (2006) and Brugi  re & Fleury (2000) on studies of primates in Tanzania and Gabon respectively. The low density estimate might also mean that size of forest fragments used by mangabeys is increasing, which has led to less crowding and less groups detected (i.e. mangabeys are below carrying capacity). The opposite argument was also brought forward by Decker (1995) to account for causes of high density in Tana River red colobus, *Colobus badius rufomitratu*s and *C. galeritus* in 1970's. The current estimates for population density which considered presence of groups as well as solitary individuals using perpendicular methods might not be suitable for comparison with these other estimates from Udzungwas, obtained via completely different methods.

The total population abundance was estimated to be 689 individuals. This is higher than that estimated by Dinesen *et al.* (2001) and almost similar to Ehardt *et al.*'s

(2005) estimate based on Wasser (1993) and Dinesen *et al.*'s (2001) data. Rodgers and Homewood (1982) estimated the mangabey density in Mwanihana to be 0.3 groups per km², which gave a total of 790 mangabeys in the whole 177 km² forest. The most current estimate of closed forest is 109 km². Mangabey groups however, use a variety of habitats such as low-elevation miombo woodland and the moist evergreen montane forest. If the current estimate of abundance is comparable to these other studies, despite decreases in closed forest size, then the mangabey population has increased in Mwanihana.

The mean cluster size was 13.5 individuals. The cluster size of 13.5 in our calculation might be overestimated, because the groups detected on the transects rarely contained more than 20 individuals. However, since mangabeys are known to form sub groups that can persist up to 6 hours before regrouping (Ehardt *et al.*, 2005), the low group counts that possibly led to minimal cluster sizes estimated might have been due to this behaviour. The estimates provided in the current work can be used (with some caution), until further investigation considers the error that the estimates are associated with during data acquisition and analysis.

Ranging

Comparison between the current study and the result of preliminary work on another group by Ehardt *et al.* (2005) showed an increase in home range of Sanje mangabeys. This result supports the hypothesis that the home range of the Njokamoni group has increased due to greater daily distances travelled associated with expanding group size. Specifically, there was an increase in amount of area the group covered, from the original forests of Njokamoni to extended wooded miombo forest in Sonjo, and lower parts of the forest close to the main road. Greater distances travelled might be a form of scramble competition, whereby larger groups are forced to travel further to obtain the amount of food needed for each individual (Chapman & Chapman, 2000; Isbell, 1991; Waser, 1977). It should be noted that the association between larger home range size and larger group size are made only in terms of group size estimates for 2005. The group contained 10 less individuals in 2005, and used to range only within Njokamoni.

The increased home range of the Njokamoni mangabeys is likely to be a function of increased intra group competition between multiple individuals feeding on smaller patches. The group's rates of aggression have also been observed to increase since 2005 (UMNP ecological monitoring data). Throughout the study, fewer intra group encounters were observed. This might also suggest larger home ranges and low population density of mangabeys in Njokamoni. Similar effects of low population density and increased home range (=unconstrained movement) have been suggested in many other primates (Butynski, 1990; Ostro *et al.*, 1999; Wieczkowski, 2005b). Low food availability might also be another explanation for the larger home range of this group, compared to 200 ha of the other habituated group. The forest in Njokamoni where the group resides is largely tangled with climbers and fewer canopy trees occur to provide fruit and seeds to support the group. Low food availability is known to favour larger home ranges (Clutton-Brock & Harvey, 1977).

The impact of rainfall on Sanje mangabey movement and ranging patterns was quite remarkable. Movement and ranging patterns during wet and dry seasons varied with shorter daily movements during the rains. In the dry season, mangabeys moved longer distances and used more area apparently to increase their chances of encountering rare food items such as fig trees, termites and fruits. There was a tendency for the group to use most direct routes, faster movements and to travel further on drier days than on rainy days. These results indicate that the group spent more time in certain areas, and moved rapidly through others, in relation to weather conditions. The patterns of movement also, I believe, relate to food and food encounter rates (i.e. abundance), rates of renewal in the patches and the animals' spatial memory ability during foraging- see (Brain, 1990; Buzzard, 2006; Erhart & Overdorff, 2008; Freeland, 1980; Homewood, 1976; Kinnaird, 1990a). Influences of rainfall on ranging patterns and range size were also reported in *Cercocebus torquatus* and *Lophocebus albigena* (Freeland, 1980; Mitani, 1989). Further investigation should be undertaken to determine other factors associated with the rainy season that might have allowed for the more concentrated use of space during rainy days.

I could not assess or directly relate effect of predation risk on ranging, because, few signs and acts of predation were observed. However, there were observations for the group's tendency to change course of travel or avoid areas where predators/signs were

encountered. Forest size and degree of fragmentation is known to affect movement patterns and home range of many species e.g. *Cercocebus galeritus* (Homewood, 1976; Kinnaird, 1990a), *Colobus guereza* and *Macaca silenus* (Anderson *et al.*, 2007; Olupot *et al.*, 1994; Onderdonk & Chapman, 2000). In these studies, fragmented forests were related to smaller home ranges. Possible increase in forest area and senescence (i.e. regeneration) may also have accounted for the larger home range of this group. Forest regeneration and increase in fragment size enhance abilities of forest to support primates (Irwin, 2008; Newmark, 1998; Onderdonk & Chapman, 2000; Tutin, 1999; Tutin *et al.*, 1997; Wieczkowski, 2005b; Wong & Sicotte, 2007). This was not tested, however, the factor contributed to range expansion in *Lophocebus albigena jonstonii* (Olupot *et al.*, 1994).

The results also showed that the group also has more than one area that is favoured (core areas) as part of their range (Figure 2.6). This result was in line with my assumptions that the group might be ranging entirely within certain parts of forest during one season before moving, and that the animals spend 'quality time' in other areas in relation to food items encountered. The use of non closed-forest habitats of Sonjo by Sanje mangebeys highlights their capability of travelling, and the importance of these habitats. Although this was observed only in this group, which might not be the case for others, the behaviour may help these animals when serious situations result in declines in food biomass or forest area. The use of more than one patch (core areas) might be associated with increased feeding competition within the group, due to increased group size and constant abundance of food, leading to lower per capita feeding efficiency (Isbell *et al.*, 1990; Wieczkowski, 2005b). In that case, I suspect, the group had to shift its diet to a more dispersed resource area and increase inter-individual distance by travelling over more space to meet its daily needs (Chapman & Chapman, 2000). By increasing the home range, the group has a greater access to more food than in the previous range. Similar responses to increased group size and feeding competition have been reported to lead to increases in the home range resulting in increased food acquisition in vervet monkeys (Isbell *et al.*, 1990; Isbell *et al.*, 1998) *Colobus vellerosus* (Saj & Sicotte, 2007) and *Lophocebus albigena* (Olupot *et al.*, 1994). More research on the ecological determinants of conditions of ranging behaviour would be valuable.

Dominance

Both males and females could be ranked in linear hierarchy according to aggressive and submissive acts during scan samples (table 2.4). There were two dyads and one triad for females, and one dyad for males in which submissive acts were observed equally in both directions. These led to unknown relationships between the dyads, to which I assign positions in the dominance hierarchy. Although female BMS and KL were several times observed to equally behave submissively towards each other, their scaled ranks differed slightly (table 2.8), rendering female KL higher ranking. For males, the higher ranking was AMR. More than 95% and 76% of aggression for males and females, respectively, produced clear cut winners. This suggests that during agonistic interactions in Sanje mangebeys, there is a high degree of power differential that predicts the outcome of agonistic interactions. Therefore, using frequencies of agonistic interactions to determine the status of individual Sanje mangabeys is a reliable measure of social position.

Aggression in this group was directed primarily down the hierarchy. Landau's (de Vries, 1995; de Vries *et al.*, 2006) test of linearity revealed that both males' and female' dominance relationships showed transitivity (i.e. the observed pattern of dominance was consistent with a linear hierarchy to a greater extent, than would be expected by chance, for both sexes $P < 0.05$). The directional consistency index, DC for both sexes was also significant, suggesting that in all age classes, dyadic aggressive interactions are bidirectional.

Although lower ranking males and females were the recipients of aggression more often than higher ranking animals, higher ranking individuals did not engage in aggression more frequently than lower ranking ones (table 2.4). Males are generally dominant over females, thus, one could expect no female-male aggression. However there were cases where females initiated intense aggressive acts towards males and won. There were no cases of adult males or females forming coalitions against members of the same or opposite sex. However, lower ranking sub adult males, SAN and SAM were often observed forming coalitions against female BMS (Rank 2), and against medium and lower ranking males AMB and AMC. In both of these cases involving the two sub adults and adult males (7 cases), higher ranking male AMR intervened when the two started to scream. Both of these coalitions against males

happened when sub adults and the males were foraging. Two occasions of AMC provoked aggression did not lead to coalition, although the two sub adults were nearby. The fact that these conflicts, which happened among adjacently ranked dyads were provoked, indicates that they might serve to reinforce dominance relationships. The results presented here provide the first measure of dominance, and initial systematic description of the agonistic behaviour in Sanje mangabeys.

Affiliative relationships

Theoretically, social relationships among individuals should be highly differentiated when contest competition over access of to resources is frequent. In Njokamoni group, adult female mangabeys were observed to associate with a limited number, but significantly, with other females. Males associated more with sub adult females than they did with adult females. As one would expect, there was strong affiliation between females and their young. Relationships between sub adults were weaker, than with adult females or males. Grooming was even less distributed among potential partners of various age classes, and reflected preferred associations. The observed correlations are similar to findings of sooty mangabeys (Range & Noë, 2002) and captive Rhesus macaques (Hinde & Rowell, 1962).

Based on present the data, I could not determine the underlying mechanisms that might have produced the observed patterns. Individual monkeys could have been attracted to associate with higher ranking monkeys (Seyfarth, 1980) or with individuals similar in rank (de Waal & Luttrell, 1986). In general, the index used, was useful in assessing the associations in this group (Cairns & Schwager, 1987). These results provide an initial measure of association and affiliative relationships in Sanje mangabeys

Grooming

Overall, my results were consistent with predictions of the biological markets model i.e. grooming is a commodity that is traded among individual Sanje mangabeys. In line with these assumptions, I found significant positive correlations between grooming contributions of partners within time-matched reciprocated bouts within all age classes in this group. In addition, there were differences in grooming intercepts, suggesting that grooming bout lengths vary across age classes (Figure 2.8). There was a tendency for grooming to be directed towards higher ranking monkeys, but the

relationship was not significant. In addition, I found a significant relationship between the duration of an initiator's first grooming episode and subsequent reciprocation by receivers in all age classes. The results are consistent with other studies of grooming in Papionins (Barrett *et al.*, 2002; Barrett *et al.*, 1999; Chancellor & Isbell, 2009; Henzi & Barrett, 1999; Henzi *et al.*, 2003).

The individuals of this group maintained, time-matched and reciprocal grooming bouts regardless of other activities in their time budget. I found that grooming tendencies influenced how much individuals reciprocated, because the amount of an initiator's grooming was correlated with the receiver's grooming ($p < 0.0001$, figure 2.9). In line with Chancellor & Isbell (2009) findings, there was no trend, nor significant relationship between the initial duration an initiator groomed and whether or not the recipient groomed. This might mean either unreciprocated grooming bouts are exchanged for other rewards e.g. tolerance and enhanced social bonds, or they were reciprocated but over longer periods of time (Chancellor & Isbell, 2009). Since reciprocal grooming provides direct benefits to individuals through removal of ectoparasites, it is possible that grooming in Sanje mangabeys acts as a 'payoff currency' as well. This result, further argues that grooming can be exchanged for its value equivalent, because it was maintained among dyads where there were no other social benefits to be gained from grooming (e.g. between females and juveniles). The results on time-matched grooming bouts also help to explain the complementary tendency for allo-grooming and for as grooming to concentrate on areas that are hard to reach (e.g. back of the head).

There was no substantive proof that grooming is exchanged for coalitionary support. However, it appears that interchange of grooming may serve to increase tolerance between dominant and subordinate individuals. This was evident in two ways; 1) reduced levels of aggression and increased access to 'favourite' food. Although it was not systematically scored, the fact that adult males were tolerant during feeding towards females who groomed them more often, is reasonable evidence that grooming in Sanje mangabeys may enhance or facilitate tolerance among individuals (de Waal, 1997; Gumert & Ho, 2008). For females, this tolerance may also help to alleviate the negative effects of ecological competition upon their reproductive success (Dunbar, 1988; van Schaik, 1989; Weisbard & Goy, 1976).

According to Seyfarth (1977), patterns of grooming in groups that have steep dominance gradients, are expected to be characterised by reciprocal rather than interchange grooming, because the time and ability of individuals to groom a large number of higher ranking conspecifics is low. Therefore, the observed low rates of female-female grooming in Njokamoni might have been brought about by high tendencies of female grooming males. Furthermore, and in line with reciprocation of biological markets theory and Chancellor & Isbell's (2009) findings, higher ranking females and males tended to reciprocate with smaller durations to all the grooming bouts from medium and lower ranking individuals. Balance between grooming (in exchange) for tolerance depends on rank order between potential traders (Henzi & Barrett, 1999). Because of this, the relationship between two traders will always be fixed and limited to one type of exchange according their dominance levels (e.g. between males and females). Henzi and Barrett (1999) argue that, these interchanges may be useful to distinguish between groups as either egalitarian (having low power differential) or despotic (steep dominance gradients). When competition for resources is high and dominance gradients are steep, relationships between distantly-ranked individuals will be based on grooming interchange Henzi and Barrett (1999), whereas relationships between closely ranked individuals will be based on reciprocal grooming. Thus, the choice of who to groom (for equivalent amount of grooming or for tolerance) are based on dominance. Both of these relationships were evident in this group, however, with more predictive value for the later. In contrast to this theory, if females were trading grooming for tolerance, male-female or female-male agonistic rates need not have increased.

Grooming reciprocity ranged from 5 % to 26%, lower than in Grey-cheeked mangabeys (18%-40%, Chancellor & Isbell, (2009)), and Chacma baboons (31%-51%, Barret *et al.* (1999)). However, these percentages were similar to capuchins (12%-27%) and higher than in bonnet macaques (5%-7%, (Manson *et al.*, 2004). The variations presented here, however, may not be necessarily species specific, but rather due to approaches used to define grooming bouts, which, determine bout length e.g. (Manson *et al.*, 2004). Reciprocal grooming might be highly evident in the wild, because, individuals can just stay out of the way of intolerant individuals (Henzi & Barrett, 1999), which might not be case for captive conditions.

Studies of *Macaca fuscata* have shown that rates of reciprocation of grooming bouts among unrelated individuals were higher than for related, and that related individuals were less likely to reciprocate (Muroyama, 1991). I do know the affinity relations for this group; however, because no cases of migrations were observed (which suggests that they are kin) and according to Muroyama's findings I may suggest that kinship minimizes the need for immediate reciprocation, and that inability to interchange (due to power differential in part) might have led to observed lower but significant levels of reciprocation in Sanje mangabeys. This group of mangabeys is characterised by higher level of rank distance among individuals. Thus, variations observed in table 2.10 for reciprocated grooming were likely to be a function of variation in ranks among age and sex classes. Similar results showing low levels of reciprocation in a group of chacma baboons that showed weak rank distance were documented by Henzi & Barrett (1999). Further investigation of how grooming is negotiated between partners is necessary, and to examine relationships to rank. Data on kinship within Sanje mangabey groups will also help to pinpoint the combined relative effects of kinship and dominance upon the patterns of grooming.

Allomothering, infant carrying and attractiveness of infants

Adult females, all adult male mangabeys were involved in allomothering. For both sexes, adults carry infants on the ventrum. There was a trend suggesting that the amount of male allomothering might predict the amount of mounts accepted by all females. However the relationship was not significant. The lack of significance perhaps was due to consideration of frequencies of male mounts accepted by all the females rather than only females whose infants were allomothered by these males. Further investigation to minimize these sampling and analytical errors should be attempted, to examine this important behaviour in these monkeys.

Interestingly, and in contrast to some other members of Papionini, males of this species were highly involved in protecting the infants from aggression by other members. Male Barbary macaques use infants in male-male interactions, apparently to reduce the likelihood of aggression (Deag & Crook, 1971). Baboon males, on the other hand carry infants, and they are known to have intense affiliations, but are not reported to protect them from aggression (Buchan *et al.*, 2003; Busse, 1984). Adult

male Sanje mangabeys stopped and intervened in aggressive encounters between other group members and females with clinging infants. The males took infants away from their mothers, confronted the individuals who directed aggression towards nursing females and often discouraged prolonged social play between juveniles and infants. These behaviours are a unique form of infant care and protection by adult male Sanje mangabeys. On the other hand, my result could suggest infant protection selectivity, probably based on paternal relations (van Schaik & Paul, 1996). Resident male Sanje mangabeys selectively supported offspring when the mother was involved in agonistic disputes, by discouraging proximity or attacking upon the infants whose mothers either reached for help by running towards these males or when the infants approached the male. This situation happened 18/57 occasions involving infant of female KM. This behavior suggests that they are probably able to differentiate their offspring from unrelated offspring (Buchan *et al.*, 2003; van Schaik & Paul, 1996).

Because there are high degrees of aggression in *C. sanjei*, which often intensively involve nursing mothers, there should be a great advantage of extra 'parent' infant care and protection; otherwise there could be high numbers of infant mortalities as result of injuries. Thus, allomothering in Sanje mangabeys could be an evolutionarily stable strategy of controlling infant mortalities.

Appendix 1. Ethogram: Activity categories and behaviour definition

Major Activity	Behaviour	Key		Definition
Agonistic		A		Activities which involve displays of hostility and/or cause the displacement of conspecifics.
	Stare	A	St	A raises eyebrows and looks directly at B for period beyond brief glance. The head can be rapidly lowered and raised while exhibiting the stare
	Lunge	A	L	While looking at B, A thrusts upper body toward B without moving from present location.
	Chase	A	Ch	A rushes toward B who runs away before aggressor can reach recipient.
	Scream	A	Sc	Loud, shrill vocalisation emitted in agonistic situations (A may be recipient or instigator of aggression).
	Bite	A	B	A uses teeth to aggressively grab fur or skin of B.
	Neck Bite	A	N	A bites neck region of B.
	Hit	A	H	A lashes out aggressively with limbs at B.
	Grimace	A	G	A pulls lips back at edges to reveal teeth. Often accompanied by kecking sounds.
	Crouch	A	Cr	A Lowers chest/belly and/or head toward ground whilst hindquarters remain and upright directed toward B. The crouch may occur during severe physical attack, signalling complete submission (Bernstein, 1976)
	Keck	A	K	Sound repeated several times at short intervals, often when animal appears nervous and uncertain.
	Run to	A	R	Having received a threat and or attack from B, A runs toward B, often kecking and/or showing other submissive behaviours.
	Confront	A	Co	After directing threats at A, B charges at A who remains stationary as B approaches.
	Flee	A	F	Having received a threat and/or attack from B, A runs away from B. May or may not be pursued by aggressor.
	Involve Third Party/ coalition	A	T	Having received aggression from B, A runs towards neutral party C, often putting C physically between A and B.
	Intervene/ A. support	A	I	A becomes involved in aggressive encounter between two conspecifics, often coming to the aid of the aggressee.
Affiliative		F		Non-hostile, socially motivated behaviour.
	Homosexual Presentation	F	P	A presents hindquarters turned toward individual of the same sex, often accompanied by kecking
	Presentation:	F	Pr	A receives homosexual presentation from B, and touches the perineum of B.

	Response			
	Homo Mount: Attempt	F	M A	A attempts to climb onto hindquarters of B, but activity is aborted before mounting occurs.
	Homosexual Mount	F	M	A climbs onto hindquarters of B. B may initiate thrusting motions.
	Homo Mount: Response	F	M R	While being mounted by B, A reaches behind and touches the perineum of A
	Contact Grunt	F	C	Short throaty grunt made with mouth closed. Often repeated several times.
	Whoop gobble			Characteristic loud call made by males, that is heard up to a distance of 1km, used for group herding or advertise group's location (a spacing mechanism)
	Bahu Call	F	B	Loud call which draws the attention of other conspecifics to some event.
	Lip Smack	F	S	Rapid succession of opening and closing of lips. Instigator is often facing and or approaching conspecific at the time.
	Groom Solicit	F	GS	A presents or exposes part of his body e.g. flank/hindquarters to B while standing or sitting stiffly (Hinde & Rowell, 1962)
	Groom	F	G	A preens pelage of B with the hands or mouth.
	Huddle/hug	F	H	A embraces B, by placing his fore limb on B's shoulders. One or both may animals may rise onto 4 limbs or remain seated and place arms on the other's ventrum (Range & Noë, 2002), this may involve more than two individuals.
	Play Fight	F	F	Tussling, challenging and chasing between individuals, which does not escalate into serious injury causing?
Sexual		X		Behaviours concerned with the acquisition and practice of sexual activity.
	Heterosexual Presentation	X	P	Female directs her hindquarters turned toward male conspecific with tail raised.
	Hetero Pres with Look	X	PL	Female directs her hindquarters turned toward male conspecific with tail raised. Female looks over shoulder at recipients face during activity.
	Inspection: Smell	X	IS	Male inspects anogenital region of female by smelling genital area. Often follows presentation.
	Inspection: Touch	X	IT	Male inspects anogenital region of female by touching genital area. Often follows presentation.
	Inspection: Look	X	IL	Male inspects anogenital region of female by observing the genital area. Often follows presentation.
	Grab	X	G	A grabs body part of B Preceded and/or followed by other forms solicitation or mating behaviour.
	Hetero Mount: Attempt	X	M A	A climbs onto hindquarters of B of the same sex. Activity aborted before intromission occurs.

	Heterosexual Mounting	X	M	A climbs onto hindquarters of B of the same sex. Accompanied by thrusting motions indicative of successful intromission.
	Pause: Ejaculation	X	E	Male involved in heterosexual mount briefly pauses toward end of sexual bout. Indicative of ejaculation.
	Copulation Call	X	C	Short grunting sounds made by female during intromission.
	Masturbation	X	W	Manual stimulation of genitalia. May result in visible ejaculation in males.
Proximity		P		Locomotive activity which is motivated by and/or involves the movement of one or more conspecifics.
	Approach	P	A	Individual moves to within 1 body length (touching distance) of a conspecific after being 2 or more body lengths apart. $R < 2\text{ m}$
	Leave/yield	P	L	Individual moves away (jumps or walks) from conspecific that had been located within 2 body lengths of individual.
	Follow: Individual	P	I	Walking/running/climbing in the direction taken by single conspecific, excludes events where multiple individuals move simultaneously.
	Follow: Unit	P	U	Walking/running/climbing in the direction taken by two or more of conspecifics.
	Ride	P	R	Individual clings to sides/back of moving conspecific.
	Avoid	P	A	Individual changes trajectory of travel or leans aside due to the likelihood of crossing the path of conspecific that approaches or walks by.
	Supplant	P	S	Individual moves from original position at approach of conspecific, moving away from direction of approach so as to avoid contact. i.e. A Approaches and replace B who moves away without overt aggression
	Pass	P	P	Individual moves within 1 body length of conspecific (who remains unmoved) but continues past beyond a length of 1 body lengths (beyond touching distance).
Self-directed		S		Behaviours in which individual is both instigator and recipient, which are associated with situations of uncertainty and stress.
	Self Grooming	S	G	Individual inspects own pelage.
	Scratch	S	S	Repeated movement in which digits of hands or feet are drawn through pelage.
	Yawn	S	Y	Brief gaping movement with mouth. Does not occur within aggressive display.
	Body Shake	S	B	A shaking movement of whole body.
	Nose Wipe	S	N	Brief circular movement of hand at end of nose.
Out of Site		OoS		Periods where observation of individual is not possible.

3. HABITAT, FEEDING ECOLOGY AND SEASONAL PARAMETERS

Abstract

The Njokamoni group of Sanje mangabeys has recently changed its ranging behaviour, visiting areas of the forest that have never been recorded before, most very close to main human roads. This might have been due decreased amount of food items in the existing range. According to optimal foraging theory, animals choose food mainly on the grounds of nutritional quality to obtain the mix of nutrients within a fixed total intake or switch to abundant food when availability of preferred one decreases. Feeding selectivity has also been related to body weight.

I studied dietary selection in relation to body size, to examine dietary components and age-sex class behaviour during feeding. The foods eaten by the individuals were recorded using focal animal sampling. Focal individuals were chosen at random from a sample of 30 individually recognisable animals. All plant, fungi and invertebrates utilized were recorded while following the group on foot for 6 consecutive days, 3 times a month; from 7am to 6pm. While quantifying actual food utilized, the habitat was quickly scanned every 2 hours for plants that are available. Habitat was then sampled across the mangabey range to quantify habitat use; from plots equivalent to >10% of home range. 7 plots consisting of 100m × 50m (0.5ha) were sampled between March and May. Mangabeys were classified in 34 age classes: adult males, adult females, sub adults and immatures. Time spent feeding; feeding level was recorded each time a focal individual was in view. The plants were identified in the field. The temperature and rainfall was also monitored from daily records over the period of 6.5 months to investigate the influence on behaviour and ecology.

The diet composition of Sanje mangabey was found to be very diverse. About 99 identifiable plant species were consumed. 68% of all feeding time was utilized on the forest floor. Heavier individuals relatively fed more on leaves, while lighter individuals fed on seeds, fruits and flowers and invertebrates more frequently. There were no differences in time spent feeding between age classes, but feeding time on different items varied significantly. This finding agrees with Jarman- Bell principle.

Key words: Diet composition, age-sex, body size, terrestriality, Jarman-Bell principle

Introduction

Feeding ecology

Studies of habitat use and influences of seasonal parameters on feeding ecology facilitate our understanding of complexities of animal behaviour and ecology including feeding strategies. There is a close relationship between body size and food habits in most homeothermic animals. Primate food habits vary from insectivorous, frugivorous to folivorous. For most forest ecosystems, leaves, which have a lower quality per unit weight (in terms readily accessible calories and protein content) than insects and fruits are more readily available (Chapman *et al.*, 2002; Hoshino, 1985; Marshall & Wrangham, 2007; Milton, 2006; Sailer *et al.*, 1985).

Dietary selection has been related to body size in variety of species including primates (Agetsuma, 2001; Leonard *et al.*, 1996; Sailer *et al.*, 1985). A general trend for most of these animals is for larger animals feeding on greater amounts of low quality foods because they need more energy, though their energy requirement per unit of body weight is low. On the other hand, smaller animals, whose energy requirement per unit of body weight is high, tend to feed on smaller amounts of higher quality food. This relationship is well known as the Jarman-Bell principle (Bell, 1971; Geist, 1974; Jarman, 1974). The principle explains differences in feeding habits among species in terms of body weight (as determined by age or sexual dimorphism).

Discussions about differences in feeding behaviour in primates have focused on nutritional requirements for growth, and reproductive needs such as occur during development of secondary sexual characteristics, and during pregnancy or lactation (Agetsuma, 2001; Chapman *et al.*, 2002; Cipolletta *et al.*, 2007; Daegling & McGraw, 2007; Erhart & Overdorff, 2008; Felton *et al.*, 2008; Hoshino, 1985; Norscia *et al.*, 2006; Saj & Sicotte, 2007; Setchell *et al.*, 2001; Struhsaker *et al.*, 2004; Wahungu, 1998; Wakibara, 2005). Influences of body size or weight on feeding behaviour within groups of mangabeys have not been examined thoroughly. In this study I attempt to show how age- sex related differences in body weight affect food selection by Sanje mangabeys.

Density of trees influences fruit abundance habitat-wide (Chapman *et al.*, 1994; Wieczkowski, 2005b), and diameter at breast height (d.b.h) provides an accurate

estimate of fruit number and biomass (Leighton & Leighton, 1982; McDiarmid *et al.*, 1977). A traditional view of the relationship between tree diversity relative to diameter at breast height with food abundance is that food abundance increases with the increasing diversity of trees of a bigger DBH along an altitudinal range (Lieberman *et al.*, 1996). However, the relationship does not take in to account species differences in size and capacity to produce food. For some forests, the relationship is not uniform (Chapman *et al.*, 2002; Chapman *et al.*, 1994).

The degree of terrestriality in Sanje mangabeys is not known apart from the fact that the animals spend a large proportion of their time foraging on the ground (Ehardt *et al.*, 2005). The present study attempts to show how dependent Sanje mangabeys are on different levels of forest for feeding and how this influences their behaviour.

Wet and dry seasons

Distribution of rainfall and variations in temperature are known to affect many aspects of social organisation, ecology, and behaviour of forest living primates (Marshall & Wrangham, 2007; Sterck, 1999; Struhsaker, 1997; Thomas, 1991; Wahungu, 1998). For example, group size and feeding behaviour of primates in a Brazilian rainforest were found to be largely dependent on rainfall and temperature (de A Moura, 2007). Rainfall can also affect the abundance of food, which in return affects animal's feeding strategies and ranging behaviour (Buzzard, 2006; Mitani, 1989; Norscia *et al.*, 2006; Olupot *et al.*, 1997). Patterns of rainfall and temperature also influence sexual behaviour and reproductive parameters of many primates (Baulu, 1976; Gust *et al.*, 1990; Setchell & Wickings, 2004b).

In many African countries, there are only two seasons, wet and dry. Traditionally, the bimodal rainfall pattern in these regions has been analysed by separating the first and second half of the year. Global climate change has led to changing seasonal rainfall regimes and reduced reliability of seasonal patterns of rainfall in most parts of the tropical rainforests. As a result, there have been great problems in attempts to quantify seasonal patterns throughout regions in which timing of wet and dry season are not reliable (Hanna, 1976; T.M.A, 2008). I present data for rainfall and temperature changes from Udzungwa Mountains National Park collected over a one year period.

The present study attempts to show how seasonal patterns of rainfall and temperature affect feeding ecology and behaviour in the Sanje mangabey.

Methods

Study group and site

This study was conducted in the Mwanihana forest. The Mwanihana forest exhibits continuous zonation from 300-2250 m above sea level, ranging from lowland forest in the Great Ruaha river valley to montane forest at higher altitudes. Habitat in Mwanihana consists of dry deciduous woodland at lower altitudes and montane forest of *Podocarp*, *Prunus* and *Hagenia* that coexists with a mosaic of bamboo at higher altitudes (Ehardt *et al.*, 2005; Lovett *et al.*, 2006). The climate in this area is highly influenced by the Indian Ocean and characterised by reliable and relatively high rainfall (up to 1800mm per year) to the eastern side of the escarpment (Lovett, 1996). Considerable effort has been made to habituate two groups of mangabeys, in order to facilitate ecological studies. The groups are called Njokamoni and Mizimu, after the river Njokamoni and the Mizimu forest fragment of the Mwanihana forest respectively. The Njokamoni group has been habituated and studied for various lengths of time since annexation of the Park in 1998. In my study, data on the climate and species feeding behaviour were collected at Njokamoni from December 2007 to June 2008.

Feeding observations

Data were collected by myself and three trained assistants. The foods eaten by the individuals were recorded using focal animal sampling. All plant species, fungi and invertebrates used by the individuals were recorded while following the group on foot. Full day follows of the group were conducted for 6 consecutive days, repeated 3 times a month, from 7am to 6pm. Twenty minute focal animal samples (Altmann, 1974) were collected at 10 minute intervals. Focal individuals were chosen at random or at fixed rotation between age and sex classes. Twenty individually recognisable animals (6 adult females, 4 adult males, 4 sub-adults, 4 juveniles and 2 infants) were sampled. All other members of the group were also sampled randomly by choosing individuals of certain age and sex class whenever the specific individual of that age/sex class was out of sight. Ten minutes were allowed to locate the focal individual by scanning the group. Once an individual was located the observer waited for 5-15 seconds before

recording feeding behaviour to ensure no over-representation of eye catching behaviour occurred (Teichroeb *et al.*, 2003).

The following parameters of feeding behaviour were recorded for each focal individual;

1. Time feeding on each food item, and the parts taken.
2. The subject's feeding level (position) from the ground (in metres) estimated by eye or by range finder.
3. Number, age class and sex of other individuals of the group utilizing similar food items (if they were within 5m of the focal animal).

To obtain an estimate of the percentage of the time spent feeding on different substrates (i.e. the degree of terrestriality) I classified feeding position into 5 categories of height, corresponding to a 'traditional' forest layer classification (Butler, 2005; Johnson *et al.*, 2002). 'This classification uses height to stratify forest as either emergent, canopy, understory, shrub layer, or forest floor (ground layer). In this case I defined heights to correspond to these layers, and assigned feeding behaviour as being either terrestrial (0m to 1m) or arboreal (≥ 16 m), and any feeding positions of animal at the other levels between the two as intermediate.

While quantifying actual food utilized, the habitat was quickly scanned every two hours for plants that are available around that specific area. An observer stood in the middle of the group, looked around and recorded all canopy and small trees, shrubs and undergrowth vegetation within a 15 metre radius. The number of each species of woody vegetation was recorded but only the presence or absence of herbaceous plant species.

Habitat sampling

Habitat was sampled for the food available across the mangabey range to quantify habitat use. Vegetation was sampled by myself and 3 assistants who are experienced at working in the Udzungwa forest. I selected plot sample sizes equivalent to $>10\%$ of mangabey home range. Seven plots were sampled, between March and May 2008. The plots consisted of $100\text{m} \times 50\text{m}$ (0.5ha) divided into 8 equal sections of $25\text{m} \times 25\text{m}$. The major trees, shrubs and invertebrates were recorded. To ensure the plots were representative of the area throughout the home range, I randomly selected area

points for vegetation sampling. I used 35 sleeping sites that were between 400m to several kilometres away from each other as reference units. Each unit was given a name and a number, and plots were chosen randomly (Greenwood & Robinson, 2006).

The direction and starting point of a plot from systematically chosen points at each identified sleeping site was randomly selected. We assigned numbers in metres from 1 to 20 for distance and 0° to 360° for direction and selected a distance and direction to start a plot from these numbers. The direction of the plots was measured using a compass. All directions and distances that led to plots falling into permanent rivers or steep cliffs were ignored. Twelve red flagged, 1.5m poles were used to mark the 25m x 25m subplots, and 50m rope was used to measure the distances. For all trees ≥ 10 cm, d.b.h was measured and height estimated within the 25m x 25m plots and total count was taken for those with d.b.h < 10 cm. All woody and herbaceous plants ≥ 1 m high but less than 10cm d.b.h were counted within the 25m x 25m plots. To sample plants that were less than 1m tall, I laid out two 2m x 2m plots within 25m x 25m plots. I also sampled all the invertebrates, seedlings and fruits or seeds that were on the ground in 1m x 1m plots laid out within the 2m x 2m plots. The phenology of the fruits on the ground was recorded as fresh, senescing or old.

Plant Identification

The plants were identified in the field. However, experienced researchers' advice was sought when identification was uncertain, by presenting specimens for verification at the National Herbarium of Tanzania (NHT). Identification was made to species level, but whenever this was not possible generic or family names were used. English names were used for invertebrate species only. During my time at the herbarium I worked with Mr Suleiman Hajji (NHT curator). Only English names were used for the invertebrate species eaten and observed in the 1m x 1 m plots.

Climatic patterns

Temperature and rainfall was documented from daily records over the period of 6.5 months. A weather monitoring station (White & Edwards, 2000) was set up in the forest about 100m from the main camp in Njokamoni ($7^{\circ} 50'.079''$ S, $36^{\circ} 52'.990''$ E). The station was 3.5 km away from the road at Park headquarters at an altitude of 450

m above sea level (a.s.l.). The station was set up in the forest to account for differences in elevation (and possibly weather patterns) between the forest and Park headquarters (where it is much hotter), and to be able to compare these data and data for 6 months prior to this study that were recorded by the Park from a station set in the forest at altitude 400 a.s.l. A rainfall gauge and maximum-minimum thermometer was used. Data were collected daily at 8am by one observer for most of the study period. The six month term of data collection was supplemented with the Park's weather records for six months prior to the start of my study. I used 100 mm rainfall per month as a cut-off amount to define rainfall during wet (November- April) and dry (May-October) seasons. This criterion was adopted because in Tanzania 82% of all regions in drier months of year receive rainfall less than 100 mm (T.M.A, 2008).

Data analysis

Inter-observer reliability - was enhanced by independent recording of feeding during scans. A list of dietary material was created by averaging the percentage contribution of each item (plants, fungi, and invertebrates) across the Njokamoni group. The averages were then ranked. Since percentage contributions to diet correlates with abundance of dietary species in the forest (canopy, understory and ground), the abundance of each of the top 15 dietary species was determined. The 10 most abundant species were then selected, these contributed to 80% of the group's diet. The 10 most important diet species in this group ranged from 53-61% of the annual diet of the Sanje mangabey (Homewood & Rodgers, 1981). The percentage of time feeding at different levels of the forest was used to assess the importance of terrestriality for feeding ecology in the Sanje mangabey.

Diet selectivity

Individuals of the group were classified into three age-sex classes according to their body sizes: Males- (5 adults) Sub adults (2males and 2 females), Females (10 adult females and 2 sub-adult females) and Immature (four large juveniles, 4 small juveniles and three suckling infants). Food items were classified into four categories 1) reproductive parts (fruits, seeds, and flowers), 2) leaves, 3) shoots and stem sap, and 4) invertebrates and mushrooms. I calculated the time spent feeding by each age-sex class, by dividing the time for number of mangabeys engaged in feeding on a particular food item by the total time mangabeys in age-sex the class were observed in

each period. Rates of arboreal or terrestrial feeding were calculated by dividing the positions of the number of mangabeys feeding at each height (i.e. 0-1 m, between 1 and 15.9 and >16m) by the total number of feeding positions of mangabeys in each class in each period. The dietary composition selectivity for each class was calculated by dividing the number of mangabeys feeding on each food category by the total number of mangabeys feeding in each class in each period.

Habitat use, food tree density and abundance

The basal area of the trees measured within 25m x 25m plots was calculated using an equation for the area of a circle. Stem density was determined from each of the 0.5ha plot and the total counts of all species over 1m tall. Reproductively sized individuals (i.e. d.b.h >10 cm) of food species were enumerated from the 25m x 25m plots. The Sanje mangabey's habitat use was then calculated for the number of plant species eaten. Density was calculated by dividing the total number of individual plants counted of each species by the total of area (hectares) sampled. The counts of food trees were then converted to abundance per individual.

Climatic data

Average monthly temperature and rainfall totals were computed. The monthly averages of temperature and rainfall totals were graphed to obtain the yearly pattern. Analysis of variance was applied to determine any significant differences in rainfall between months. The temperature and rainfall patterns were then correlated with patterns of feeding and behaviour.

Results

Feeding behaviour

On average, 56-72% of the group members were observed in each focal scan and 52-81% of feeding individuals were identified each time. My study found the dietary composition of Sanje mangabeys to be very diverse. Their diet encompassed fruits, seeds, nuts, flowers, leaves, shoots, roots, gum/sap, bark, ferns, lizards, fungi, and invertebrates.

The invertebrates and fungi eaten were from the forest floor, decomposing wood and trees. The diet included 6 species of fungi, 2 ferns, lizards, 3 species of millipede,

snails, and three species of termites (Genus *Microtermes*), grasshoppers, and spiders. Other food items are yet to be identified, and are shown in Figure 1. During the entire study, Sanje mangabeys consumed approximately 99 identifiable plant species, but spent 68% of their feeding time on < 34 species. The plant dietary composition is presented in table 3.1.

Table 3.1. Plant species consumed by Sanje mangabey in December 2007 to June 2008

Family	Species	Part eaten ¹	Form ²
Agavaceae	<i>Dracaena mannii</i>	Sh	T
Anacardiaceae	<i>Sorindeia madagascariensis</i>	S,B	T
Annonaceae	<i>Annona senegalensis</i>	Fr	T
Annonaceae	<i>Lettowianthus stellatus</i>	Fr,S,N	T
Annonaceae	<i>Monanthes trichocarpa</i>	Fr	T
Bambusoidea	<i>Olyra ratifolia</i>	Sh	G
Annonaceae	<i>Monanthes buchananii</i>	Fr,L	C
Bignoniaceae	<i>Markhamia lutea</i>	Fr	T
Adiantaceae	<i>Pellaea angulosa</i>	Fr	F
Adiantaceae	<i>Pellaea quadripinata</i>	L	F
Apocynaceae	<i>Tabernaemontana pachysiphon</i>	Fr,L,G	T
Apocynaceae	<i>Euclea divinorum</i>	Fr	T
Apocynaceae	<i>Voacanga africana</i>	Fr	T
Apocynaceae	<i>Saba comorensis</i>	Fr	C
Apocynaceae	<i>Saba florida</i>	Fr	C
Aspleniaceae	<i>Asplenium lobatum</i>	L	F
Araceae	<i>Culcassia scandens</i>	Fr	C
Araliaceae	<i>Cussonia kirkii</i>	Fr	H
Chrysobalanaceae	<i>Parinari excelsa</i>	N,Fr,L	T
Combretaceae	<i>Combretum molle</i>	S	T
Commelinaceae	<i>Commelina africana</i>	Sh	H
Cucurbitaceae	<i>Coccinia</i> sp.	Fr	C
Cucurbitaceae	<i>Piponium vogelii</i>	Fr	C
Cucurbitaceae	<i>Telfairia pedata</i>	S	T
Clusiaceae	<i>Harungana madagascariensis</i>	Fruit	T
Cyperaceae	<i>Carex</i> sp.(cf <i>C. geminata</i>)	Sh	H
Dichapetalaceae	<i>Dichapetalum stuhlmannii</i>	Fr,L	T
Euphorbiaceae	<i>Ricinodendron heudelotii</i>	S	T
Ebeneceae	<i>Diospyros zombensis</i>	Fr	T
Fabaceae (Leguminosae)	<i>Brachystegia spiciformis</i>	Fr	T
Fabaceae (Leguminosae)	<i>Codyla africana</i>	Fr	T
Flagellariaceae	<i>Flagellaria guineensis</i>	shoot	H
Fabaceae	<i>Dalbegia obovata</i>	Fr	C
Fabaceae (Leguminosae)	<i>Desmodium adscendens</i> sp. <i>robustum</i>	S	C
Fabaceae (Leguminosae)	<i>Brachystegia bursei</i>	Fr	T
Dioscoreaceae	<i>Dioscorea sansibarensis</i>	Sh	C
Flacourtiaceae	<i>Dovyalis</i> sp.	Fr	T
Gentianaceae (Loganiaceae)	<i>Anthocleista grandiflora</i>	Fr	T
Guttiferae	<i>Harungana madagascariensis</i>	Fr,G	T

Graminaceae	<i>Panicum brevifolium</i>	Fr,sh	G
Graminaceae	<i>Panicum chionene</i>	Sh	G
Isotomoidea (Sapoteceae)	<i>Afrosersalisia cerasifera</i>	Fr,L	C
Icacinaceae	<i>Rhaphiostylis beninensis</i>	Fr,L	C
Labiataeae	<i>Huslundia opposita</i>	Fr	H
Leguminosae	<i>Milletia sp.</i>	FL	T
Liliaceae	<i>Asparagus africana</i>	Fl,Fr	F
Liliaceae	<i>Asparagus ?cetaceus</i>	Fr	F
Mellaceae	<i>Terraefloribunda</i>	FR,L	F
Mimosaceae	<i>Albizia gummifera</i>	Fr,S,L,B	T
Mimosaceae	<i>Parkia filicoidea</i>	Fr,S	T
Moraceae	<i>Antiaris toxicaria</i>	Fr	T
Moraceae	<i>Ficus sur</i>	Fr	T
Moraceae	<i>Ficus natalensis</i>	Fr	T
Moraceae	<i>Ficus sp. 1 (?cyastipula)</i>	L	T
Moraceae	<i>Ficus sp. 2</i>	L,G	T
Moraceae	<i>Ficus exasperata</i>	Fr,L	T
Moraceae	<i>Treculia africana</i>	Fr,S	T
Papilionaceae	<i>Mucuna pruriensi</i>	Fr	C
Piperaceae	<i>Piper sp. (?capensis)</i>	Fr	T
Piperaceae	<i>Piper umbretum</i>	Sh	H
Rubiaceae	<i>Vangueria infausta</i>	Fr	T
Rubiaceae	<i>Didymosalpinx norae</i>	Fr	T
Rubiaceae	<i>Mallotus mauritania</i>	Fr	H
Rubiaceae	<i>Pentas ulugurica</i>	L,Fr	H
Rubiaceae	<i>Psychotria capensis</i>	Sh,B	T
Rubiaceae	<i>Paveta comostyla spp. nyassica</i>	Fr	T
Rubiaceae	<i>Catunaregum spinosa</i>	Fr	T
Rubiaceae	<i>Leptactina platyphylla</i>	Fr,L,B	T
Rubiaceae	<i>Tricalysia pallens</i>	Fr	T
Rubiaceae	<i>Tricalysia allocalyx</i>	Fr	T
Rubiaceae (Rutaceae)	<i>Toddalia asiatica</i>	Fr,S,L	C
Salicaceae	<i>Oncoba spinosa</i>	Fr	C
Sapindaceae	<i>Paullinia pinata</i>	Fr	H
Sapindaceae	<i>Zanha africana</i>	Fr,L	C
Sapindaceae	<i>Zanha golungensis</i>	Fr	C
Sapotaceae	<i>Pachystela brevipes</i>	Fr,L	T
Sapotaceae	<i>Synsepalum cerasiferu</i>	Fr,S	H/ST
Simaroubaceae	<i>Harrisonia abyssinica</i>	Fr	T
Solanaceae	<i>Solanum kitiviense</i>	Fr	H
Scrabaeoidea	<i>Cussonia zimmermannii</i>	Fr	H/ST
Sterculiaceae	<i>Leptonychia usambarensis</i>	Fr,L	T
Sterculiaceae	<i>Sterculia quinqueloba</i>	Fr,B	T
Smilacaceae	<i>Smilax anceps</i>	Sh	C
Tiliaceae	<i>Grewia goetzeana</i>	Fr	T
Tiliaceae	<i>Grewia sp.</i>	Fr	T
Thymelaceae	<i>Synaptolepis kirkii</i>	Fr	T/H
Ulmaceae	<i>Trema orientalis</i>	Fr	T
Ulmaceae	<i>Celtis africana</i>	Fr,L	T
Verbenaceae	<i>Lantana camara</i>	Fr	H
Ulmaceae	<i>Celtis gomphophylla</i>	Fr	T
Vitaceae	<i>Cissus rhondensis</i>	Fr	H
Vitaceae	<i>ciccus sp.</i>	Fr,S	C
Verbenaceae	<i>Vitex doniana</i>	Fr,Fl	T

Zingiberaceae	<i>Aframomum sp.</i>	Sh	H
Zingiberaceae	<i>Costus ?afer</i>	R,Fl	H
?	<i>Oxyanthus pyrisformis</i>	Fr	T
?	<i>Diospyros mespiliformis</i>	Fr	
?	<i>Landofia buechanani</i>	Fr	T
?	<i>Tetracera litoralis</i>	Fr	Sh

¹Fl = Flower, Fr = Fruit, G = Gum, L = Leaf, S = Seed, N = Nut, R = Root, Sh = Shoot
 2 C = Climber, H = Herb, T = Tree.

The Sanje mangabey is largely frugivorous. The percentage of total fruit eaten was 43%. The mangabeys spent up to an average of 47% of their time feeding on fruits, seeds, flowers and roots, 19% feeding on small vertebrates, invertebrates and fungi. The group spent 15% feeding on shoots and stems (gum or sap) of various species, and 9 % on leaves.

The feeding time (minutes) mangabeys spent on different items varied significantly (Individuals $n = 30$, $F_{\text{Leaves}} = 28.7$, $F_{\text{reproductive parts}} = 51.3$, $F_{\text{Shoot/stem}} = 32.6$ and $F_{\text{Invertebrate/Fungi}} = 48.0$ all $P < 0.001$). Figure 2 shows time spent feeding on each food item for each age-sex class. Time spent feeding on leaves was longer in heavier individuals in January, May and June ($\chi^2 = 7.25$, $P < 0.05$). Females spent relatively longer time feeding on fruits, seed and flowers than any other group members ($\chi^2 = 8.43$, $P < 0.01$). Higher amounts of shoots and stems were eaten by sub adults and juveniles than adults ($\chi^2 = 8.11$, $P < 0.05$).

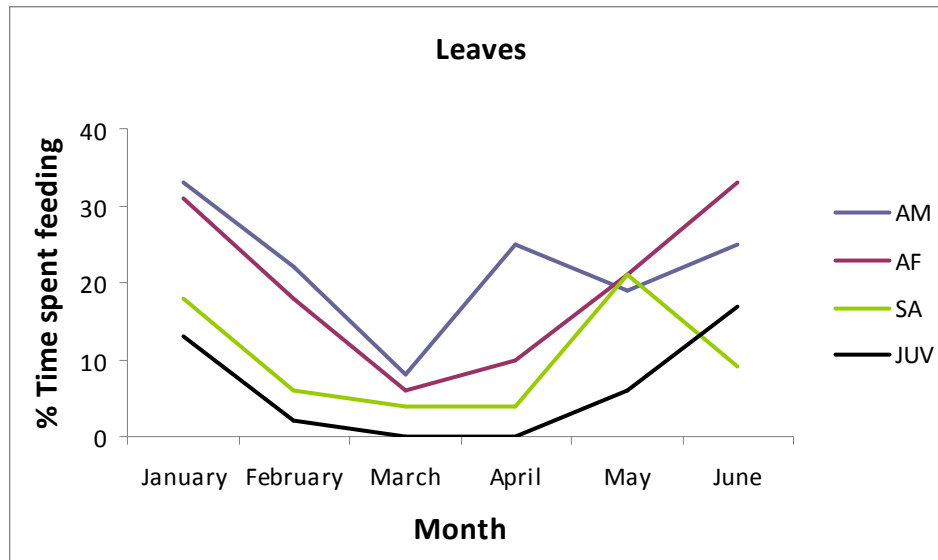
Heavier individuals tended to forage in trees more in January, May and June when there was relatively little rain, than during other months (Figure 3.1). They also tended to use the canopy layer of the forest more often than immatures and sub adults. Sub adults and females foraged in trees more frequently than males and juveniles. Lighter individuals fed on seeds, fruits and flowers more in March throughout June. 68% of all feeding time for the group was spent on the forest floor (i.e. between 0 and 1 m). Thus, Sanje mangabeys are generally terrestrial. The arboreal layer was utilized for 19% of feeding time. Males used the arboreal layer more (64%) than females (46%), sub adults (51%) and juveniles (25%).



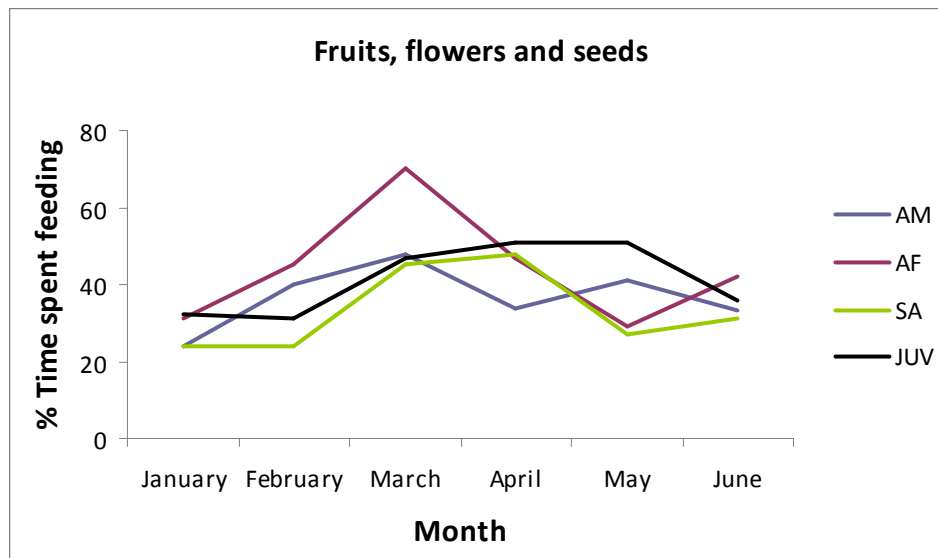
Fig. 3.1. Other food items consumed by Sanje mangabey

Food tree density

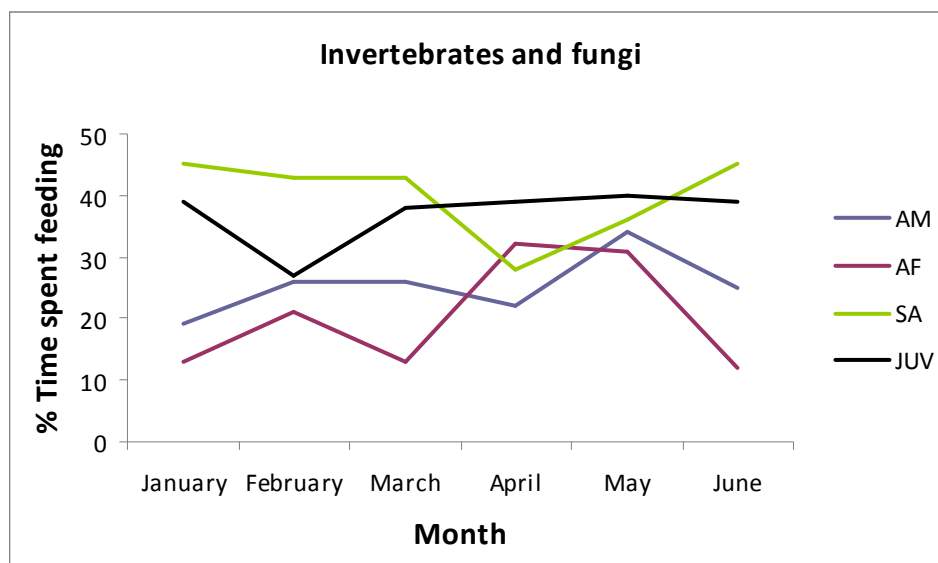
The density of reproductively sized individuals of the 34 most consumed food species in a 7.0 ha area of Njokamoni was 183 trees per hectare. The 34 species were selected because they contributed up to 71-95% of group diet per month for the whole data collection period, and 82% of them occur in Njokamoni. The abundance of food trees per individual was 95. These estimates were probably lower before the group expanded its range to infrequently used areas of Sonjo.



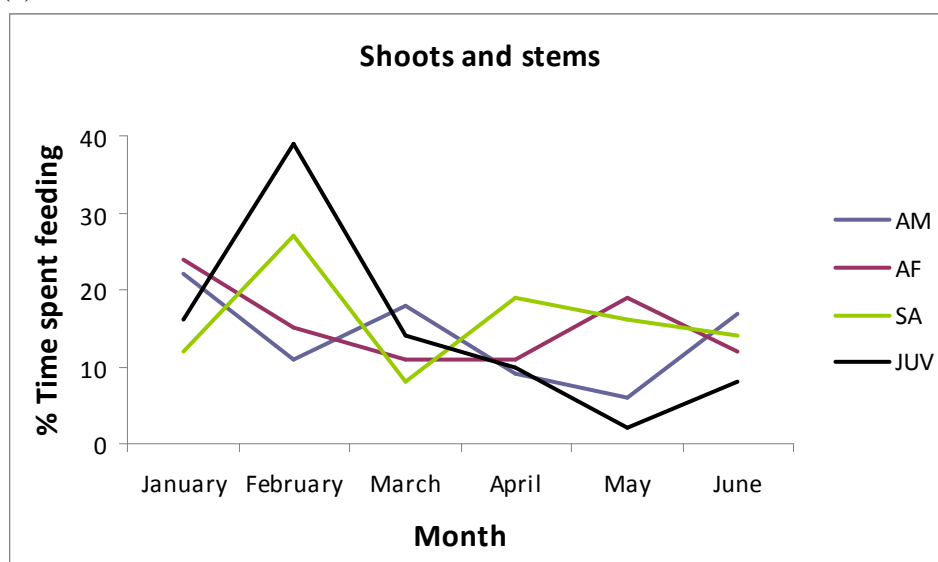
(a)



(b)



(c)



(d)

Fig. 3.2. Percentage time feeding on each food item (a, Leaves; b, reproductive parts; c, invertebrates and fungi; and d, shoots and stems).

Patterns of rainfall: Wet and dry seasons

The total annual rainfall at Udzungwa's Mwanihana forest in July 2007 to June 2008 was 2384.9 millimetres (mm). The mean monthly rainfall was 198.7 mm (range 13-667mm). Rainfall was lowest between May and November and greatest between December and April, with a peak in March. Figure 3.3 summarizes the monthly total rainfall in Mwanihana. The annual total amount of rainfall received in Mwanihana was quite high compared to that estimated for 1996 and mid 2005-2006 (Lovett, 1996; Lovett *et al.*, 2006). The rainfall was also high compared to the 2000 mm average rainfall received for all regions of Tanzania per year (T.M.A, 2008).

The wet season in Udzungwa starts in mid December to April. The dry seasons lasts from May to November (when the total rainfall drops significantly). Variations in the onset of rainfall in the Udzungwas (which are used to define seasons in each particular region), cause slight variations in the wet (November- April) and dry (May-October) season estimates in this area.

Temperature

The mean annual temperature in Mwanihana at 450 m a.s.l. from July 2007 to June 2008 was 25.2°C. However, days with rain had relatively cooler temperatures than in drier days. This estimate compares to 26 °C (range 24 °C - 28°C) temperature recorded at 300 m a.s.l. reported by Lovett in 1996. My data show that there are minimal differences in the mean temperatures per month per year in Udzungwas (Figure 3.4). The data thus, suggest some temperature decreases with altitude.

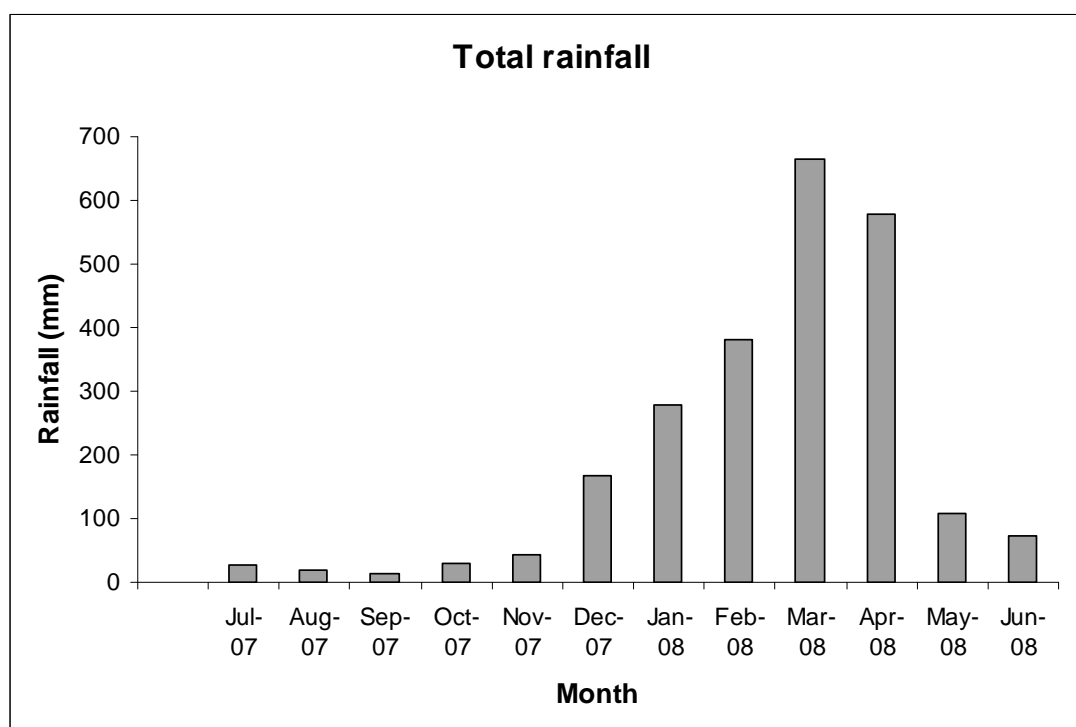


Fig. 3.3. Rainfall patterns for Mwanihana forest in July 2007 to June 2008

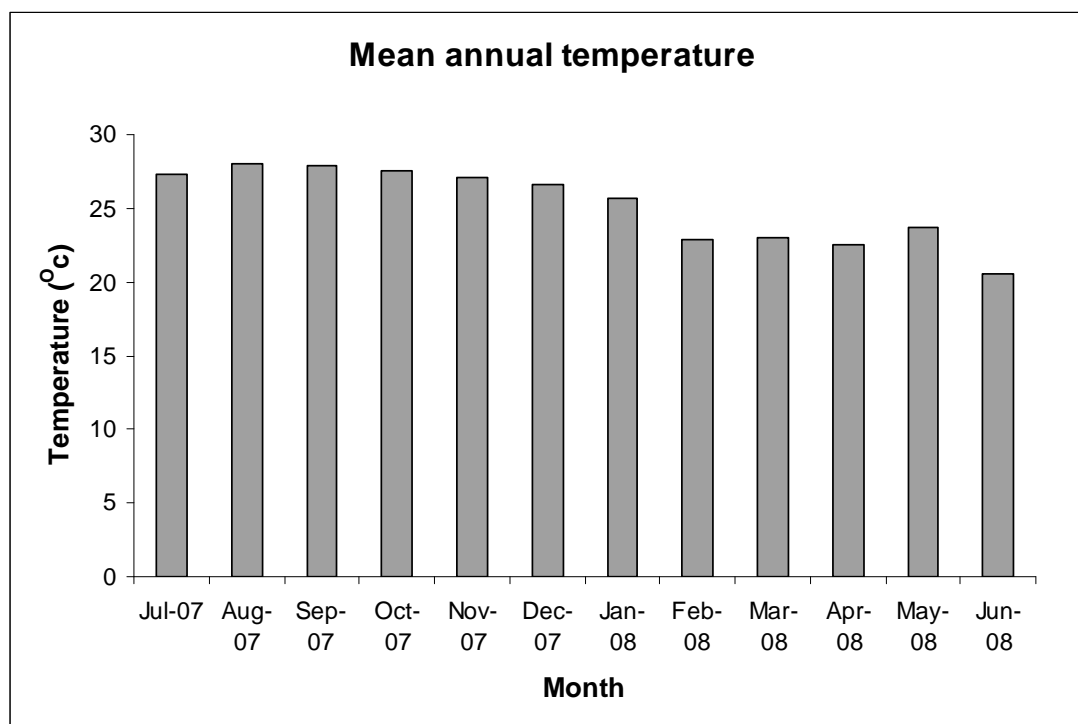


Fig.3.2. Mean monthly temperature in Mwanihana forest from July 2007 to June 2008

Discussion

As evidenced by the dental and facial characteristics (McGraw & Fleagle, 2006) and available field data, Sanje mangabeys, like other *Cercocebus* species, share a common foraging regime with mandrills. The group was observed feeding on a variety of food items, ranging from fruits, seeds, nuts, flowers, leaves, shoots, roots, gum/sap, and ferns, to small vertebrates such as lizards, fungi, and invertebrates.

Before this study, virtually nothing was known of the Sanje mangabey's dietary ecology or the parameters of the forest it occupies (Ehardt *et al.*, 2005). My results confirm Ehardt's speculation that this species might be largely frugivores. The percentage of total fruit eaten was slightly lower than the 60% estimate by Ehardt *et al.* (2005). The mangabeys spent an average of 47% of their time feeding on fruits, seeds, flowers and roots, 29% feeding on small vertebrates, invertebrates and fungi. The group spent 15% time feeding on shoot and stems, gum or sap of various species, and 9% on leaves.

The numbers of plant items utilized was also higher than previously estimated (Ehardt *et al.*, 2005; Wasser, 1993). These previous estimates of mangabey diet were probably too low because they were based on preliminary general surveys of all primates and

reliance on non systematic observations. My study, in addition was able to prove a measure of mangabey use of forest strata. I found out that the species spends up to 68% of all focal feeding time on the forest floor (lower than 1 m). Ground and intermediate layers combined were utilized for 79% of focal time. The arboreal layer was utilized for 19%. This is higher than the 51% estimate by Ehardt *et al.* for heights less than 10 m above the ground.

The density of food trees that are most often utilized by mangabeys is quite low compared to closely related Tana River mangabey living in a similar habitat, in Kenyan forest. The smaller estimate of food trees per hectare was due to a smaller area sampled, which also might not have been a truly representative of their favoured habitats. Wieczkowski (2005b) sampled 16.25 ha, where in my study, only 7 ha were sampled. Furthermore, my findings suggest that food abundance available per individual mangabey was quite high, considering the 183 available trees in each hectare. Food abundance per mangabey was 95 trees. Also, since the animals take other food items, I can say that the estimated plant food abundance might be quite accurate.

Based on optimal foraging models, primates, like most other mammalian species, can choose food items based on their nutritional qualities or, alternatively be influenced by food availability, and switch to more abundant food when preferred items are not available. The amount of time Sanje mangabeys spent feeding was not significantly different with each class in each period. This suggests that each class had its own dietary preferences, which were reflected by the actual time spent feeding on different food items.

As per the Jarman-Bell principle, the time spent feeding on leaves was longer for heavy bodied individuals (figure 3.1). On the other hand, juveniles and sub adults spent relatively larger percentages of time feeding on invertebrates and mushrooms than adult males and females. Leaves are readily available in the forest (Agetsuma, 2001; Leonard *et al.*, 1996; Sailer *et al.*, 1985), but they were not, on an average, selected over other nutritious foods. The findings of my study suggest that the Jarman-Bell principle of feeding selectivity based on body size does apply to Sanje mangabeys, whose body sizes differ with respect to sex and age.

Seasonality in feeding behaviour: There were few obvious seasonal effects upon feeding behaviour, to tentatively suggest that feeding behaviour in Sanje was influenced by seasons. The animals showed some slight increases in the amount of time spent on the forest floor during dry days than on days with rain. However, my observations were conducted for quite a short period of time, so it is difficult to draw conclusions about important aspects of Sanje mangabey ecology. Comprehensive investigations will be required to further address this issue.

Climatic patterns

A annual rain season is evident in this area, with rainfall of up to 2100 mm starting in December and lasting until May. The dry season starts in June and lasts until November. The total amount of rainfall received per year in Mwanihana was high compared to previous estimates (Lovett, 1996; Lovett *et al.*, 2006). This might be due to two factors; either climatic conditions in the area have improved, or there were technical differences in the way data were collected. The total annual rainfall was 2384.9 millimetres (mm), with a mean monthly rainfall of 198.7 mm. Wet months in this area are December to April, and drier months last from May to November. The rainfall received was also higher compared to general Tanzania's estimates per year (T.M.A, 2008).

There were minimal differences in the mean temperatures per month per year in Udzungwas (Figure 3.4). The temperature recorded in this study was slightly cooler than that estimated by Lovett in 1996 and by Lovett *et al.* in 2006. These studies estimate an average temperature of 26°C. The mean annual temperature in Mwanihana at 450 m a.s.l. in July 2007 to June 2008 was 25.2°C. The estimates in these other studies were made at altitude of 300 m a.s.l. The data thus, suggest some temperature decreases with altitude.

CHAPTER 4: SEXUAL BEHAVIOUR AND REPRODUCTIVE STATUS

Abstract

Basic knowledge on reproductive biology of Sanje mangabey which is crucial for effective conservation planning and management is lacking. Data obtained over a 6 months period from one habituated group of free-ranging Sanje mangabeys were analysed in order to examine the sexual behaviour in relation to patterns and changes in reproductive cycle and sexual skin morphology. Menstrual cycles were monitored in 10 individually identifiable females. Cyclical changes in the female sexual skin swelling and in patterns of sexual behaviour in both sexes were quantified, and seasonal effects on reproduction were monitored. Females exhibited large oestrogen-dependent sexual skin swellings during the follicular phase of the menstrual cycle. I report the description of the morphology of sex skin and changes in its appearance at various cycle stages and during pregnancy. The reproductive parameters and sexual behaviour are explained. Morphology of sex skin of this mangabey differs from that of other *Cercocebus* sp. *Cercocebus sanjei* is comparable to other *Cercocebus* species in terms of reproductive parameters, although variability is exhibited within and among female subjects. The estimated swelling cycle length is 32.1 ± 2.4 days. Individual females differed significantly in swelling duration ($F = 12.43$, $P = 0.043$), but there was no group variation in cycle length ($H = 30.2$, D.F. = 6, $P > 0.05$). Mean menses length was 3 ± 0.2 days ($n=3$). Maximum swelling lasted for an average of 4.4 ± 0.9 days and swelling detumescence averaged 14.7 ± 3.9 days. All cycling females, except CT, showed days with regular swellings of both sizes. It appears that social factors and stressful incidents altered cycle length of some females. The mean interval between birth and resumption of swelling cycle is 184 days. Gestation length averaged 173 days. The swellings have shown to be sexually attractive signals of female reproductive condition. Although mating occurred in all stages of female cycle, a peak was observed during maximum swelling size and breakdown. Births and occurrence of sexual swellings did not show a seasonal distribution. These data illustrate the utility of sex swellings as signal used by males to determine female reproductive status and show its value in mating interactions.

Key words: *C. sanjei*, sexual skin swellings, sexual behaviour, swelling cycle.

Introduction

The two sexes of most animal species use specific signals to advertise their fertility and to attract potential mates e.g. *Holbrookia propinqua*: (Cooper Jr *et al.*, 1983); *Drosophila grimshawi*: (Droney & Hock, 1998); *Loxodonta Africana*: (Leong *et al.*, 2003). These signals may be substantial and conspicuous (Dixson, 1983), and can be physiologically and energetically costly (Setchell & Dixson, 2001b). For females, such signals generally increase their attractiveness towards male conspecifics and encourage copulation by stimulating male sexual arousal (Dixson, 1998; Girolami & Bielert, 1987). In primates the most obvious morphological signal of fertility and or impending ovulation is the sexual swelling of females (Dixson, 1983). Olfactory cues may also play role in signalling fertility in primates (Johansson & Jones, 2007; Michael & Keverne, 1968). However, studies of higher primates indicate, apart from behavioural and morphological cues displayed by female, males do not rely on olfactory cues to a large extent (Reichert *et al.*, 2002). This makes swellings the primary and probably the most important cue used by males.

Sexual selection has led to the evolution of a number of secondary sex traits in various animal species, sex swellings being amongst them (Anderson, 1994; Darwin, 1871; Zinner *et al.*, 2004). Occurrence of exaggerated swellings is mostly restricted to Old World monkeys with multi-male multi-female mating systems (Clutton-Brock & Harvey, 1976). The evolution of sexual skin swellings in Old World monkeys has occurred a number of times during primate evolution; secondary reduction of the sexual skin may have occurred in some lineages (Dixson, 1983; 1998).

Swelling size is basically due to water retention, and its colour is influenced by vascular changes (Bielert & Anderson, 1985; Bielert *et al.*, 1989). Changes in the morphology of the sex skin are triggered by oestrogen which stimulates the sex skin around the perineum to swell or redden, during the follicular phase, showing maximum size around the time of ovulation (Baulu, 1976; Dixson, 1983; Girolami & Bielert, 1987; Hrdy & Whitten, 1987). The swelling then decreases in size under the action of progesterone during the luteal phase of the menstrual cycle e.g. *Hylobates lar*: (Barelli *et al.*, 2007). The duration of tumescence of sex skin varies considerably between and within species.

The size of skin swelling has been associated with various functions. For example, the size of swelling has been related to female fitness (Domb & Pagel, 2001), to cycle quality (Deschner *et al.*, 2004) and to serve for social identification during inter-group transfer (Goodall, 1986). Swellings have been associated with reproductive success, increasing the chance of fertilization and signalling reproductive status (Nunn, 1999a; Pagel, 1994). It may also play some 'mechanical' role during mating (Dixson, 2002; Dixson & Anderson, 2004).

The function of swellings, particularly with respect to their influence on mating patterns has been much debated, and a number of theories have been advanced to account for their evolution (see reviews in Dixson (1998) and Nunn (1999a)). Sex swellings, based on their size and stage were initially proposed to function as a rough indicator of female reproductive condition (Dixson, 1983). Swellings have also been reported to function as obvious indicators of timing of ovulation (Hamilton, 1984), hence assuring paternity to dominant males, if they were to mate with females that have swollen sex skin. In contrast, a study of *Macaca fascicularis* suggests that it is female sexual behaviour rather than skin swellings that indicates the timing of the fertile phase (Engelhardt *et al.*, 2005). The 'many males hypothesis' (Hrdy, 1981; Hrdy & Whitten, 1987) suggests that females use the attraction of males to swellings to mate with many partners, and so reduce the chances of infanticide by confusing paternity. These hypotheses are based on the assumption that ovulation is distributed over different stages of swelling, such that males are unable to pinpoint the timing of ovulation.

Swellings might also encourage sperm competition (Harvey & May, 1989) by increasing male-male mating competition and thus indirect female mate choice. This could result in the female's infant benefiting from the male's superior quality (best male hypothesis: Clutton-Brock & Harvey, 1976). Furthermore, swellings are also considered as honest signals of female reproductive fitness (the reliable- quality indicator hypothesis: (Pagel, 1994). This theory is based on fact that females are fertile and sexually receptive when they are swollen. Alternatively, the graded signal hypothesis (Nunn, 1999a) suggests that swelling sizes only act as approximate indicators to males concerning the likelihood of ovulation. The graded signal

hypothesis proposes that most of the follicles ovulate at peak swelling size, and that high ranking dominant males tend to guard females only when they are maximally swollen. This gives less dominant males a small but significant chance of passing on their genes when swellings are smaller in size, and when females are not monopolized by dominant males. It appears nevertheless, that the dominant male has the best opportunities to reproduce, and rank can be an indicator of potential reproductive success. However, male rank and mating success do not invariably reflect reproductive success (Marvan *et al.*, 2006).

Other hypotheses are more focused on male-female socio-sexual relationships, such that males tend to form consortships with females at peak swelling (The male services hypothesis: Manson, 1997). Consortship serves a number of functions for both sexes such as mate guarding, mate assessment and courtship. It also offers the female protection against predators and assistance in territorial defence since male consorts are believed to be the most effective at excluding other individuals or predators (Nunn, 1999a). The protecting male may also minimize harassment towards the female with a swollen skin, even though this male is only guarding to maintain exclusive mating access. Each of these hypotheses makes assumptions about swelling sizes in relation to female reproductive status and fertility, most of which have been difficult to verify.

In African papionins (baboons, mandrills and mangabeys) and most other Old World monkeys that live in multi-male multi-female groups, females have conspicuous sex swellings. Female attractivity increases during the maximum tumescent phase of the sex skin (Dixon, 1983; 1998) and patterns of skin swelling and behaviour change during this period, reflecting cyclic fluctuations in ovarian hormones (Dixon, 1998). Females of the Sanje mangabey (*Cercocebus sanjei*) exhibit exaggerated sex swelling typical of other African papionins. During this period the anogenital region becomes bright pink or red and swells.

Although members of the Afro-papionin group have diverse ecologies and social structure, their reproductive parameters are considered to be uniform. Menstrual cycles and gestation periods are approximately 4-5 weeks and 6 months respectively with no evidence for intertaxon variability (Altmann *et al.*, 1981; Campbell *et al.*,

2007; Gust & Gordon, 1991b; Setchell *et al.*, 2006). Due to insufficient information generalisations about mangabey sexual behaviour are, however, still based on inadequate evidence.

While data on menstruation are of great importance, they are very difficult to collect in the wild. Accordingly, captive studies can contribute vital information to complement that collected in the wild. With the exception of baboons, female cycle variability, sexual and breeding behaviour are poorly studied in the African papionin group. There are few studies describing reproductive parameters in mangabeys (Gust, 1994a; Gust *et al.*, 1990; Gust & Gordon, 1991b; Wallis, 1983; Whitten & Russell, 1996). These studies of mangabeys, so far, have either analysed cyclic changes in swelling-hormone interactions, without considering behaviour. These studies have also produced contradictory results concerning the duration of the menstrual/swelling cycle (Wallis, 1983).

Swelling characteristics and sexual behaviour are moderately characterised in a few species of mangabey, and no information is available for *C. sanjei*, possibly because this is a relatively newly discovered species. *C. sanjei* is clearly important among mangabeys because it has an unusual combination of behaviour and ecology typical of both the phylogenetically closely related mandrills and other terrestrial mangabeys. Given the lack of information on mangabey reproduction and behaviour, detailed behavioural studies that focus on mating patterns in relation to sexual swelling in the Sanje mangabey are necessary.

The aims of this study were therefore to document female sexual skin morphology in the Sanje mangabey and examine temporal relationships between sexual skin swellings and sexual behaviour. My specific objectives were: (1) to describe the morphology of sexual skin in female Sanje mangabeys; (2) to characterize changes in swellings in different reproductive states; (3) to measure changes in sexual behaviour during various swelling stages; (4) to test various hypotheses underlying the functional significance of sex swellings; (5) To obtain a preliminary estimate of gestation length for the Sanje mangabey.

Methods

Study group

I collected data on sexual behaviour and on female reproductive status of free ranging Sanje mangabeys living in the forests of Udzungwa from December 2007 to June 2008. The Njokamoni group of Sanje mangabeys had 62 individuals during the study, which comprised 14 reproductively active females and 5 sexually mature adult males. The rest of the animals were juveniles, infants and sub-adult males and females. My observations focused upon 10 females and 6 males. Supplementary data on sexual behaviour were also recorded for other group members. Assessment of reproductive status and sexual skin swellings were made for the 10 individually recognised females. An 11th female (possibly pregnant) was excluded as she disappeared and may have died or migrated to another group during the study period. Seven females cycled throughout the 6 months of observations, one was lactating, and two were pregnant and later gave birth. The decision to track swelling morphology from a sub-sample of 10 females was due to difficulties in finding and identifying all the females in a group of 62 free ranging animals in a dense rainforest.

Female Sexual skin swellings

The morphology of sexual skin swellings in *Cercocebus sanjei* is undescribed. As a starting point we used the morphological criteria known for other mangabeys and especially for other members of *Cercocebus* to describe sex skin swellings in this species. (Gust *et al.*, 1990; Rowell & Chalmers, 1970; Walker *et al.*, 2004) Photographs of Sanjei mangabey taken with Fujifilm 9.0 megapixel digital camera were used to define morphological traits of the sexual skin.

Female reproductive status and the menstrual cycle

Considering the structures of external genitalia of other *Cercocebus* (Rowell & Chalmers, 1970; Walker *et al.*, 2004), baboons (Domb & Pagel, 2001) and the related *Mandrillus sphinx* (Dixon & Anderson, 2004; Setchell & Dixon, 2001b), the size, colour and wrinkling of the pubic lobe, dorsal lobe and circumanal region were taken as the main parameters for assessing changes in female sexual skin. Assessments of reproductive status and sexual skin morphology were made and compared to the size and colour of the ischial callosities, which are pink and unfused in females but fused in males.

Swellings were inspected daily when females were sitting on branches, standing or walking. Qualitative characteristics of the appearance of the genitalia (shape, tumescence, size, colour and distribution) were examined with the aid of Bushnell 10 x 50 perma focus binoculars. Systematic records were made on check sheets to include the female's name, time of record and notes on degree of the wrinkling and colour of the genitalia.

Considering the pre-used swelling scoring system for mangabeys e.g. (Gust *et al.*, 1990; Walker *et al.*, 2004), and to allow comparison with other studies from the behaviourally and phylogenetically closely-related mandrill, I used Dixon & Anderson's (2004) four point scoring system to rate female skin swelling morphology. This method is based on the size and degree of tumescence (firmness) of the sex skin. I had no quantitative measures of sexual skin size. However, a swelling classified as flat to small would protrude several millimetres to 3.5cm, and above 3.5cm to 8cm was classified as medium to large (Domb & Pagel, 2001; Pagel, 1994). Swelling was assigned a score from 0 to 1 coinciding to early follicular phase and before it starts to increase in size. It was scored 3 at end of swelling phase and when it started to decrease in size (detumescence) in luteal phase or gestation (in case of conception cycles). Four swelling stages were defined as follows;

Flat/no swelling (score 0): maximum detumescence of genital structures, vulva appears as a tiny pink spot similar in colour to the ischial callosities, and surrounded by wrinkled skin.

Small swelling (score +1): Genital structures partially tumescent, vulva and pubic lobe visible with shallow wrinkles and pink colouration.

Medium swelling (score +2): The dorsal lobe of the sexual skin and pubic lobe are partially tumescent, and with a pink or reddish colouration. The peri-vulval area is swollen also and forms a small distinct protrusion dorsal to the pubic lobe.

Fully swollen (score +3): The dorsal and pubic lobes of the sex skin are fully swollen and turgid; and the swelling is bright red or reddish pink. The peri-vulval swelling is also maximal at this stage.

It was not possible to observe breakdown days except in rare cases. Detumescence was recorded whenever observed (i.e. regardless of whether its onset was observed or not during that or the previous day). The breakdown and deflating stages are defined as follows:

Breakdown: The dorsal lobe of the sex skin loses turgidity; the peri-vulva area is less turgid at this stage and has bright red or reddish pink colouration.

Detumescence (-2): The peri-vulval region loses its turgidity and brightness, the pubic lobe is partially tumescent but still retains its bright pink colouration and the sexual skin has shallow wrinkles.

Detumescence (-1): maximum detumescence of most of genital structures, the pubic lobe is moderately tumescent, 'pointy' and with pink colouration similar to the ischial callosities. The sex skin has shallow to deep wrinkles at this stage.

Sexual swellings were analysed relative to possible changes in female proceptivity, receptivity and sexual attractiveness. Changes in sexual presentations and behaviour throughout different reproductive states of the females were examined in relation to swelling sizes. Sex skin swellings were scored and data was collected by myself and one trained assistant. Inter-observer reliability was assured by independent rating of swelling stage periodically throughout the study.

Pregnancy and lactation

To detect patterns of swellings outside the menstrual cycle, 3 non-cycling (2 pregnant and one lactating female) were included in the sample. For pregnant females, data were collected during the last month of gestation for female numbers 7 (KMH) and 3 (KM), and the first three months after parturition and throughout one entire gestation for female number 1 (KL). For most of the period these 3 females were lactating. Photographs taken of females that were pregnant and lactating form the basis of the description of sex skin swelling morphology.

Ovulation and duration of swelling cycle (cycle length)

A detailed analysis of ovulation and the potentially fertile period requires hormonal data. Menstruation was difficult to observe, except for three cases. It is not possible to

define precisely when ovulation occurs in relation to sexual skin swellings in wild mangabeys. However, it is likely that the fertile period occurs during the last 5 days of maximum swelling and day of breakdown of the sex skin (Dixson, 1998). Endocrine studies of baboons and other monkeys (Barelli *et al.*, 2007; Shaikh *et al.*, 1982; Wildt *et al.*, 1977) show that about 60% of follicles ovulate during the last few days of maximum tumescence and at breakdown.

Since menstruation was not discernible in all females' cycles, we based the overall female cycle length on the sex skin swelling cycle. The duration of the swelling cycle was therefore measured as the interval between the days of successive periods of no swelling. Data on how long it takes for female mangabeys to attain maximum swelling size are not available. I thus measured the interval between maximum swelling to the next maximum size, which is referred to here as the Inter-swelling Interval (Paoli *et al.*, 2006). Mean cycle length calculated this way was found to be more consistent with the calculation based on menstrual and endocrine records (Deschner *et al.*, 2003; 2004).

Patterns of births, infants in the group and breeding season

Records were kept for births that occurred during the time spent in the field and presence of young infants (still clinging to the mother) in order to address whether seasonal patterns of reproduction occur in this species. Patterns of female sex swelling and copulatory frequencies were used to further to investigate this question.

Supplementary data were collected on gestation and resumption of swelling after parturition. The gestation period was estimated by counting backwards from the day of parturition to the last observed sex skin swelling that was bright pink in colour with successive days of sexual behaviour. This same method has been applied to the Tana River mangabey (*Cercocebus galeritus galeritus*) by Kinnaird (1990a; 1990b). To determine when females resume menstrual cycling following parturition, I considered the day each female exhibited a small swelling (recorded as score 1) to delineate resumption of swelling. The purpose was to calculate the likely period of lactational amenorrhea. I used this criterion instead of later stages of swelling tumescence because the onset of sexual skin tumescence indicates the possibility of ovarian stimulation and hence likelihood of impregnation.

Sexual Behaviour

Sexual behaviours were recorded for all members of the group of reproductive age. Data were collected for an average 10 hours, 18 days a month. A combination of scan sampling and *ad libitum* sampling (Altmann, 1974) was used to record the group's sexual behaviour. The occurrence of sexual behaviours was recorded, and the frequencies generated from all 20 minute scans and *ad libitum* samples. Social behaviour was also recorded concurrently with sexual behaviour (i.e. during scan sampling times as reported in Chapter 2).

During observations, all sexual behaviours involving adult and sub adult males and sexually mature females were recorded during instantaneous scans (S) or *ad libitum* (A) sampling. Sexual behaviours were assessed relative to proceptivity, receptivity and sexual attractiveness of females towards males. The behavioural patterns recorded for females are defined as follows;

- a. Presentation (P): The female presents her hindquarters towards male with tail raised, and often looks over her shoulder at the recipient's face.
- b. Copulation call (C): Short grunting sounds made by female during and or after termination of intromission.
- c. Pre-copulatory calls (PC): These are similar to copulation calls but they are made when female is very near to (or up to 7m from) the male, often accompanied by head-flagging.
- d. Female acceptance: The female accepts male's mount attempt and allows copulation to occur.
- e. Female refusals: The female prevents the male from mounting or actively avoids his attempts to copulate.

The following were scored for males;

- a. Genital inspection (I): Male inspects the anogenital region of female by sniffing (IS), touching (IT) or by looking at it (IL). This often follows presentation by the female.
- b. Male follows female: Male follows female beyond normal or brief proximity. This often leads to other forms of sexual behaviour.

- c. Grab: Male grabs female in a dorso-ventral position. This is typically preceded and/or followed by other forms of solicitation or mating behaviour.
- d. Mount attempts (MA): The male grasps the female's hips and attempts mounting in a dorso-ventral position. Erection may, or may not accompany this behaviour.
- e. Mount: Male mounts a female in a dorso-ventral position, while clasping her calves with his feet. Occasionally, the female initiates pelvic thrusting prior to intromission. Successful intromission starts with shallow rapid, pelvic thrusts followed by slower, deep thrusting motions (often more than 9) after intromission was attained.
- f. Ejaculation: This is signalled by a pause in pelvic thrusting. The male often held onto female by pulling her close to him.
- g. Masturbation: Manual stimulation of penis which may result in erection.

Sexual behaviour is undescribed for this species; details will thus be included in the results. To determine whether intromission is performed more than once before the male ejaculates I noted the intervals between mounts and intromissions. When two copulations (involving the same partners) followed each other in less than 5 min, these were counted as a single mount series. Adult male mangabeys vary in the amount of time spent interacting with sexually mature females. The number of mounts and interactions with females by each mature male ($n=5$) was noted whenever possible. This was used to determine whether some males are more sexually active than others and if these males have greater mating success (e.g. in terms of female acceptance of their mating attempts). Variations in sexual behaviour during wet and dry seasons of the year were also quantified.

Data analysis

Because menstruation was difficult to detect, I used two measures, as interval markers of the swelling cycles. First, the final stage of deflation (from -1 to 0- i.e. the period of last signs of detumescence) to the first signs of next swelling tumescence. The other measure was the duration between first day of maximum swelling to the first day of next maximum swelling. Profiles of swelling spanning the entire study period were constructed for each of the 10 females separately, and mean values were calculated.

The 7 cycling females were observed for 3.98 ± 0.67 hours when swelling was flat, 7.06 ± 0.32 when swelling was small, 7.84 ± 0.66 when swelling was medium swollen (+2), and 3.88 ± 0.31 hours when swelling was fully swollen (+3). Also females were observed for 4.18 ± 0.3 (-1 & -2) during detumescence. Mount frequency (number of mounts) was calculated for each female (n=10) at each stage of female swelling (i.e. when swelling is flat, small, medium or maximal, pregnant and lactating) from all observations. Frequencies of mounting behaviour at different swelling cycle stages were compared using repeated measures analysis of variance. Post-hoc comparisons were conducted using t- tests and LSD statistics provided with the mixed linear model were used. Subjects were the 7 cycling females and the repeated measures were the five stages of female reproductive cycle (i.e. small swelling (+1), medium swelling (+2), maximum swelling (+3), detumescing (-1, -2)). Analyses were then restricted to 5 days before detumescence and 5 days following detumescence. Chi square (and Wilcoxon matched pair Z) tests was used to test whether frequencies of mating differ significantly during these periods.

To determine whether male dominance ranks affects mating success, I calculated the frequencies of mating involving adult males (n=5) in relation to rank (as detailed in chapter 2). Only mounts involving intromission with more than 9 pelvic thrusts were included. The percentage of matings by females at swelling phases +2, +3, and or breakdown -2, -1, was computed. It was also predicted that high ranking male individuals would have higher mating success, and would be less challenged or interfered than lower ranking individuals. Mounting and mount attempt times for each male were defined as percentage of instantaneous samples during scan and *ad libitum* observation the focal male mounted or attempted to mount. The phase of sex swellings and percentage of time female mate with either of these males were analysed in relation to dominance rank. Dominance ranks are based on rank orders as presented in Chapter 2.

In cases where parametric tests were used, I first checked the distribution of data for normality and equal variance. Hypotheses were tested with either a *t* test for dependent samples or one way ANOVAs. Tests were performed using SPSS 16.1. All tests are two tailed.

Results

Morphology of sex skin /appearance of the perineum

The morphology of the sexual swelling is illustrated in the Figure 1. The female Sanje mangabey menstrual cycle is characterised by swelling of the sex skin during the follicular phase and prior to ovulation. During this period the anogenital region becomes bright pink or red and swells. It is not known at what age sex swellings start or first conception occurs in Sanje mangabeys. However, studies of agile (*Cercocebus agilis*), golden-bellied (*C. agilis chrysogaster*), grey-cheeked (*C. albigena*) and sooty mangabeys (*Lophocebus atys*) and mandrill report 2.5 to 3 and 4.3 to 5 years respectively (Deputte, 1992; Gust, 1994a; Rowell & Chalmers, 1970; Walker *et al.*, 2004). Similar ages have been reported for the yellow baboon and mandrill (Altmann *et al.*, 1981; Setchell & Wickings, 2004b).

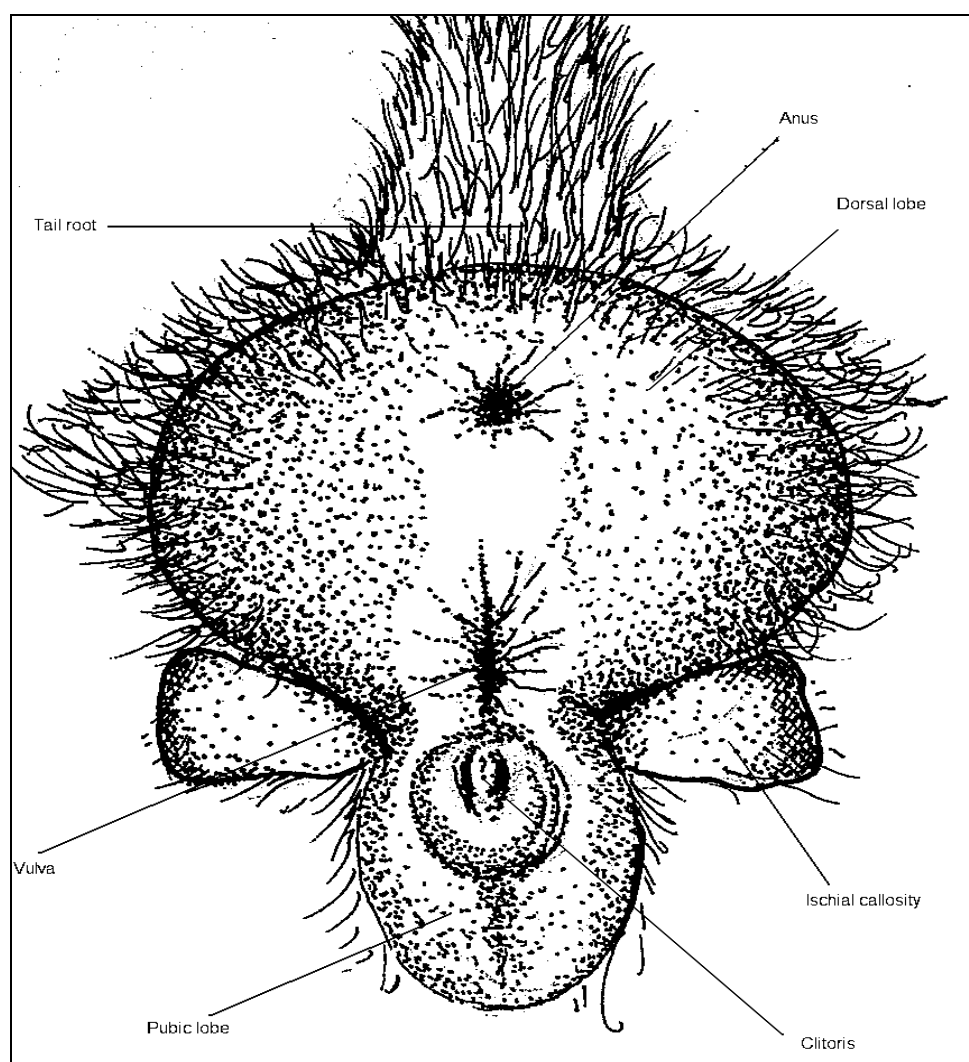
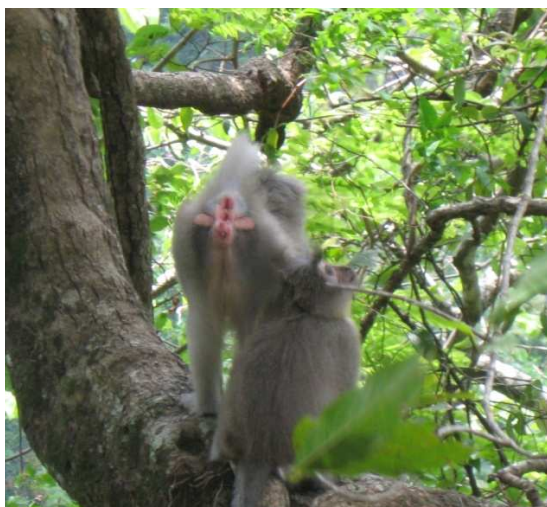


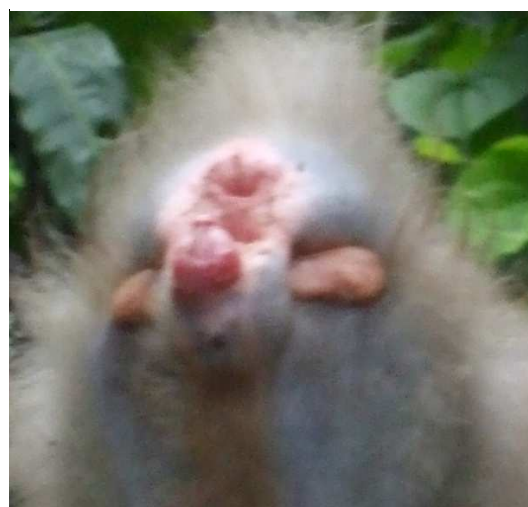
Fig. 4.1 Diagram showing the morphology of Sanje mangabey sexual swelling at full size (+3).

Female Sanje Mangabeys have a hairless sex skin in a small area between the tail root and ischial callosities. The hairless sex skin includes the area dorsal to anus, vulva/vagina extending ventrally to the pubic lobe and the clitoris. The hairless skin is surrounded by moderately haired area dorsal to the anus (perianal region) and tail, extending ventrally (but not laterally) to the ventral parts of the pubic lobe. The swelling starts as small pointed dorsal lobe, and then gradually increases in size, appearing as soft, dull-dusky pink in colour at first, becoming bright pink or red and about 8cm in depth at maximum tumescence. This condition lasts for about 1-9 days before the skin deflates and becomes completely non oedematous, wrinkled and dusky pink in colour. Figure 2 shows the general appearance of the sexual skin swelling of a wild female Sanje mangabey.

The Sanje mangabey sex skin differs from that of other mangabeys because, during the swelling cycle, the moderately haired skin also swells together with the pubic lobe, the peri-vulval region and area surrounding the anus. The other difference in Sanje mangabey is that the prepuce of the clitoris swells markedly, so that the clitoris stands out markedly from the pubic lobe at full swelling. The ventral area of sex skin (pubic lobe) from which the swelling is derived is small and pointed when the female is not swollen. And at the onset of tumescence, the pubic lobe, unlike *Lophocebus* mangabeys, swells together with other parts of the sex skin and is oriented upward, distinct from other species of mangabey.



a. Small swelling



b. Medium swelling



c. Maximum swelling

d. Detumescence

Fig. 4.2. Photograph of a wild Sanje mangabey sex skin showing swelling stages: (a) Small (+1) (b) Medium (+2) (c) Maximum (+3) and (d) Detumescence (-2).

Cycle length and other reproductive parameters

Menstruation was rarely visible in these animals except for eight occasions involving 3 females (MDK, BMK, and MWK). For these 3 females bleeding was adequately visible from approximately 1 metre. In four cases, menstruation was visible for 3 days for female MDK and BMK. The swelling of the skin started 2 and 4 days later respectively. On another occasion BMK showed menses for 1 day and swelling started 3 days later. MWK menstruated 3 times for 2, 4 and 5 days, and the sex skin began to swell in 2, 3 and 4 days respectively. During menstruation, the sex skin becomes bright red at the pubic lobe and while other regions may remain pink.

In total, 6, 5, 5, 4, 4, 5, and 4 complete swelling cycles were recorded for females CT, BMS, MDK, SN, MWK, MT and BMK respectively (Table 4.1). Some additional incomplete cycles for CT, SN, MWK MT and BMK provided supplementary information on cycle characteristics.

The individual swelling profiles over the whole study period (Fig. 4.3) illustrate some inter-individual differences on the number of days of each swelling phase. Table 4.2 shows lengths of various swelling stages (i.e. tumescence (+1, +2,) maximum (+3), and swelling breakdown (-2, -1), and respective means and ranges for each phase, for 7 cycling females. The swelling tumescent phase lasted for 12.7 ± 3.9 days. The average duration of maximum swelling was 4.4 ± 0.9 days, with the most frequent duration 4 being days. Detumescence lasted an average of 14.7 ± 3.9 days. Swellings

stayed in a resting state (before inflating again) for an average of 1.8 ± 0.5 days. All cyclic females, except CT, showed days with regular swellings of both sizes (i.e. small=score 1, medium=score 2 and large=score 3). Swellings of all 3 size classes combined were most common in cycling females (mean =93.3%, median= 94.4%) and were rarer in lactating females (mean= 18.4%, median = 12.4). Not enough samples were available to test for changes in pregnant females.

Table 4.1. Female identification name, code, and number of cycles analysed (cycles N=33; cycling females N=7).

Identification name	Code	Reproductive state	Cycles analysed
Kubwa lao	KL	Lactating →cycling	N/A
Chokstaa	CT	Cycling	6
Kuvimba mkia	KM	Lactating	N/A
Baka mkono kushoto	BMS	Cycling	5
Mdogo kuliko	MDK	Cycling (cycle with menses)	5
Sura nyeusi	SN	Cycling	4
Kijivu mbeba hovyoy	KMH	Pregnant→lactating	N/A
Mwembamba kuliko	MWK	Cycling (cycle with menses)	4
Manywele timtim	MT	Cycling	5
Baka mkono kulia	BMK	Cycling (cycle with menses)	4

N/A= Not applicable.

Table 4.2. Duration of tumescent, maximum and detumescence swelling phase for each female's individual cycle.

Female	Cycle No.	Duration from start to maximum swelling	Days of maximum swelling	Days of detumescence (Luteal phase)	Days of no swelling
CT	-	-	4	6	3
	I	10	4	4	3
	II	22	2	10	1
	III	14	1	17	6
	IV	4	4	13	1
	V	19	2	1	1
	VI	10	3	13	1
Range		4-22	1-4	1-17	1-6
Mean \pm SEM		13.2 ± 2.7	2.8 ± 0.5	10.2 ± 1.9	2.5 ± 0.8
BMS	I	5	1	9	2
	II	5	1	14	1
	III	16	1	12	1
	IV	36	7	14	1
	V	17	4	19	3
	Range	5-36	1-7	9-19	1-3
Mean \pm SEM		15.8 ± 5.7	2.8 ± 1.2	13.6 ± 1.6	1.6 ± 0.4
MDK	I	4	3	11	1
	II	11	7	5	1

	III	9	8	34	3
	IV	15	4	12	3
	V	13	4	20	1
Range		4-15	3-8	5-34	1-3
Mean \pm SEM		10.4 \pm 1.9	5.2 \pm 1.0	16.4 \pm 5.0	1.8 \pm 0.5
SN	-	-	7	2	1
	I	4	7	8	1
	II	3	6	60	1
	III	15	3	22	1
	IV	7	5	20	2
Range		3-15	3-7	2-60	1-2
Mean \pm SEM		7.3 \pm 2.7	5.6 \pm 0.7	22.4 \pm 10.1	1.2 \pm 0.2
MWK	-	-	2	3	3
	I	15	8	7	8
	II	29	2	20	1
	III	10	7	13	1
	IV	10	5	18	2
Range		10-29	2-8	3-20	1-8
Mean \pm sem		16.0 \pm 4.5	4.8 \pm 1.2	12.2 \pm 3.2	3.0 \pm 1.3
MT	I	6	1	11	1
	II	5	2	24	1
	III	5	2	8	2
	IV	32	5	21	4
	V	7	3	18	1
	-	14	-	-	2
Range		5-32	1-5	8-21	1-2
Mean \pm SEM		11.5 \pm 4.3	2.6 \pm 0.7	16.4 \pm 3.0	1.8 \pm 0.5
BMK	-	-	8	5	1
	I	12	9	10	1
	II	30	5	18	1
	III	10	7	12	2
	IV	11	6	18	1
Range		10-30	5-9	5-18	1-2
Mean \pm SEM		15.8 \pm 4.8	7 \pm 0.7	12.6 \pm 2.5	1.2 \pm 0.2
All 7 females					
Range		3-36	1-9	2-60	1-8
Mean \pm SEM		12.9 \pm 3.8	4.4 \pm 0.9	14.8 \pm 3.9	1.9 \pm 0.6

Table 4.3 shows reproductive parameters measured for 10 females. The mean swelling cycle length was 32.4 ± 2.4 days (females, $n = 7$), and the interval between maximum swelling and the next maximum swelling (i.e. the inter-swelling interval, ISI) was 33.1 ± 2.4 days. The median cycle length was 32, 29, 31, 36, 31.5, 28, and 33 for CT, BMS, MDK, SN, MWK, MT and BMK respectively. Mean menses length was 3 ± 0.2 days ($n = 3$). There were inter-individual differences in swelling duration ($F = 12.43$, $P = 0.043$). The group, unlike the individuals, showed no significant variation in cycle length (Kruskal Wallis test, $H = 30.2$, d.f. = 6, $P > 0.05$).

To determine if there is any significant difference between the two measures of cycle length (i.e. end of deflation (from -1 to 0), to next end of deflation = cycle length, and inter swelling interval (maximum swelling to next maximum swelling); I compared the means of the two measures of cycle length using a paired t-test. The test statistic and associated *p*-value indicate that the difference between the two means is not statistically significant ($t = 0.125$, $P = 0.09$, $n=25$), and the two measures were highly correlated (paired sample correlation, $t= 0.53$, $P = 0.05$).

Table 4.3. Reproductive parameters in wild Sanje mangabey

Reproductive parameter	Cycle length	Interval swelling Interval	Menses length	Lactational amenorrhea	Gestation length
Median, (n)	31, (31)	32, (31)	3, (24)	-, (2)	-, (2)
Mean \pm SE	33.1 \pm 2.4	33.2 \pm 2.6	3 \pm 0.2	184 \pm 26.5	173 \pm 14
Range	15-69	14-82	1-5	158-211	159-187

There were unusually long cycles for all females which deviated from the normal by a range of 15-69 days. Irregular cycles or females not showing swelling at all might be associated with specific factors such as sickness, receipt of aggression from males, challenges from other females in the group or other social traumas. Table 4.4 shows irregular, long cycles for 6 females and their possible correlates. Some females also had at least one cycle shorter than the mean. CT had two unusually short cycles, the reason for this is suspected to be physiological, since the female was exceptionally slender, and suspected to be under-weight. CT's swelling also, had an unusual morphology, and most of the time it did not reach maximum size. This female has been observed copulating but has not been observed with infant for the past 4 years (Mselewa pers. communication). CT was also ill at intervals. During those times she was observed salivating excessively and sleeping intermittently.

Table 4.4. Irregular cycles and their possible correlates

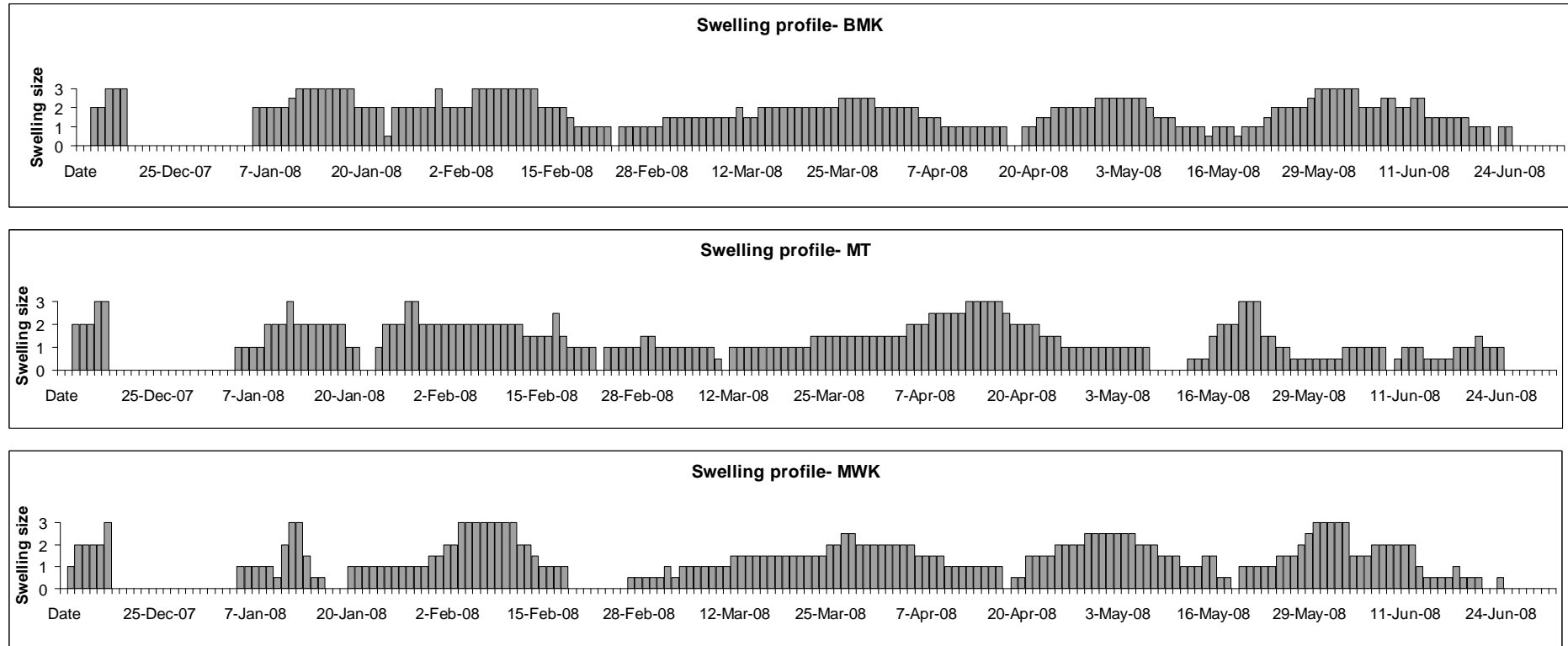
ID	Cycle length	Small (+1)	Med. (+2)	Max. (+3)	Detum. (-2 & -1)	Presumed correlate
BMS	40	8	8	5	19	Problem and aggression from female BMK, MWK and male AMc
	57	15	21	7	14	Aggression from male AMc & AMm during early days of her

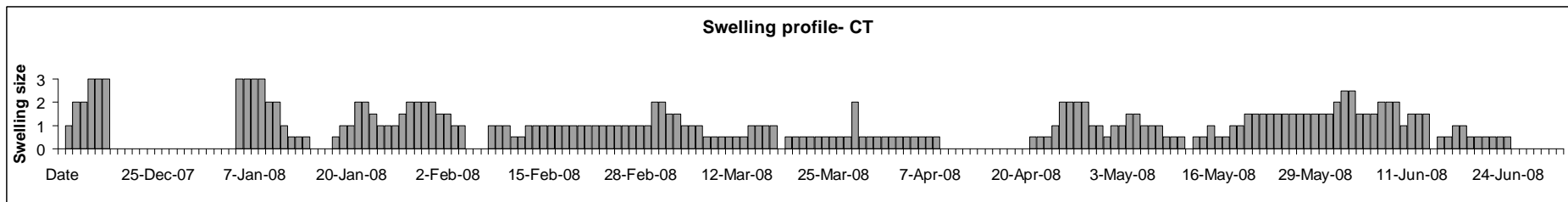
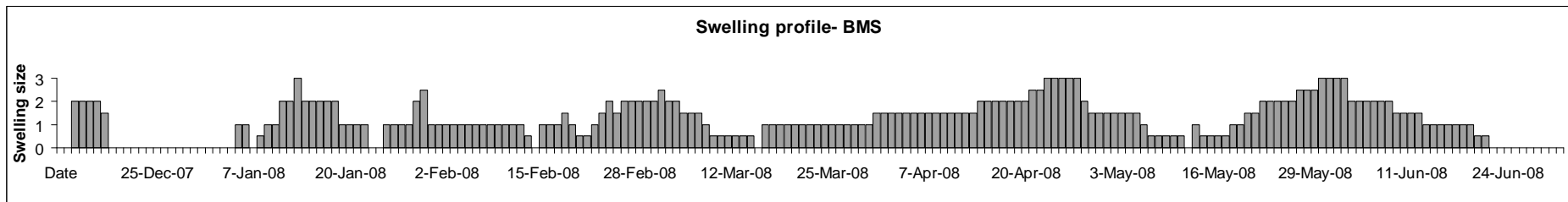
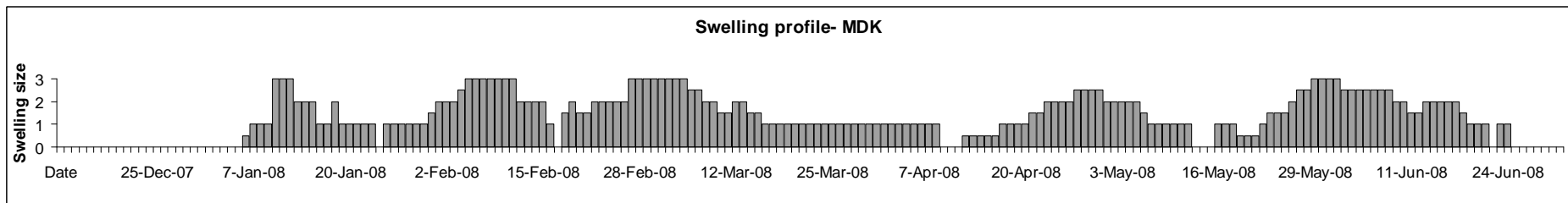
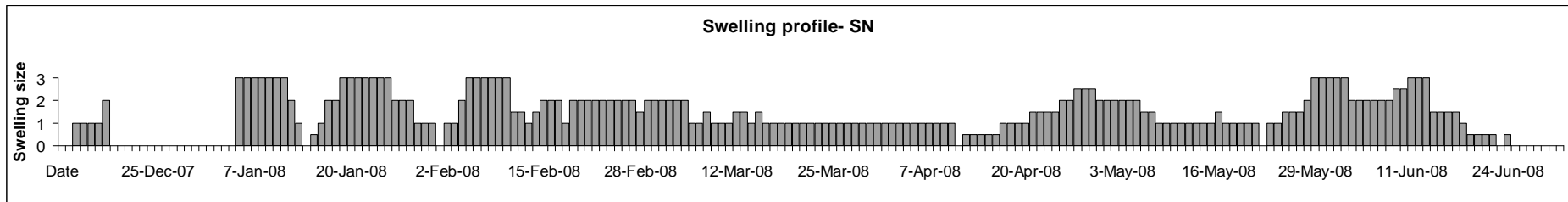
						cycle
						Aggression from sub adult males during AMr & AMb mate guarding
MDK	51	4	5	8	34	Persistent aggression from male AMb soon after mating with 2 non resident males
	37	8	5	5	19	Sickness following back injury from a fight with baboons
SN	69	2	1	6	60	Aggression (during feeding) from male AMr & AMb
	40	9	6	3	22	Aggression from BMK and lactating female KL& KMH
MKW	51	15	13	3	20	Persistent aggression from 2 sub adult males
MT	58	13	20	5	20	Aggression and subsequent injury from male AMk during her early mid cycle
BMK	53	14	16	5	18	

Pregnant and lactating females

Wild female Sanje mangabeys exhibit post-conception swellings near the end of first trimester (day 67 after last observed copulating while fully swollen = approximately 2 months after conception). These swellings are similar to normal fertile swellings in general morphology. However, unlike normal swellings, they have a dark reddish colouration during deflation. The swellings are distinguishable from fertile swellings associated with ovulation by being less pronounced (attaining a medium size, i.e. score 2 in this study) and do not have as much degree of turgidity as during menstrual cycles. I did not have a large sample of pregnant animals. However, for one female the swelling cycle averaged 40 days (n=2, range= 39-41) including a slow detumescence of 22 days. During pregnancy, the nipples redden and become slightly elongated and the abdomen becomes quite enlarged. During swelling, the female presented to males and they mounted and attempted to copulate with the female. Most of these copulations, however, involved sub adult males and only rarely adult males (e.g. Jan 10th and 14th 2008 and Dec 17 2007 for female KMH and KM respectively).

Individual swelling profiles for 10 study females





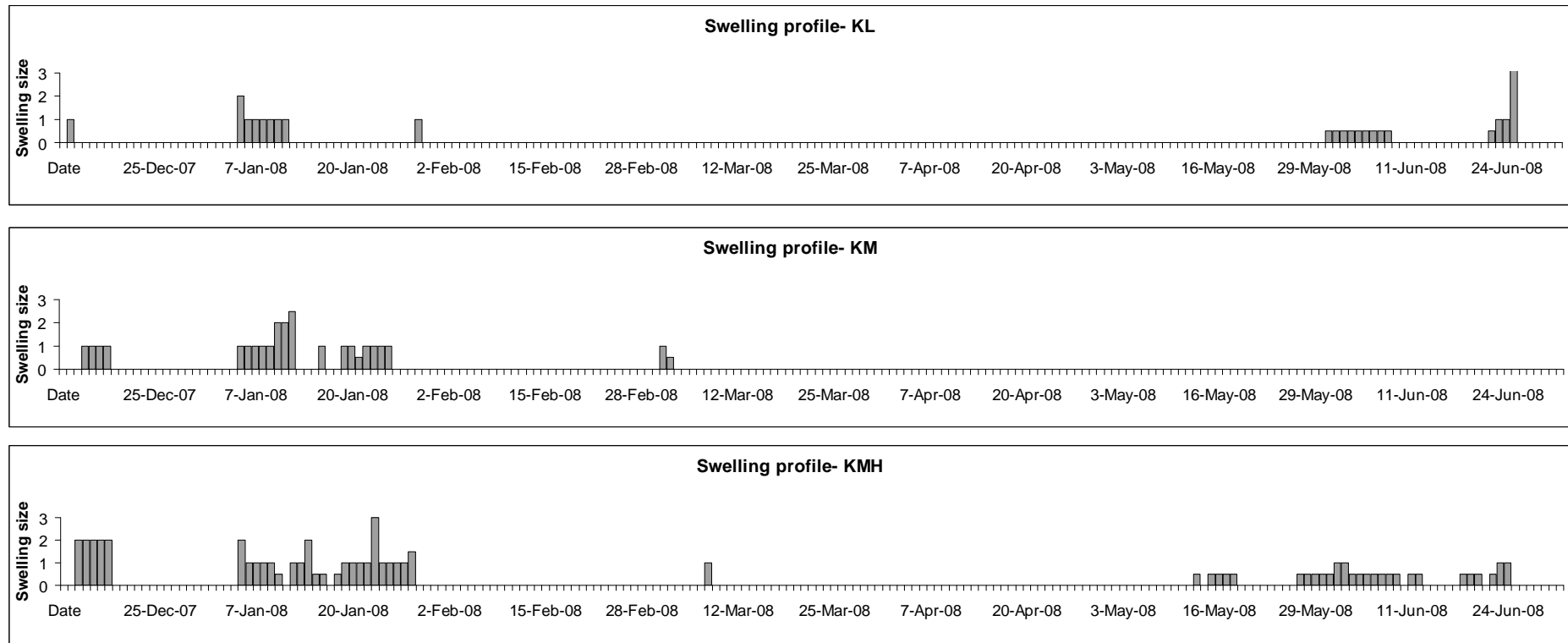


Fig. 4.3. Ten individual females swelling profiles during the entire study period (178 days) for 3 lactating females KMH, KL, KM and 6 cycling females, CT, BMS, SN, MDK, MWK, MT and BMK.

Swelling changes during late pregnancy and lactation

The perineum of a pregnant Sanje mangabey swells slightly during the week before birth. The sex skin then deflates, and remains small in size (score 1) or flat (0) lacking bright pink colouration. The female gives birth while the swelling is flat (in the case of KMH) or small (KM). After birth the sex skin inflates and goes through short (3-8 days) inflations and deflations (swelling size 1, 2 and -1, 0). The sex skin remains at this stage (size 0) for 24 days before it suddenly swells for 1 or 2 days, then becomes flat throughout the entire lactation period. During the periods of short inflation and deflation, the females presented to adult males, who did not make mount attempts, except in the case of one female, KM. Female KM was observed copulating with 4 different males on four consecutive days (once with each). This unusual circumstance occurred 2 days after the day of parturition.

Female Sanje mangabeys nurse their infants even when they resume cycling (this was observed in two females, KL and KMH). At times, it was difficult therefore to distinguish late lactating from cycling females. The mean interval between birth and resumption of normal swelling cycles (i.e. lactational amenorrhoea) was 184 days ($n = 2$, range = 158-211). This is only a preliminary estimate of lactational amenorrhoea in the Sanje mangabey however, due to the small sample size. Gestation length averaged 173 days (or 5.8 months, range = 159 -187, $n = 2$).

Sexual behaviour

In Sanje mangabeys, it is usually the male that solicits mating (only 37% of all the mounts were initiated by females. Table 4.5 shows number of female initiated mounts for the seven cycling females. As a means of inviting males to mate, females present their hindquarters towards males and often utter pre-copulatory calls, which associate with head flagging. Pre-copulatory calls are given by females when in close proximity to males. These calls, unlike copulation calls start as deep grunting sound emitted at long intervals, then become fast before fading away at the end. Usually when pre-copulation calls fade, the female makes eye contact with the male. The male inspects the female by either sniffing, touching or looking at the genitalia or performing a combination of these activities. The male may then make a mount attempt.

Table 4.5. Numbers of mounts with intromission initiated by males (in red) and in response to female invitations (in black).

	CT		BMS		MDK		SN		MWK		MT		BMK	
Female														
Jun	0	13	1	9	6	3	5	11	2	11	1	16	0	9
May	10	8	4	16	4	23	8	24	10	11	6	12	7	12
Apr	1	3	14	13	5	17	5	13	6	15	7	8	6	11
Mar	0	0	1	1	6	8	4	2	8	4	4	5	10	8
Feb	2	4	6	9	17	14	6	11	1	4	4	7	7	18
Jan	7	3	1	6	3	4	10	9	1	3	6	10	12	12
Dec	1	0	0	0	0	0	1	0	0	0	4	0	2	2
Total	21	31	27	54	41	69	39	70	28	48	32	58	44	72
% of female initiated mounts														
	40.4		33.3		37.3		35.8		36.8		35.6		37.9	

The copulatory posture of wild Sanje mangabey consists of male holding onto the female's ankles with his feet and her hips with his hands. This mounting posture is well-known as the double foot-clasp (Dixon, 1998). The female often turns to look back towards the male during the mount. Upon intromission, the female may utter a copulation call. Copulation calls often start immediately after the male intromits and during ejaculation. These calls start as soft, short grunting sounds which become deep and fast and may (or may not) end with a 'kre-kre-kre' sound. After copulation the female moves away from male and continues vocalising. Copulation calls often begin during copulation but in some cases begin immediately after mating. The females also often displays a clutching reaction during copulation, by arching her head and or reaching back to grasp the male's leg, shoulder or face and his hair. Soon after copulating with one male, the female may utter a pre-copulatory call while in close proximity to similar male or other males. These calls are usually followed by mounts by either the previous or a different male. Copulation calls are occasionally uttered during non copulatory contexts such as in proximity to adult lactating females; the meaning of this behaviour is not understood.

Mounts and female reproductive cycle

Mount with successful intromission comprised of male thrusting motions ≥ 9 accompanied by male pulling female closer and holding on to her. The counting of pelvic thrust of more than 9 was chosen as criteria of successful intromission because 89% of all mounts with ejaculation had 9 or more pelvic thrusts. It was not possible to determine if ejaculation occurred on all mounts, however, male pause in pelvic

thrusting and body tremor was considered indicative of ejaculation. More than one mount often occurred before ejaculation, and single mounts were rare. In my sample, only 4.9% of all mounts with intromission were ejaculatory. Mating intensity was skewed towards morning with 71 % of all mounts occurring between 6:30 am and 12:00 noon. The average intromission duration was 86 seconds (range, 12-104s, n=1509 mounts).

The age for onset of male sexual behaviour in Sanje mangabeys is not known. Sub adult males of this mangabey exhibit mounting (with successful intromission) behaviour at a rate much higher than mature adult males (e.g. Sub adult mounts, N=617). Mounting behaviour at this age class was usually directed at mature cycling females, not females similar in age to them. By the time these males reach reproductive maturity, the frequency of mounting behaviour and copulation decreases from the rates seen in adolescence e.g. one case with AMc (Mselewa & Mvelege pers. communication).

Table 4.6 shows number of intromission mounts, mounts with ejaculation, intromission duration and intromission thrusts for five adult males (AMb, AMc, AMk, AMr, and AMm) and sub adults (SAMo) with 7 study females in relation to their ranks. The most sexually active adult male, third in dominance rank order, AMb monopolised sexual partners at times, and mated in high frequency than other males. This strategy, usually maximise sperm volume to outcompete other males (Dixon, 1998). AMb was also the most consorting male in the group. Sneak copulations by other males, and sub adult males occurred during these periods. The dominant male however, AMR, was not observed sneak mating.

Table 4.6. Intromission mounts, mounts with ejaculation, intromission thrust and intromission duration of males with 7 female in relation to their ranks.

Male	Rank	Mounts with intromission	mounts with ejaculation	Thrusts range (mean \pm se)	Intromission duration (mean \pm se)
AMr	1	105	14	5-19 (9 \pm 0.02)	92-104 (98 \pm 0.3)
AMm	2	21	6	3-12 (8 \pm 0.03)	76-100 (85 \pm 0.2)
AMb	3	205	9	5-16 (8 \pm 0.02)	71-102 (86 \pm 0.3)
AMc	4	78	1	3-15 (9 \pm 0.01)	91-101 (91 \pm 0.3)
AMk	4	64	3	6-11 (9 \pm 0.02)	75-101 (87 \pm 0.3)
SAMo	5	161	0	3-13 (9 \pm 0.04)	12-78 (65 \pm 0.2)

SAMo = Other sub adult males, Intromission duration is in seconds

Mate guarding in Sanje mangabey is characterised by males walking very close to the female (usually behind), possibly to prevent any female attempts to invite other males. During these period, the males often gave grunting vocalisations, chased other males and they repeatedly hit the female when attempted proximity to another male. The males also involved in physical aggression whenever another male attempted to mount the female (whether invited or not). Also, in all cases (involving BMS), AMr was observed to devote more energy chasing other adult and sub adult males.

Mate guarding is probably an energetically costly pursuit in Sanje mangabeys, only 13 female guarding occasions involving males AMr (rank 1) and AMb (rank 3) and females MDK, MWK, BMK and MT were observed. The guarding displayed however, was only 9% of the days females had maximal swelling (where fertilization could be possible). Encounters with other groups as well as solitary, non-group, males were common, and these occasionally resulted in copulation with receptive females (5 out of 17 encounters =29% resulted in copulation). During the encounters, non resident males attempted proximity with females (both had maximum swellings) and resident males fought the other male instantly, after persistent grunting vocalizations from both. In 4 encounters that these other males copulated, AMr (rank 1) was defeated. The other group males (AMb, AMc, AMm, and AMk) chased but did involve themselves in the physical dispute with these other males. One solitary individual copulated with female MT.

Figure 4.4 shows copulatory parameters in terms of attempted mounts, mounts with intromission, number of intromitted thrusts, mounts with female copulation call, and mounts in response to female invitations during all cycle days. It appears that all mounts with successful intromission were accompanied by female copulation calls. Females MDK, SN AND BMK received more mounts as a result of their invitational behaviour. Although males initiate mating, not all of their attempts were successful, females refused male attempt as well. Mounts attempted by all males but refused by females are shown in this figure as well.

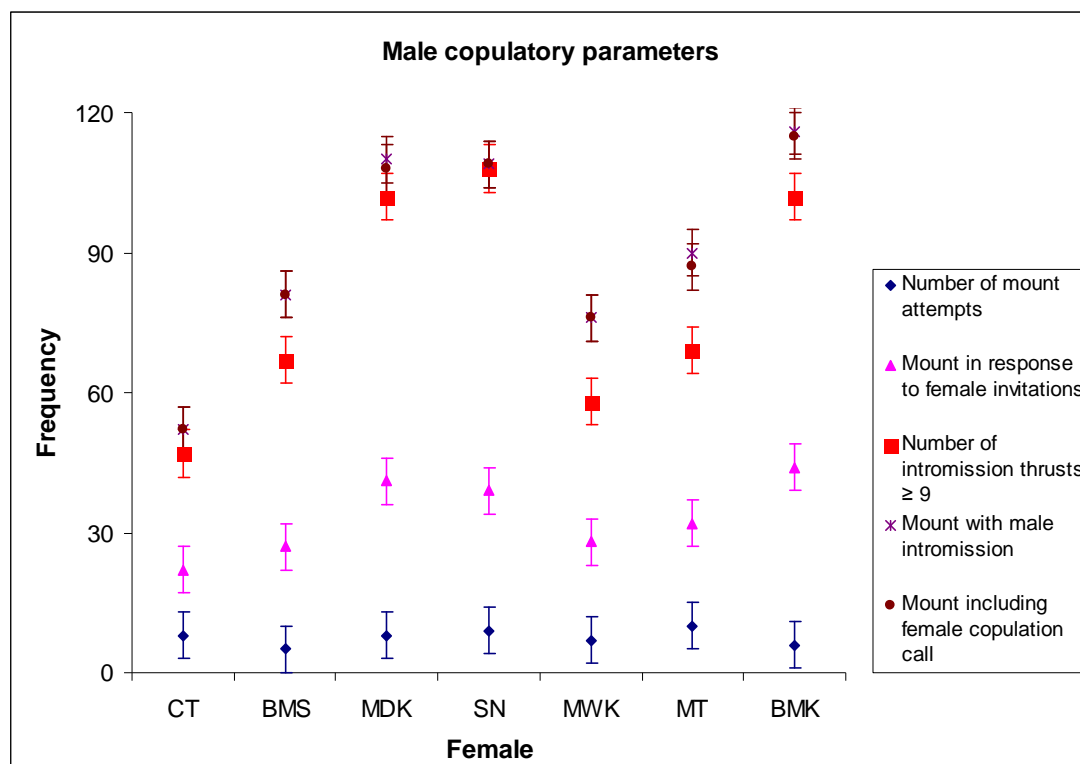


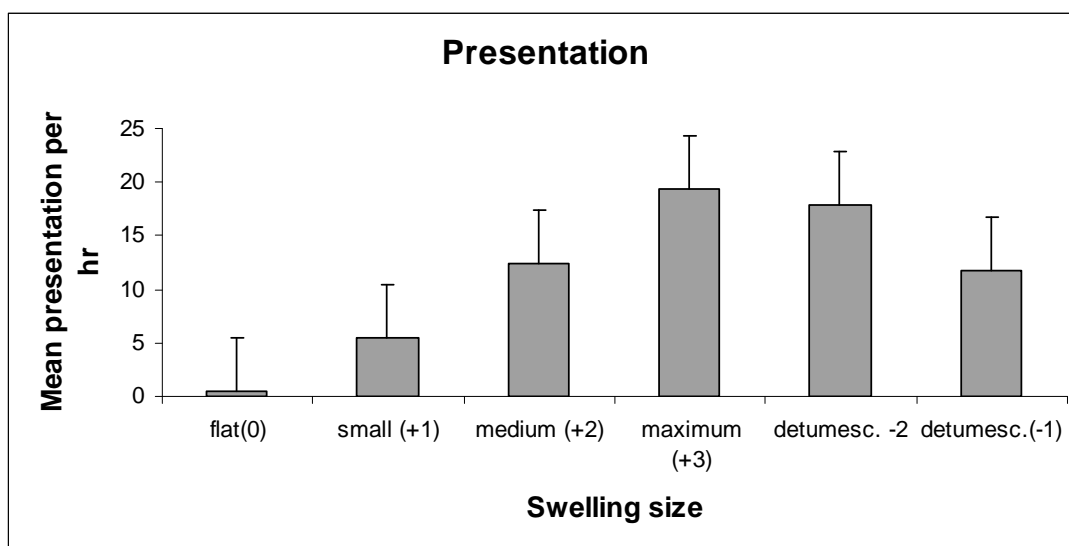
Fig 4.4. Male *Sanje mangabey* copulatory behaviour.

Male mounts do not guarantee that the female is receptive or that there is a chance for a female to conceive, but rather indicate male is sufficiently aroused and that the female is sufficiently attractive. Figure 4.5 shows total per hour frequencies of female presentations, male inspections of female sex skin and copulations during the different swelling phases. This figure illustrates that, for all males, inspection of sex skin was most frequent during swelling inflation stages +1 and +2 and deflation stage -1.

Whether male *Sanje mangabeys* distinguish between females on the basis of individual differences in swelling size or its colour is not clear. However, copulations were most frequent during the period of maximum swelling, decreasing during breakdown and detumescence (Figure 4.5). Males seem to devote more effort mating with females in a window of days of the cycle where chances of fertilization are high. Females with flat sex skins received 0.14 ± 0.0 mounts per hour; females with small swellings received 1.19 ± 0.03 mounts per hour; medium swollen females were mounted at a rate of 3.07 ± 0.04 ; fully swollen females 7.14 ± 0.09 mounts per hour, 3.54 ± 0.06 mounts per hour for females at detumescence (-2) and females at detumescence (-1) stage received 3.76 ± 0.08 mounts per hour. Mounting behaviour in *Sanje mangabeys* is therefore highly correlated with the morphology of the sex skin.

Of 638 observed copulations involving 7 study females, 184 (29%) occurred 1-2 days before swelling maximal tumescence, 196 (=30.9%) at swelling maximal tumescence and 210 (33.1%) at or swelling breakdown (swelling size -2 & -1). Although copulations occurred at higher rates in maximum (+3) compared to non maximum swelling stages in 6 of the study females the observed difference did not reach statistical significance (paired t-test: $t=1.742$, $n=7$). Thus, the frequencies of mounting were analysed in relation to cycle days. Mounting behaviour of males highly correlated with size of sex swelling size. ($F=13.59$, $P<0.05$, Repeated measures post-hoc Scheffe's test $P<0.05$).

Individuals showed some variations e.g. females MDK was inspected more and CT received less inspection during their maximum swelling period than in any other stages (Appendix 4.1). Female presentation increased with an increasing swelling size for all females except MT. This female demonstrated similar amounts of invitational behaviour, mounts and inspection throughout her cycles. For most females, proceptive behaviours decreased at maximum swelling towards deflation (Appendix 1).



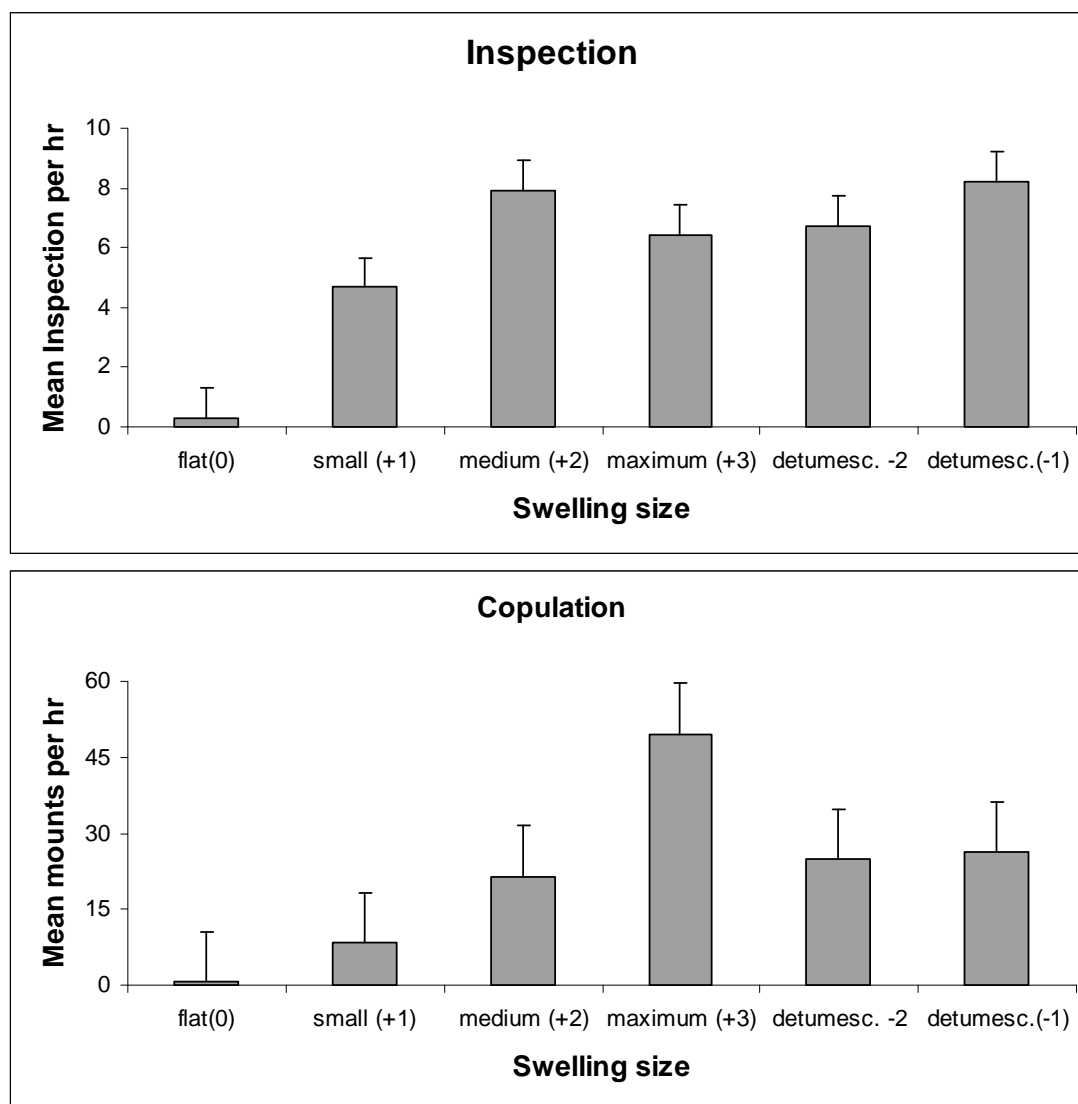


Fig. 4.5. Mean number of presentations (top), male's inspection of sex skin (middle) and copulations (bottom) during small (+1), medium (+2), maximum (+3) and detumescence (-2 & -1) stage.

Male matings during maximum swelling

An investigation was done to find out how many males each female Sanje mangabey mates with during her maximum swelling. The data are summarised in table 4.7. On average, females mate with 2.6 ± 0.1 males during the maximum swelling phase. The likely chance of female conceiving each of these males is approximately 43% (provided sperm half-life, vaginal track conditions and sperm competition are constant). Despite several females cycling at the same time, sub-adult males were not observed to get the chance or compete for mating with adult males during swelling maximum tumescence. Figure 4.6 summarises changes in swelling morphology and sexual interactions of one female (BMK) with various males. On average, males

attained ejaculation while mating with females with swollen skin of all sizes (figure 4.7 a & b.)

Table 4.7. Total number of male partners during maximum swelling size for each female cycle.

Cycle Number → Female	I	II	III	IV	V	VI	All cycles Mean ± SEM
CT	6	2	0	0	1	0	1.5 ± 1.0
BMS	1	1	0	6	5	?	2.6 ± 1.2
MDK	2	3	5	3	4	?	3.4 ± 0.5
SN	3	2	5	4	1	?	3.0 ± 0.7
MWK	1	2	2	5	3	?	2.6 ± 0.7
MT	1	2	5	3	?	?	2.8 ± 0.8
BMK	3	4	4	3	4	3	3.5 ± 0.2
Total	2.4	2.3	3	3.4	3	1.5	2.6 ± 0.1

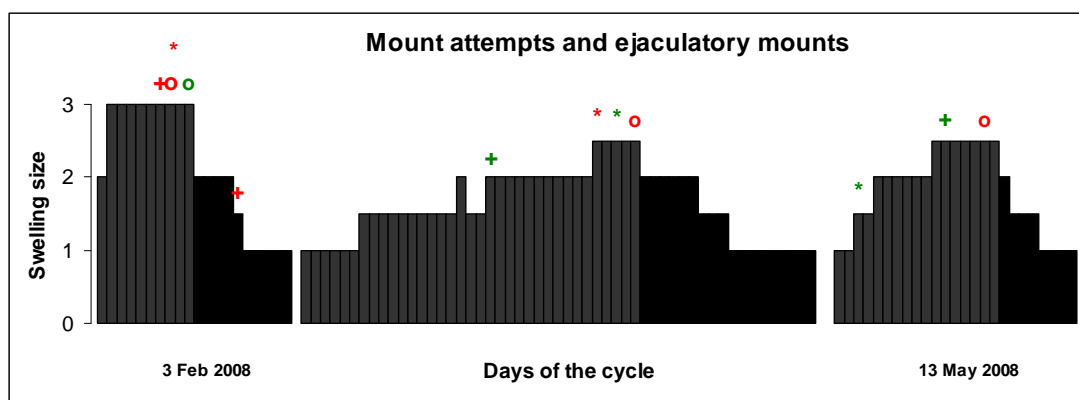


Fig.4.6. Changes in swelling size morphology and sexual interactions of female BMK with male AMr - rank 1 (o), AMb –rank 3 () and AMk –rank 4 (+). Symbols show ejaculatory mounts (in red) and attempted mounts (in green).*

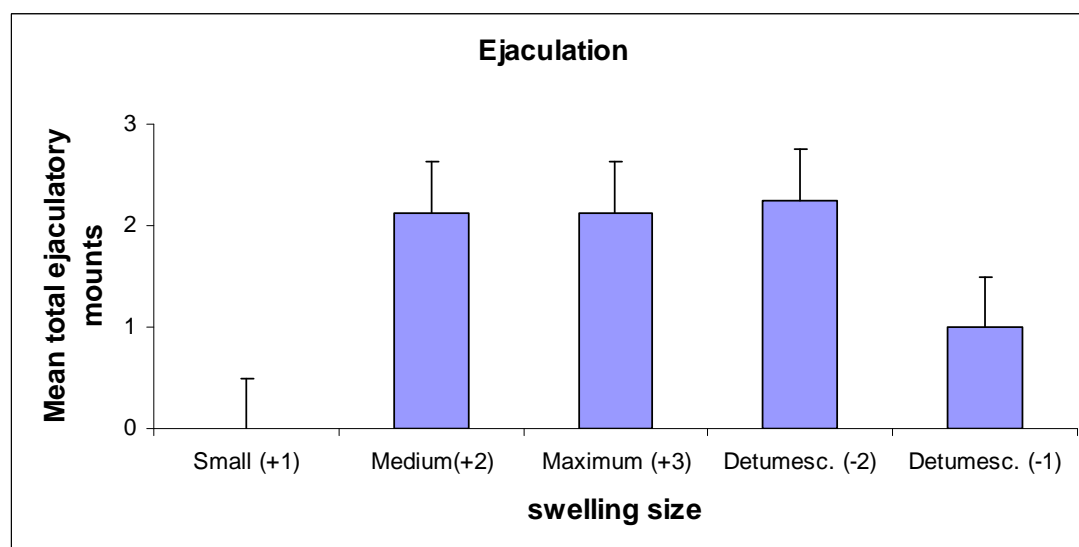


Fig. 4.7 (a)

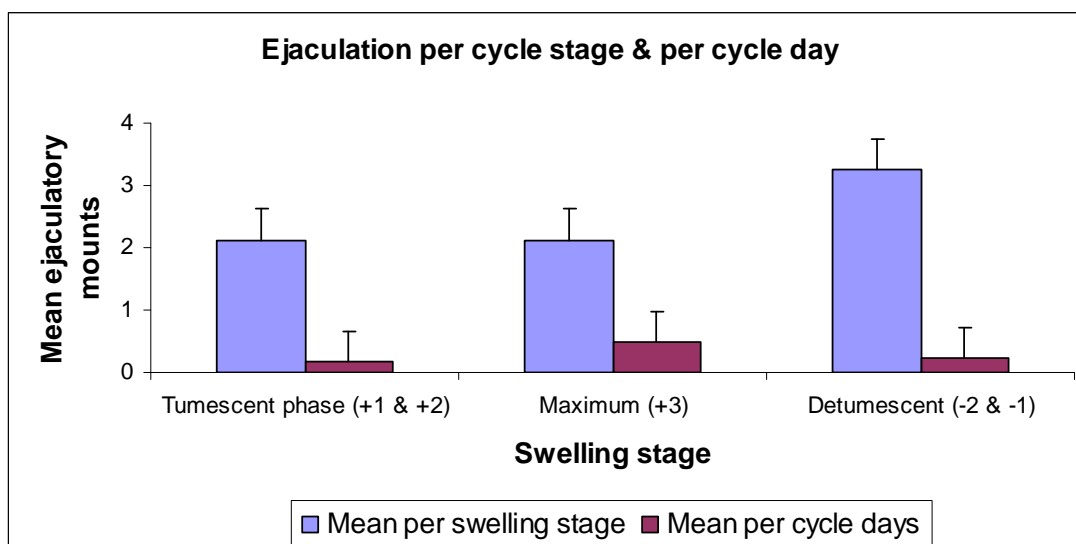


Fig. 4.7 (b)

Fig. 4.7. Relationship between ejaculatory mounts and stage of skin swelling. Top (a) mean total ejaculatory mount in all stages, (b) bottom, Ejaculatory mounts per cycle stage and per phase per day.

To examine the relationship between skin swellings and sexual behaviour, I compared the occurrence of swellings during days with sexual behaviour to days with swellings when no sexual behaviour was observed. During the entire study period, 7 females that showed proceptive behaviour (i.e. presentation and vocalisation) on an average had swellings on 76% of those days (median= 55%). On days with no proceptive behaviours, female had a swellings on 44% of those days (median= 36%). The numbers were very similar for days with swellings and receptive behaviour present (mean=55%, median=50%) or absent (mean 51.2%, median 46=.2%), as well as for days with female attractivity present (mean 51.2%, median=50.0%) or absent (mean= 54.4%, median= 42.4%). The values for cycling females (n=7) were somewhat related and substantial in number especially for the proceptivity sample. This suggests that, females were equally likely to be receptive and attractive but not proceptive, when they were swollen and occasionally when not swollen. On 91% of all days with swellings, female proceptive behaviours occurred, and proceptivity seemed to be more related therefore to swelling phases. For four adult females, inspection was highly performed on days when they were also proceptive. Attractivity and proceptivity were, however, strongly linked.

Copulation calls

Figure 4.8 shows numbers of copulation call given by 7 females. However, an increase in percentage of number of calls was observed for all females except CT as the sex skin enlarged in size and peaked at swelling maximum size (figure 4.8). A summary of all female copulation calls is presented in figure 4.9. In general, copulation calls were given by all females and in all stages of a swelling cycle. A decrease in calls was observed when females mated with males at swelling breakdown (-2) and fewer copulation calls were heard for all females at small (+1) swellings compared to swelling stages (+1 and +3).

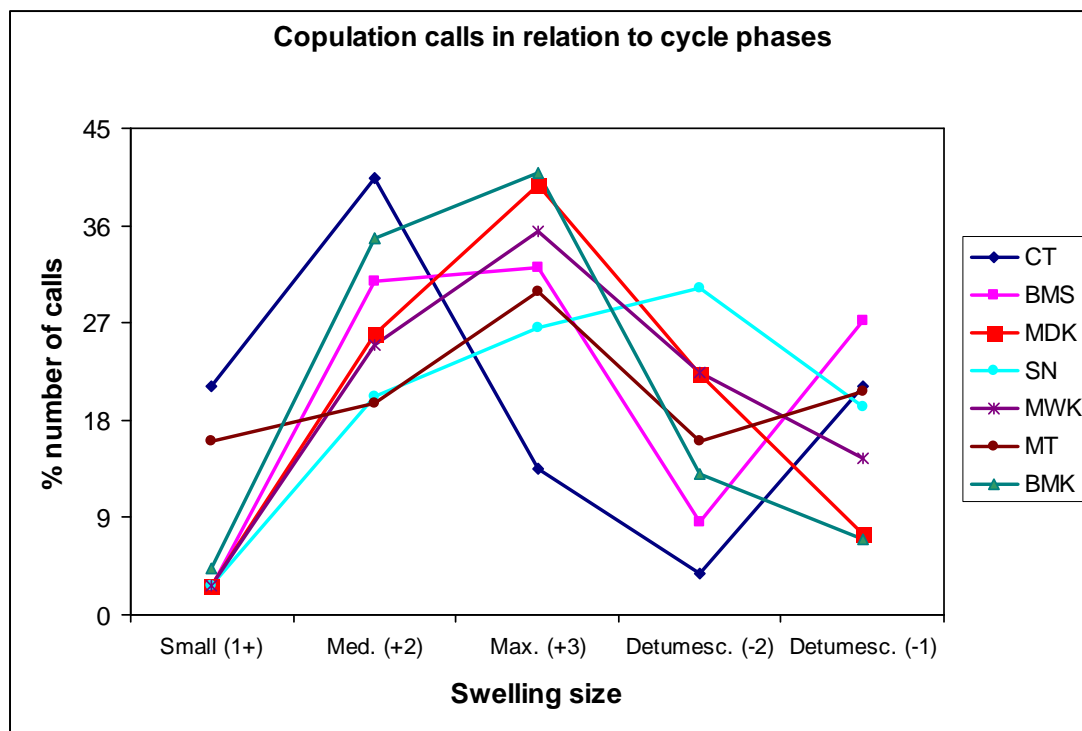


Fig.4.8. Individual female copulation calls in relation to swelling stages.

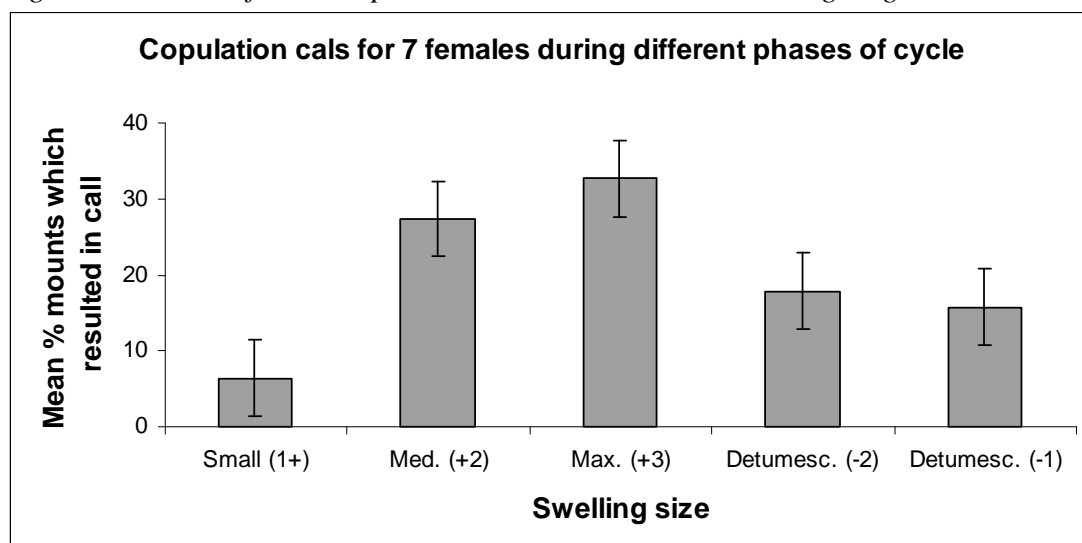


Fig. 4.9. Relationship between copulation calls and swelling stage for all 7 females.

Copulation calls and male dominance

To answer the question whether some females give copulation calls more or less than others, and if calls occur more often when a female mates with certain males, I quantified female copulation calls in relation to each male partner. Variation in female tendency to call after copulation can be explained by the copulatory success of males with which each female mate with (i.e. the more the male mounts are accepted, the more the female will call, Dixon, Pers. comm.). I tested the hypothesis that female copulation calls are a form of post-copulatory female choice. Females are expected to give more calls when copulating with higher ranking males. The prediction was that calls are likely to be associated with copulation with preferred males, according to their rank. It was thus expected for females to give more calls when mating with higher ranking males than would with low ranking males.

The results show that more calls are given by females when mating with some males than with others. There was a strong significant negative relationship between the total number of calls given and male dominance rank (Spearman's $\rho = -0.82$, $P = 0.0012$). Figure 4.10 shows the relationship between number of copulation calls and male dominance rank. AMr (rank =1) had less number of calls than AMb (rank 3). All females gave least number of calls when mating with AMm (rank 2) than any other male. Males AMk and AMc (3rd in rank) had almost similar amount of calls given by the females they met with. Females BMK, SN and MDK had the highest number of calls as a result of male' intromission, followed by MT, BMS and MWK (Table 4.8). CT was the only female with least number of calls when mating with all adult males, but she called more when mating with sub adult males of the group.

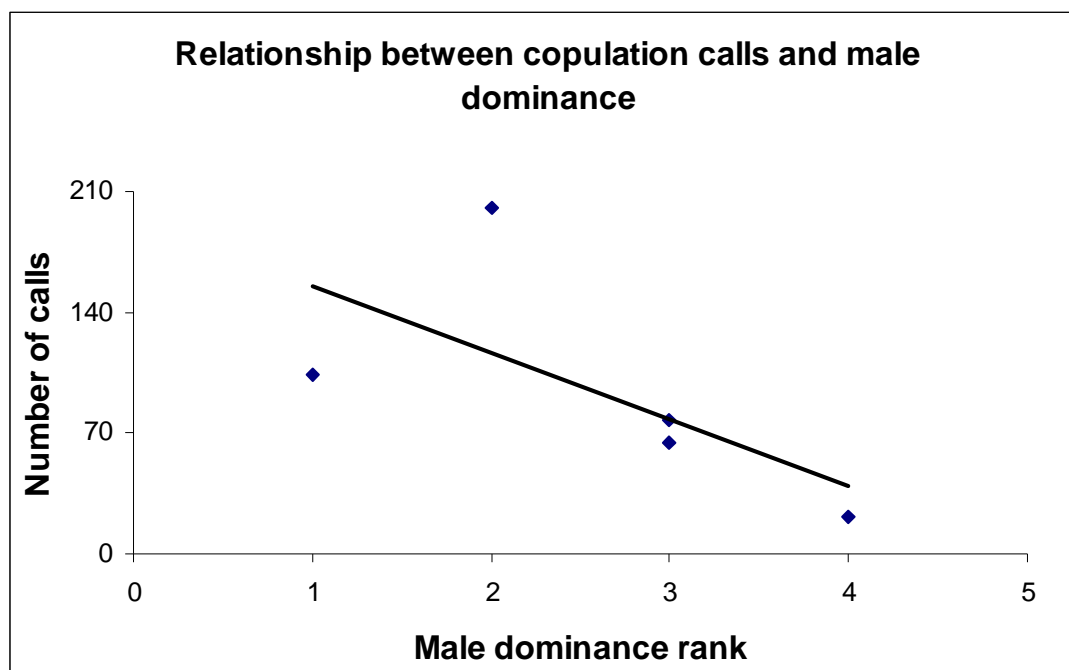


Fig. 4.10. Copulation calls given by female *Sanje mangabey* during and immediately after mating with different males are significantly related to male dominance rank ($p = 0.0012$).

Table 4.8. Total copulation calls (black) and intromissions (in red) in relation to male mates

Male	AMb ³		AMc ⁴		AMk ⁴		AMr ¹		AMm ²		SAMo ⁵	
CT	8	8	2	4	0	1	1	1	1	1	40	81
BMS	22	29	13	18	4	6	10	10	5	6	27	63
MDK	26	28	19	29	13	25	27	28	3	3	20	42
SN	31	32	12	21	12	19	14	14	2	2	38	59
MWK	29	37	12	19	12	16	12	12	4	4	7	13
MT	36	41	13	20	8	9	13	14	1	1	16	31
BMK	49	59	7	9	15	24	27	27	5	6	12	39
		23										32
Total	201	4	78	120	64	100	104	106	21	23	160	8
% intromission with female vocalization	85.9		65.0		64.0		98.1		91.3		48.8	

SAMo = other sub-adult males, 1, 2, 3, 4, 5, indicate male dominance rank orders

Reproductive/breeding seasonality

Sanje mangabeys reproduction was examined in a forest setting that is characterised by slight annual variations in day length and temperature. One yearly rainy season is evident in this area, with rainfall of up to 2100 mm starting in December to May. The dry season starts in June and lasts until November (see chapter 3).

The reproductive status of female Sanje mangabeys is not influenced by seasons and no evidence of breeding seasonality was found. The animals did not show any distinct mating or birth periods in relation to seasonal changes of rainfall, and swollen females have been observed all across the year in this population (F. Mselewa, S. Mvelege pers. Observations), suggesting absence of breeding seasonality. However, my observations and data on frequencies of copulation suggest that sexual activity peaks occur near the end of rainy season in April to June. Up to 68 % of all copulations occur during this period.

Discussion

Cercocebus sanjei is still poorly known in terms of its behaviour, ecology and reproduction. This is partly because the species was only described 3 decades ago. The results of this study show that female sex skin morphology is a little different from other terrestrial mangabeys. The reproductive parameters are comparable to those of mangabeys, mandrills and baboons in terms of cycle length, inter-swelling interval, menses length, gestation and lactational amenorrhoea. The cycle characteristics are comparable to those of other *Cercocebus* species and mandrills; perhaps due to their close phylogenetic relationship. Sexual behaviour of this mangabey is also similar to these other taxa as well. Sanje mangabeys mate throughout the year and births were likewise observed throughout the year.

Sex skin morphology and reproductive cycle

The reproductive cycles in female Sanje mangabeys are very similar to those of other *Cercocebus* species, mandrills, *Lophocebus* mangabeys and baboons. However, there are some differences in the sexual skin morphology of this mangabey, compared to these other genera. In *Lophocebus albigena* the swelling is restricted to the vulva and anterior margins of the anus (Rowell & Chalmers, 1970), and in *Cercocebus agilis chysogaster*, the swelling extends from the vulva and the anus to the pubic lobe where the clitoris is located (Walker *et al.*, 2004). The sexual skin swelling is also different from that of baboons. Baboons have swellings that involve mostly the perianal area, with an extensive bare area lateral to the callosities (Domb & Pagel, 2001; Zinner *et al.*, 1994; Zinner *et al.*, 2004). *C. sanjei* swelling also differs from that of the mandrill that has 'almost circular' skin when fully swollen with a naked, shiny, purplish area

around it. The mandrill sex skin swells around the vulva, pubic lobe and in areas round the anus.

My estimates for Sanje mangabey reproductive cycle are comparable to most other mangabeys. The reproductive swelling cycle length reported for *Cercocebus galleritus* is 32 ± 3.2 days (Homewood, 1976), 30.1 ± 4.0 days for *C. torquatus* (Gordon & Busse, 1984; Gust *et al.*, 1990) and *C. agilis agilis chysogaster* has cycle length of 30.7 ± 4.7 (Walker *et al.*, 2004). The Sanje mangabey cycle is longer than that of *Lophocebus* species e.g. *Lophocebus aterrimus* 26.0 ± 0.8 (Celle, 1990). Although the average 32-days cycle length of 7 *Cercocebus sanjei* was longer than these other taxa, this estimate fits well within the terrestrial mangabey range of 29 – 34.5 days. *Mandrillus sphinx* has a longer cycle length than *C. sanjei*: in captivity the estimated cycle average is 39.6 days (Bettinger *et al.*, 1995) and in the wild the average was 32.6 (median 38 days) (Hadidian & Bernstein, 1979; Setchell & Wickings, 2004b; Zuckerman, 1937). In spite of these small differences in cycle characteristics, there is a high similarity in the relative timing of behavioural and physiological events associated with probable timing of ovulation in Sanje mangabey and these species.

Menstruation and cycle phases

As Rowell and Chalmers (1970) point out, it appears that menstruation in this mangabey as in most species, occurs immediately before the sex skin begins to swell. The 3.0 ± 0.2 days duration of menstruation is comparable to other mangabeys (e.g. *C. agilis* 3 ± 1.2 days (Walker *et al.*, 2004)). Sanje mangabeys, unlike other terrestrial mangabeys (Celle, 1990; Deputte, 1991), had comparatively light menses, and these were only visible for 3 females. The findings on duration of cycle phases such as maximum swelling, detumescence and duration from start of swelling to maximum swelling are in accord with the results of previous studies on other mangabeys (Rowell & Chalmers, 1970; Walker *et al.*, 2004; Wallis, 1983) which demonstrate some inter specific differences in these parameters. The duration of maximum swelling for the Udzungwa's Sanje mangabey is similar to that reported for wild *Cercocebus agilis* and as *C. torquatus* at Sacramento zoo (Gordon *et al.*, 1991; Gust *et al.*, 1990; Walker *et al.*, 2004) except for unusually longer maximum swelling duration for *C. torquatus* (Table 4.9).

Table 4.9. Inter-species comparison of reproductive cycle characteristics

Species	<i>C. sanjei</i>	<i>C. torquatus</i>	<i>C. agilis</i>	<i>L. aterrimus</i>
Cycle length	32.4 \pm 2.4	30.1 \pm 4.0	30.7 \pm 4.7	26.0 \pm 0.8
Median cycle length	31	30	30	29
Max. tumescence	4.4 \pm 0.4	16.6 \pm 3.3	5.8 \pm 3.1	5.6 \pm 0.5
Detumescence	14.7 \pm 1.7	14.3 \pm 0.8	14.0 \pm 3	12.1 \pm 0.6
Menses length	3 \pm 0.2	-	3 \pm 1.2	3.8 \pm 0.3
Cycles analysed	32	7	164	26

Irregular cycles

Cycles of exceptionally long and short durations have been observed in various species. However, little is known about these events or their significance in an individual's life history. Sexual skin swelling may be indicative of reproductive success and competence e.g. *Papio cynocephalus anubis* (Domb & Pagel, 2001). Thus, for species that exhibit exaggerated signs of ovulations, irregularities in swelling cycle length might be of a particular significance, such as to indicate poor reproductive fertility and incompetence. This however, might not be the case for some species (Tokuda *et al.*, 1968). Apart from cycle irregularities due to social stress, the above mentioned situations do not occur in most Papionins. Comparable effects of social stress have been observed in mangabeys, and these usually rapidly disappear with removal of stress (Chalmers, 1968; Rowell & Chalmers, 1970; Walker *et al.*, 2004)

In most monkey groups, dominance rank and foraging skills influence resource availability, hence reproductive success. Dominant females can restrict a subordinate female's access to resources. In such a system, acquisition of resources should be positively correlated with dominance rank. As a consequence of uneven resource acquisition, the reproductive success of higher-ranking females in such systems is higher than that of low-ranking e.g. *Macaca fuscata* (Saito, 1996), *M. fascicularis* (van Noordwijk & van Schaik, 1987), *Theropithecus gelada* (Dunbar, 1980), and *Papio cynocephalus ursinus* (Busse, 1982).

Male behaviour affects female, thus intra-group aggression might have a great effect on cycle patterns. The irregularities in morphology of sex skin and cycle length in Sanje mangabeys, apart from male aggression, are affected and can be explained by

female rank orders. For example, female CT, who had an abnormal swelling morphology and whose cycles were shorter than the mean, ranked 7th in the dominance order (see Chapter 2). Longer cycles in other females are more difficult to correlate with dominance, given with available data, might as well be influenced by female status in the group. Thus I am not certain whether such cycles were influenced by female status.

Gestation period, Lactational amenorrhoea and post-conception swelling

The Sanje mangabey has an estimated mean gestation length of 174 days (or 5.8 months) and lactational amenorrhoea lasted 184 days. These estimates refer to very few cases as detailed in the results. This current estimate compares with gestation length of 180 ± 4.49 days in the ecologically closely-related Tana river mangabey (Kinnaird, 1990b). A gestation length of 6 to 10 months in this species was proposed by Homewood in 1975. On the other hand, Homewood (1976) estimated gestation in *C. galeritus* at 124-139 days based on the duration between swelling detumescence and the day of birth. Studies of Sooty mangabeys estimate gestation lengths at 167 days (Stebenfeldt & Hendrickx, 1973), and 169 days (Gordon & Busse, 1984; Gust *et al.*, 1990). *Cercocebus torquatus atys* has gestation length of 7.2 months (Gust *et al.*, 1990) and 5.8 months for *Cercocebus agilis chysogaster* (Walker *et al.*, 2004) in captivity, with a lactational amenorrhoea of 8.6 months. *Lophocebus albigena* has a reported estimated gestation length of 176 ± 1.4 days (Rowell & Chalmers, 1970), and 174 ± 2.5 days (Gautier-Hion & Tutin, 1988). Both of these above mentioned studies report post-conception swellings near the end of first trimester (however, exact number of days are not given). The gestation length estimates are also comparable to the 181 to 184 days reported for baboons (Altmann, 1990; Altmann *et al.*, 1981; Zinner *et al.*, 1994; Zinner *et al.*, 2004).

My preliminary results on lactational amenorrhoea are similar findings on semi-free ranging mandrills. Mandrills may conceive while still caring for a previous offspring who are about only 7 months of age. They are thus able to produce one offspring per year (Hadidian & Bernstein, 1979; Setchell & Wickings, 2004a; 2004b; Wickings & Dixon, 1992). However, the estimates of gestation period for captive mandrills are much shorter, and lactational amenorrhoea is much longer than is the case for the Sanje mangabey (Bettinger *et al.*, 1995). Lactational amenorrhoea in *Lophocebus*

albigena ranges from 117-140 days (Rowell & Chalmers, 1970). The exact life history of the Sanje mangabey was not known, thus the presence of other dependant infants was used to draw these comparisons. The relationships and comparisons drawn in this study were based on studies that estimated the two parameters from multiparous females. Variability between studies except for Homewood (1975) are most likely due to small sample sizes used, species-specific differences, minimal variations in criteria used to estimate resumption of swellings or possible hormonal imbalances between individual females due to infant suckling (Steklis & Fox, 1988). Although hormonal data were not collected during this study, it is likely that similar mechanisms apply to *C. sanjei*.

Post-conception (pregnancy) swellings started approximately 67 days (= first trimester) after conception. These swellings were smaller and did not reach normal maximum tumescence. During pregnancy, the nipples redden and become slightly elongated. Changes in the abdomen also become quite obvious (Rowell & Chalmers, 1970). Pregnancy swellings took longer to deflate than normal swellings associated with ovulation, as is the case for the Tana River, sooty and golden-bellied mangabeys (Gordon & Busse, 1984; Kinnaird, 1990b; Walker *et al.*, 2004). Female Sanje mangabeys presented to males and males mounted the pregnant females. Previous studies of other mangabeys have documented copulations by pregnant females e.g. (Gordon & Busse, 1984; Gust, 1994a; Gust *et al.*, 1990; Gust *et al.*, 1995; Homewood, 1976; Kinnaird, 1990b; Walker *et al.*, 2004; Wallis, 1983). Similar behaviour has also been noted for chimpanzees and bonobos (Deschner *et al.*, 2003; 2004; Goodall, 1986; McArthur *et al.*, 1981; Paoli *et al.*, 2006), gorillas (Atsalis & Margulis, 2006; Nadler, 1975; Stewart, 1977) and baboons (Alberts, 1999; Altmann, 1990; Rowell, 1969; Zinner *et al.*, 1994). Mandrill males, however, do not mount pregnant females (Setchell & Dixson, 2001b).

It has been suggested that pregnancy swellings may function to confuse paternity, thus increasing the chances of multiple male care of infants (Busse & Hamilton III, 1981; Gumert, 2007; van Schaik & Paul, 1996). It may also be an adaptation to decrease risk of infanticide by males (Alberts, 1999; Gordon *et al.*, 1991; Hrdy, 1979; Hrdy & Whitten, 1987). My observations of Sanje mangabeys support the idea that female swelling during pregnancy might increase total male care of infants as males not

infrequently interact with infants in the mangabey species (see details provided in Chapter 2).

Sexual behaviour during menstrual cycle and theory of sex skin functions

Using patterns of sex skin swellings and sexual activities of males in the Njokamoni group, I have shown that sex skin swellings Sanje mangabeys are likely to represent an approximate indication of female reproductive condition (Dixson, 1983) but do not provide precise information about the time of ovulation (Hamilton, 1964b). Copulations in this group were observed days before maximum tumescence of the sexual skin, during maximal swelling and breakdown for all females. The occurrence of a majority of copulations during maximal tumescence suggests that swellings are, apparently, more attractive to males during this period, and thus may function as approximate indicators of likelihood of ovulation (Nunn, 1999a). On the other hand, however, according to Nunn's hypothesis, if males are able to tell probable fertile days, they would be expected to compete for or guard females during periods of maximum swellings. In these mangabeys, only a few mate guarding episodes occurred during female maximum swelling size where ovulation was likely (only 60% did), but rather 1-2 days before. No guarding was observed during detumescence. High ranking male, AMR and third ranking male, AMB were the only males involved in guarding. During guarding, the males maintained proximity to females and copulated more regularly, male AMR guarded more (9/13) than male AMB as expected for dominant males.

These findings stress the idea that swellings provide more than general information about the reproductive status of females, and can be considered as reliable indicators of fertile period i.e. graded signals (Dixson, 1983; Nunn, 1999a). The results are the first to help improve our understanding of functions of sex skin swellings in Sanje mangabeys. They also have implications for studies of behaviour relying on sex skin swelling data to understand the reproductive significance of mating events.

Since my data show a relationship between dominance and female copulation calls, a detailed study to investigate this in the light of possible sperm competition (Harvey & May, 1989) to understand evolution of male sexual behaviour at sperm level would be interesting. A study on the relationship between swelling size and long term

reproductive success of female mangabeys (Domb & Pagel, 2001) would also be useful. There were no data to support the ‘many males hypothesis’ on paternity confusion and decreasing chances of infants being victims of male infanticide (Hrdy, 1981; Hrdy & Whitten, 1987). Moreover, existing studies have not ruled out infanticide in Sanje mangabey (Struhsaker, 1997; Struhsaker *et al.*, 2004).

I also investigated functions of swellings besides their role as sexual signals and possible indicators of reproductive condition. My results show that swellings may be significant in strengthening social-sexual bonds through female consortship formation with males (Manson, 1997). Male Sanje mangabeys were observed to be less aggressive and more tolerant towards females that were maximally swollen during feeding interactions (86% of females with swollen skin did not receive aggression from males as a result of proximity during feeding within a patch). These females, in addition, were observed to run towards the males that are usually tolerant to them whenever they encountered intense aggression from other members. Comprehensive data to test hypotheses concerning this behaviour are required.

Copulation calls and male dominance

It is not clear from my results what function of copulation calls maybe. Due their timing, they might function as a form of post-copulatory female choice (Nikitopoulos *et al.*, 2004; Troisi & Carosi). Females displayed calls irrespective of male ranks (Spearman’s $\rho = -0.82$, $p = 0.0012$). However, intromissions by males higher in rank were more likely to end up with copulation call (Table 4.7). This suggests that females use copulation calls as form of indirect mate choice. Copulation calls have been suggested to correlate with male dominance in Japanese macaques and Guinea baboon (Maestripieri *et al.*, 2005; Nikitopoulos *et al.*, 2004; Troisi & Carosi, 1998). Copulation calls may play a role in sexual selection as a way of expression of female mate choice, where opportunity of a female to choose a mate are little or costly.

Breeding seasonality

My data do not indicate that breeding seasonality occurs the in Sanje mangabey. However, there is some evidence of peak in mating activity near the end of rain season in April throughout June. Deputte (1992) and Rowell & Chalmers (1970) found no evidence of seasonal influences on breeding in *Lophocebus albigena* living

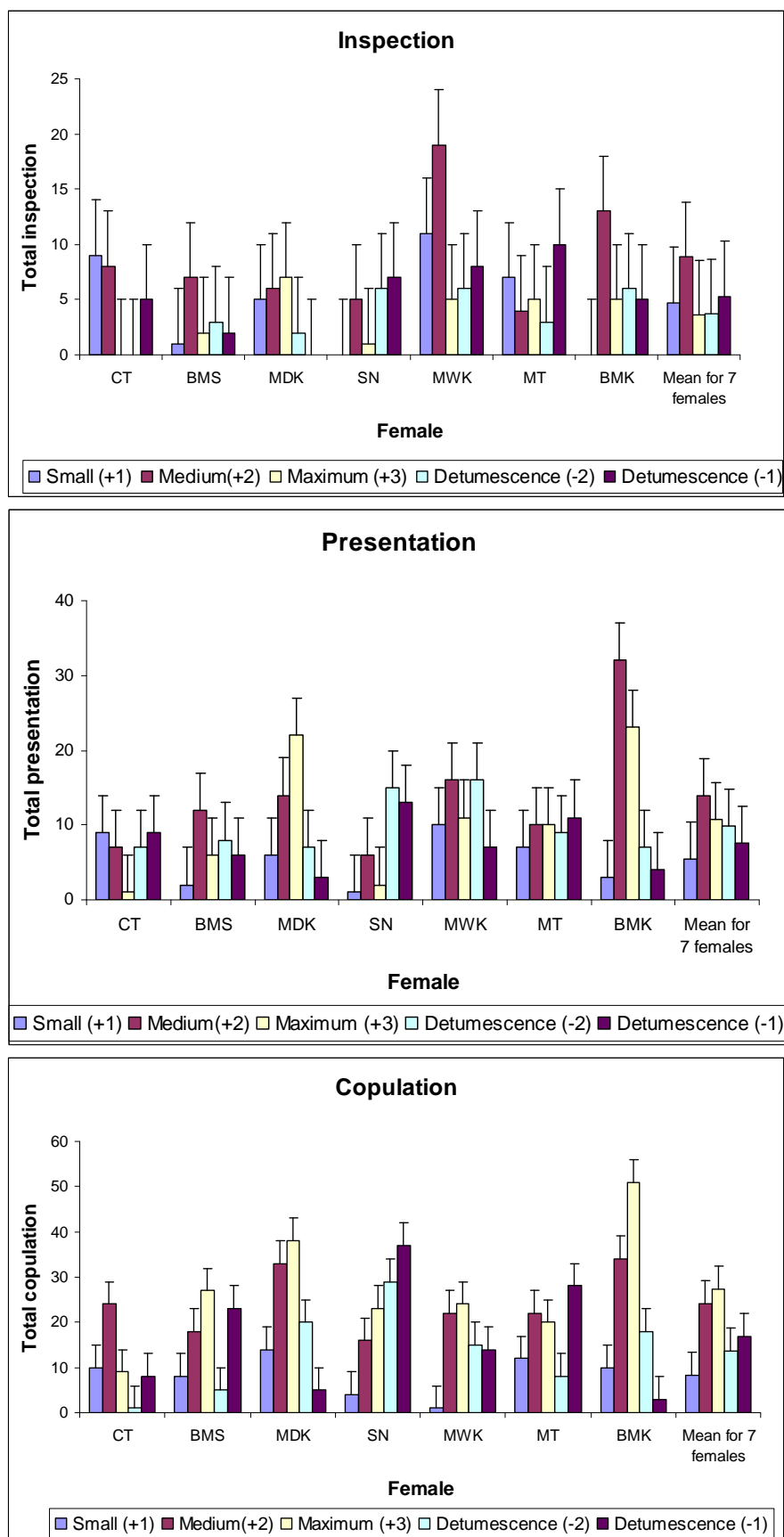
in similar Ugandan setting. A recent study of *C. galeritus* (Wieczkowski, 2005b) found no support for seasonal reproduction, nor was there evidence in the sympatric baboons from Kenyan riverine forest as well (Rowell, 1969). However, Gust *et al.* (1990) and Gordon *et al.* (1991) found evidence for seasonal influences in births and onset of swelling in young females in the related *Cercocebus torquatus atys*. My data, however, were too limited to decide whether the intensity of reproductive activity was uniform throughout the year or whether there is one or more slight seasonal peaks. From these results, I tentatively suggest that, patterns of Sanje mangabey reproduction are not affected by seasons.

Conclusion

The morphology of Sanje mangabey sex skin and characteristics of 32 cycles of 7 cycling females are described. Changes in the appearance of sex skin of cycling females, and during pregnancy are differentiated. Details of the sexual behaviour in the Sanje mangabey and its patterns for both males and females are described. Changes in appearance of sex skin during cycling, pregnancy and the gestation period are documented. The similarities in reproductive patterns with other *Cercocebus* and *Lophocebus* mangabey and of the related mandrills and baboons are stressed, and implications for evolution of sexual skin and Papionini sexual behaviour are discussed.

In conclusion, the reproductive parameters of wild Sanje mangabey are comparable to those known for other mangabeys, particularly in the terrestrial group. The knowledge presented about female reproductive cycle and sexual behaviour together efforts to enhance understanding of Sanje mangabey biology, which will help to manage the populations to enhance its conservation. The information also contributes to knowledge that might be of use for captive management of this endangered monkey whenever necessary.

Appendix 1. Total numbers of presentations (top), inspection of the sex skin (middle) and copulations (bottom) during small, medium, maximum and detumescence stage.



5. Summary of findings and conservation context

Degradation of tropical forests is a major concern for conservation biology, basic studies of biology for many endangered species that useful for conservation management are lacking. I studied the social organisation and reproduction of the Sanje mangabey in the Udzungwa Mountains of Tanzania to examine group size, age and sex composition, feeding, ranging behaviour and social relationships. The study also focused on examination of the influences of swelling cycle phases on male and female sexual behaviour. What follows is the summary of findings from these studies.

Social organisation, Group size, age and sex composition

Mangabeys live in bisexual groups. The social structure of *Cercocebus sanjei* is multimale-multifemale. The group that I studied contained 5 adult males, 13 adult females and the immatures. The group consisted of 48 individuals at the onset of the study and 62 animals at its end; with 3 births occurring during that period. The sociometric sex ratio for the Njokamoni group was 2.8.

The group often broke into up to four smaller foraging groups, for 3-7 hours. Foraging group remained an average of 43 metres away from each other before re-grouping in mid afternoon. During data collection periods, the mangabeys were observed to associate with other primates such as Sykes monkeys, Iringa red colobus, and black and white colobus. They also often interacted with red duikers. The associations with black and white colobus and Iringa red colobus were very interactive (lasting for up to 2 hours together; members also often groomed each other). The two colobus species are mainly folivores. Associations with a potential feeding competitor, the Sykes monkey, mainly involved pairs and solitary individuals that spent up to two and a half hours with the group. Previous observations of another habituated group have documented similar findings. The associations have been related to predation risks from crowned eagles and leopards, which associated with solitary foragers or small groups (Ehardt *et al.*, 2005; Struhsaker *et al.*, 2004; Wasser, 1993). The other primate species that mangabeys associate with are largely arboreal, and make relatively high pitched vocalizations, which may function to alert the more terrestrial Sanje mangabey to sightings of predators.

Population density investigations using three transects in Mwanihana reveal that the density of Sanje mangabeys is decreasing. However, since this comparison was based on limited information concerning previous estimates, and because there are other indicators suggesting increasing population, these estimates may not provide a true picture of the density of this rare primate. Analyses show that *Cercocebus sanjei* group sizes are related to many habitat variables, particularly vegetation structure and composition. Groups encountered on the transect along wooded and forested habitats varied markedly, with fewer numbers of individuals for those groups living in undisturbed forests. The effective strip width (i.e. 30.4m) might have influenced the estimated density, which in turn gave a low estimate of density in the area. Detection probability might also have affected the estimate. Mangabey detection decreased at strip widths greater than 25 m, partly due to uneven topography of the study area. Similar topographic effects were reported by Rovero *et al.* (2006) and Brugiére & Fleury (2000). The population abundance estimate for the Sanje mangabey was 689 individuals, far higher than that estimated by Dinesen *et al.* (2001), but similar to Ehardt *et al.*'s (2005) estimate. The most current estimate of the closed forest at Mwanihana is 109 km² (Marshall, 2007). However, mangabey groups use a variety of habitats such as low-elevation miombo woodland and moist evergreen montane forest. If the current estimate of abundance is comparable to these other studies, despite decreases in closed forest size, then the mangabey population has increased in Mwanihana.

Ranging behaviour

My overall observations indicate that the home range of the Njokamoni Sanje mangabey group has increased, when compared with a previous estimate of home range reported for another habituated group. The animals utilised habitat in proportion to its availability and food distribution. Based on my results (chapter 2) showing four different core areas in the range, I can infer that Sanje mangabeys are selecting some habitat types more, and are avoiding others. However, it is not clear how dependent their movements are affected by these habitat types; this requires further investigation. The mangabey's daily range was quite high as well, reaching up to 1760 m; this is higher than in any of the other terrestrial mangabeys (Wieczkowski, 2005). Mangabeys travelled to non-forested habitat quite often. The ability of the Sanje

mangabey to travel to non forest habitats is an important aspect of its ecological flexibility.

Movements and ranging patterns varied markedly during the wet and dry seasons. Sanje mangabeys moved at an average speed of 303m/hr. On days when the group visited distant forest patches, the mangabeys travelled significantly further and significantly faster, and with fewer stops compared to days when they visited closer patches. The days they travelled further also increased the home range size from 173.7 ha to 343.4 ha. These results indicate that rainfall has important effects upon range use and home range size in the Sanje mangabey.

Social relationships

Relationships among individuals are highly variable across species. Male and female relationships in this species were characterised by competition, intolerance and clear dominance relations. Both males and females could be ranked in stable dominance hierarchies (Landau's linearity index, h' were > 0.9 , $P = 0.05$ for both sexes). Agonistic interactions were very common in the group, and the group showed quite remarkable affiliative relations as well. Adult males were involved in aggressive acts more often than any age class in this group. The rate of aggression per hour for males was 1.69, compared to 0.68 per hour for females. The male- female rate was 1.03 per hour, and the female-male rate was 0.88 per hour. The juveniles were least involved in aggressive acts. The rate for juveniles was 0.27 per hour. There were significant variations in rates of aggression between the wet and dry seasons ($P < 0.001$). During the rainy season, rates of aggression were lower (group rate per hour = 40.2) than during dry days (81.7 per hour). Results from this study suggest that the social organisation of Sanje mangabeys in their natural environment resembles the social systems described for other primate species that exhibit contest competition. In such groups, there are linear stable dominance hierarchies among individuals with members forming well-differentiated relationships with each other.

Results of studies on group association showed that females associate more with males and with their young than with other females or any other group members. Males associated with sub adult females a little more than with adult females. The association indices between classes varied between 0.01 to 0.98, suggesting that in

this group, there are individuals who are always nearest neighbours and some that are rarely, or never nearest neighbours. Rank distance and association was positively correlated for both males and females (Pearson's r rank distance-proximity correlation for female-female = 0.69, male-male = 0.73, $P < 0.001$).

In some species, grooming bonds among individuals are well developed. Grooming was basically unidirectional in Sanje mangabeys (i.e. grooming was distributed evenly among members and no partner specificity was evident). Providing grooming, or receiving grooming, affected the subsequent decision of whether individuals reciprocated or not. On an average, 53% grooming bouts were reciprocated. There was a significant relationship between duration of initiator's first grooming episode and subsequent reciprocation by receivers in all age classes. There was a tendency for grooming to be directed towards higher ranking individuals, and for adult females to groom young. The observed differences, however did not reach statistical significance. The total time spent grooming by recipients was positively and significantly correlated with the total duration of time spent grooming by the initiators. There was no substantive proof that grooming is exchanged for coalitionary support. However, it appears that interchange of grooming may serve to increase tolerance between dominant and subordinate individuals. Overall, my results were consistent with predictions of the 'biological markets model' i.e. grooming is a commodity that is traded among individual Sanje mangabeys. The results are also consistent with studies of grooming in other Papionins (Barrett *et al.*, 2002; Barrett *et al.*, 1999; Chancellor & Isbell, 2009; Henzi & Barrett, 1999; Henzi *et al.*, 2003). There was no trend, nor significant relationship, between the initial duration and initiator groomed and whether or not the recipient groomed. This suggested that unreciprocated grooming bouts may be exchanged for other rewards e.g. tolerance and enhanced social bonds, or they were reciprocated but over longer periods of time (Chancellor & Isbell, 2009). For some species, like Japanese macaques, grooming is communicated with special types of vocalization which differ when individuals attempt to groom and when receiving grooming (Muroyama, 1991). On the basis of my present data, I could not confirm or refute these findings. In general, the studies of Sanje mangabey social relationships suggest that the social behaviour of this species was heavily impacted by rank and dominance relations among group members.

Feeding ecology: Diet and food selectivity

Due to the increasing threats from human influence, food acquisition for most tropical primates has been challenging. Selective pressures have favoured behavioural traits that enhance the efficiency of foraging, such as improved behavioural flexibility and ability to learn and remember locations that can provide edible materials (Milton, 2006). As a consequence of these threats, primates may also adapt to travel further, and to increase the chances of encountering rare food items.

During my 6 months of study of Sanje mangabeys in the Udzungwas, I realized that their dietary composition is quite diverse; encompassing different parts of plants, fungi, insects, lizards, snails, millipedes and frogs. To obtain this mixture of food materials, Sanje mangabeys travelled far from their sleeping sites and back again during the evenings or sleep in new sites. The dietary composition of this species comprised of materials which were both readily digestible and full of energy, and foods that had high amounts of fibres. Furthermore, to maximize nutrient acquisition, Sanje mangabeys opted to feed selectively on certain kinds of foods. Adult males and females, whose energy requirements per body unit weight are low, often fed on leaves more than did the lighter individuals. Larger amounts of shoots and stems were eaten by sub adults and juveniles than adults ($\chi^2 = 8.11$, $P < 0.05$). The time spent feeding on different items varied significantly (Individuals $n = 30$, $F_{\text{Leaves}} = 28.7$, $F_{\text{reproductive parts}} = 51.3$, $F_{\text{Shoot/stem}} = 32.6$ and $F_{\text{Invertebrate/Fungi}} = 48.0$ all $P < 0.001$).

Sanje mangabeys spent 68% of all feeding time on the forest floor. This result confirms that *C. sanjei* is terrestrial, and able to obtain much of its food requirements by feeding on a variety of materials on the forest floor. Selectivity and food acquisition largely depend on density of food trees and abundance. I also investigated this.

Food tree density: The density of reproductively sized individuals trees in a 7.0 ha sampled in Njokamoni was 183 trees per hectare. The abundance of food trees per individual monkey was 95.

Sanje mangabeys also made use of woodland and gallery forest. Yellow baboons are sympatric with the Sanje mangabey; however, they distribute themselves differently

within the forest, and the two species are often very competitive and aggressive to each other whenever group encounters occurred. This suggests that competitive exclusion has played a part in shaping their distribution, given that both species are large, omnivorous monkeys.

Female reproductive biology and sexual behaviour

The morphology of Sanje mangabey sex skin and characteristics of its menstrual cycle were described in chapter 4. The swelling cycle length of female Sanje mangabey averaged 32 ± 2.4 days. The swelling tumescence phase lasted for 12.7 ± 3.9 days and the average duration of maximum swelling was 4.4 ± 0.9 days. Swelling detumescence lasted an average of 14.7 ± 3.9 days. My study shows that there are inter-individual differences in swelling duration among females ($F = 12.43$, $P = 0.043$). All cyclic females showed days with regular swellings of both sizes. Changes in the appearance of sex the skin during the menstrual cycle, and during pregnancy showed marked differences. For example, I showed that Sanje mangabeys exhibit post-conception swellings that are much smaller in size compared to normal swellings associated with ovulation; these swellings started to develop approximately 67 days after conception.

Details of the sexual behaviour of the Sanje mangabey have been described for the first time in this study. Similarities with other *Cercocebus* and *Lophocebus* mangabeyS and with mandrills and baboons were stressed. Implications for evolution of sexual skin sexual behaviour in the Papionini were discussed. In general, most aspects of Sanje mangabey sexual behaviour resembled that of mandrills and other terrestrial mangabeys, and baboons rather than the arboreal mangabeys.

Sanje mangabeys did not mate exclusively in the dry or wet season, unlike some *Cercocebus* species (Gust *et al.*, 1990; Gust & Gordon, 1991). Reproductive status was not influenced by seasonal changes in the amounts of rainfall or temperature in the area. However, my data also suggest that there may be some seasonal peaks in reproductive behaviour. Mating activity peaked near the end of rain season in April throughout June. Patterns of male sexual activity were associated with the occurrence and size of female sexual swellings. This influenced the behaviour of both males and females. I found that female Sanje mangabeys mate with approximately 3 males

during the maximum swelling phase. Females presented relatively more often, males copulated more but inspected the females less often during their maximum swelling phase. However, the frequency of copulations and inspections was not limited to this phase; sexual behaviour occurred in the other swelling phases. Copulations in this group were observed some days before maximum tumescence of the sexual skin, during maximal swelling and sex skin breakdown in all females. The occurrence of a majority of copulations during maximal tumescence suggests that swellings are more attractive to males during this period, and thus may function as approximate indicators of the likelihood of ovulation (Nunn, 1999). These findings stress the idea that swellings provide more than general information about the reproductive status of females, and can be considered as reliable indicators of fertile period i.e. graded signals (Dixon, 1983; Nunn, 1999). In contrast to Nunn's hypothesis concerning male mate guarding during maximum swelling to maximize mating access, male competition for access to females was not found to be very intense in this species. Further studies on the Sanje mangabey's ability to defend exclusive mating need to be undertaken, to further explain evolution of mating systems.

In the majority of mammals, females are sexually receptive for only a limited (periovarian) period during the ovarian cycle. This period of sexual receptivity or "oestrus" (as defined by Walter Heape) is under rigid control by ovarian secretion of oestrogen and progesterone. Many researchers have talked about oestrous in female primates, persistently associating or relating it with the menstrual cycle (i.e. female reproductive status) and patterns of sexual behaviour e.g. (Altmann, 1990; Atsalis & Margulis, 2006; Bielert & Anderson, 1985; Domb & Pagel, 2001; Girolami & Bielert, 1987; Nunn, 1999; Pagel, 1994; Paoli *et al.*, 2006; Steklis & Fox, 1988). However, these studies give little clarity concerning oestrus or its precise definition. Results from this study suggest that there is no oestrus in Sanje mangabeys, because female receptivity occurred throughout the entire course of the female cycle. This is not to imply that the menstrual cycle has no effect upon mangabey sexuality, because effects of the menstrual cycle upon sexual interactions do occur, and the attractiveness of female swellings is remarkable.

The knowledge presented here on the social organisation, ecology and female reproductive cycle and sexual behaviour contributes to greater understanding of Sanje

mangabey biology. This information may be useful for management and conservation. The information might also be of use for captive management of this endangered monkey should this become necessary.

Conservation concerns which impact the Sanje mangabey population

There has been continuous immigration and growth of the human population around the Udzungwa Mountains National Park. This has impacts on forest biodiversity, both directly and indirectly. Good environmental conditions and fertile soils are thought to attract people in to the udzungwas (Institute of resource assessment, cited in Ehardt *et al.* 2005). The continuous forest loss to agriculture and human settlement over the past 30 years is one the major problems affecting the Sanje mangabey. Rodgers and Homewood (1982) estimated forest size to be 450 km². Newmark (1998), Ehardt *et al.* (2005) and Marshall (2007) report that the closed forest area in Udzungwa has decreased to 389 km², 131 km² and 106 km² respectively which is about 14% to 34% of forest loss in ten years. This renders the small and fragmented mangabey populations vulnerable to extinction, as a result of low dispersal possibilities and the possible loss of genetic diversity. The threats faced by the animals may also disrupt their social structure and organization (Altmann *et al.*, 1996; Chapman *et al.*, 2007; Chapman *et al.*, 2005; Kappeler & van Schaik, 2002; Onderdonk & Chapman, 2000; Sterck, 1999; Tutin, 1999; Tutin *et al.*, 1997).

The mangabey population has also experienced local extinction. Thus, a population reported to occur in the adjacent lowland forest of Magombera no longer exists. Generally, apart from habitat loss, other threats to Udzungwa mangabeys include bushfires, commercial logging, hunting and large scale farming. Bushfires are a threat during the dry season; because there are some forest patches that are surrounded by grass. Apart from natural occurrences of fire, due to long months without rain, there are established traditions of burning, to extend open areas. As mentioned earlier, the land in Udzungwa is very fertile, and the presence of major rivers (the Kilombero and Ruaha) maximizes its potential for new immigrants. Most of the new comers in the area involve themselves in sugar cane farming. The agricultural policy in Tanzania favours conversion of land for other uses (e.g. low protected forested area) and expansion of land for agricultural purposes to increase per capita production to meet

the needs of a approximately 60% of Tanzania people who are deemed poor and leaving under 1US\$ a day (URT, 2006).

Commercial logging is still a problem. The Udzungwa forests particularly were subject to widespread and intense logging during the 1970s. There was heavy exploitation of *Milicia exelsa* and *Khaya anthoceca* in the Matundu forest, south west of Mwanihana by the Chinese (Dinesen *et al.*, 2001). Small and large scale logging was also carried out by the local Hehe people in these areas, and has continued to the present day. Some of these forests are only recovering after improved protection levels (Marshall, 2007). Hunting for bushmeat is common, especially in areas surrounding the west Udzungwa forests of Matundu. The Northern and southern parts of the Udzungwa Scalp forest, where the remaining population of mangabeys resides, are subject to high hunting pressures as well. Evidences of disrupted adult sex ratio are evident, with group counts in the area showing lower numbers of adult individuals than in other areas of the Sanje mangabey's range (Rovero *et al.*, 2006).

References

- Agetsuma, N. (2001). Relation between age-sex classes and dietary selection of wild Japanese monkeys. *Ecological Research*, 16(4), 759-763.
- Alberts, S. C. (1999). Paternal kin discrimination in wild baboons. *Proceedings of the Royal Society of London, Series B*, 266, 1501-1506.
- Alberts, S. C., & Altmann, J. (1995). Balancing costs and opportunities: dispersal in male baboons. *American Naturalist*, 145, 279-306.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227-266.
- Altmann, J. (1979). Age cohorts as paternal sibships. *Behavioral Ecology and Sociobiology*, 6(2), 161-164.
- Altmann, J. (1990). Primate males go where the females are. *Animal Behaviour*, 39(1), 193-195.
- Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., *et al.* (1996). Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Science USA*, 93(12), 5797-5801.
- Altmann, J., Altmann, S. A., & Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *American Journal of Primatology*, 1(4), 389-399.
- Altmann, J., Hausfater, G., & Altmann, S. A. (1985). Demography of Amboseli baboons, 1963-1983. *American Journal of Primatology*, 8(2), 113-125.
- Anderson, D. R., Laake, J. L., Crain, B. R., & Burnham, K. P. (1979). Guidelines for Line Transect Sampling of biological populations. *The Journal of Wildlife Management*, 43(1), 70-78.
- Anderson, J., Cowlishaw, G., & Rowcliffe, J. M. (2007). Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. *International Journal of Primatology*, 28(3), 637-655.
- Anderson, M. J. (1994). *Sexual selection* Princeton: Princeton University Press.
- Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J., & Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, 71(1), 117-127.
- Arlet, M. E., Grote, M. N., Molleman, F., Isbell, L. A., & Carey, J. R. (2009). Reproductive tactics influence cortisol levels in individual male gray-cheeked mangabeys (*Lophocebus albigena*). *Hormones and Behavior*, 55(1), 210-216.
- Asner, G. P., Knapp, D. E., Broadbent, E. N., & Oliveira, P. J. C. (2005). Selective Logging in the Brazilian Amazon. *Science*, 310(5747), 480.
- Atsalis, S., & Margulis, S. (2006). Sexual and hormonal cycles in geriatric gorilla, *Gorilla gorilla*. *International Journal of Primatology*, 27(6), 1663-1687.
- Baillie, J. E. M., Hilton-Taylor, C., & Stuart, S. N. (2004). *The IUCN Red List of Threatened Species*. Gland: IUCN.
- Barelli, C., Heistermann, M., Boesch, C., & Reichard, U. H. (2007). Sexual swellings in wild white-handed gibbon females (*Hylobates lar*) indicate the probability of ovulation. *Hormones and Behavior*, 51(2), 221-230.
- Barnicot, N. A., & Hewett-Emmett, D. (1972). Red cell and serum proteins of *Cercocebus*, *Presbytis*, *Colobus* and certain other species. *Folia Primatologica*, 17, 442-457.

- Barrett, L., Gaynor, D., & Henzi, S. P. (2002). A dynamic interaction between aggression and grooming reciprocity among female Chachma baboons. *Animal Behaviour*, 63(6), 1047-1053.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceeding of Biological Sciences*, 266, 665-670.
- Batchelder, W. H., & Bershad, N. J. (1979). The statistical analysis of a thurstonian model for rating chess players. *Journal of Mathematical Psychology*, 19(1), 39-60.
- Baulu, J. (1976). Seasonal sex skin coloration and hormonal fluctuations in free-ranging and captive monkeys. *Hormones and Behavior*, 7(4), 481-494.
- Bell, R. H. V. (1971). A grazing system in the Serengeti. *Scientific American*, 225, 86-93.
- Bernstein, I. S. (1966). An investigation of the social organisation of pigtail monkey groups through the use of challenges. *Primates*, 7, 471-480.
- Bernstein, I. S. (1971). The influence of introductory techniques on the formation of captive mangabey groups. *Primates*, 12(1), 33-44.
- Bernstein, I. S. (1976). Activity patterns in a sooty mangabey group. *Folia Primatologica*, 26, 185-206.
- Bernstein, I. S. (1981). Dominance: the baby and the bathwater. *Behavioral and Brain Sciences* 4, 419-457.
- Bernstein, I. S. (2007). Social mechanisms in the control of primate aggression. In C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger & S.K. Bearder (Eds.), *Primates in Perspective*. New York: Oxford University Press
- Bernstein, I. S., Williams, L., & Ramsay, M. (1983). The expression of aggression in Old World monkeys. *International Journal of Primatology*, 4(2), 113-125.
- Bettinger, T., Wallis, J., & Morris, A. (1995). Reproductive parameters of mandrills at the Tulsa Zoo. *Zoo Biology*, 14(2), 115-121.
- Bielert, C., & Anderson, C. M. (1985). Baboon sexual swellings and male response: A possible operational mammalian supernormal stimulus and response interaction. *International Journal of Primatology*, 6, 377-393.
- Bielert, C., Girolami, L., & Jowell, S. (1989). An experimental examination of the colour component in visually mediated sexual arousal of the male Chachma baboon (*Papio ursinus*). *Journal of Zoology London.*, 219, 569-579.
- Bolwig, N. (1978). Communicative signals and social behaviour of some African monkeys: A comparative study. *Primates*, 19(1), 61-99.
- Brain, C. (1990). Spatial use of desert environments by baboons (*Papio ursinus*). *Journal of Arid Environments*, 18, 67-73.
- Brown, L. H. (1971). The relations of the crowned eagle *stephanoaetus coronatus* and some of its prey animals. *Ibis*, 113(2), 240-243.
- Brown, L. H., Urban, E. K., & Newman, K. (1982). *The birds of Africa* (Vol. 1). New York: Academic Press.
- Brugiere, D., & Fleury, M.-C. (2000). Estimating primate densities using home range and line transect methods: A comparative test with the black colobus monkey *Colobus satanas*. *Primates*, 41(4), 373-382.
- Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature*, 425(6954), 179-181.

- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (1993). *Distance sampling: Estimating abundance of biological populations*. Suffolk, Great Britain: Chapman and Hall
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. New York: Oxford University Press, USA.
- Burgess, N. D., Balmford, A., Cordeiro, N. J., Fjelds , J., K per, W., Rahbek, C., Sanderson, E. W., *et al.* (2007a). Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation*, 134(2), 164-177.
- Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjelds , J., Howell, K. H., Kilahama, F. B., *et al.* (2007b). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, 134(2), 209-231.
- Busse, C. D. (1982). Social dominance and offspring mortality among female Chachma baboons. *International Journal of Primatology*, 3(3), 267.
- Busse, C. D. (1984). Spatial structure of Chachma baboon groups. *International Journal of Primatology*, 5(3), 247-261.
- Busse, C. D., & Hamilton III, W. J. (1981). Infant carrying by male Chachma baboons. *Science*, 212(4500), 1281-1283.
- Butler, R. (2005). Forest Stratification: The canopy. Retrieved October, 2008, from <http://rainforests.mongabay.com/0401.htm>
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecological monographs*, 60(1), 1-26.
- Buzzard, P. (2006). Ranging patterns in relation to seasonality and frugivory among *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* in the Ta  forest. *International Journal of Primatology*, 27(2), 559-573.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5), 1454-1469.
- Campbell, C. J., Fuentes, A., Mackinnon, K. C., Panger, M., & Bearder, S. K. (Eds.). (2007). *Primates in Perspective*. New York: Oxford University Press.
- Celle, P. P. (1990). Menstrual cycle characterization and artificial insemination in the black mangabey (*Cercocebus atterrimus*). *Zoo Biology*, 9, 11-24.
- Chalmers, N. R. (1968). Group composition, ecology and daily activities of free living mangabeys in Uganda. *Folia Primatologica*, 8, 247-262.
- Chance, M. R. A. (1967). Attention structure as the basis of primate rank orders. *Man*, 2(4), 503-518.
- Chancellor, R. L., & Isbell, L. A. (2009). Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*). *Behaviour Ecology*, 20(1), 79-86.
- Chapais, B. (1988a). Experimental matrilineal inheritance of rank in female Japanese macaques. *Animal Behaviour*, 36(4), 1025-1037.
- Chapais, B. (1988b). Rank maintenance in female Japanese macaques: Experimental evidence for social dependency. *Behaviour*, 104(1/2), 41-59.
- Chapais, B., Girard, M., & Primi, G. (1991). Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*, 41(3), 481-491.

- Chapman, C. A., & Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: Examining the generality of the ecological constraints model. *International Journal of Primatology*, 21(4), 565-585.
- Chapman, C. A., Chapman, L. J., & Gillespie, T. R. (2002). Scale issues in the study of primate foraging: Red colobus of Kibale National Park. *American Journal of Physical Anthropology*, 117(4), 349-363.
- Chapman, C. A., Struhsaker, T. T., & Lambert, J. E. (2005). Thirty years of research in Kibale National Park, Uganda, reveals a complex picture for conservation. *International Journal of Primatology*, 26(3), 539-555.
- Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1994). Indices of habitat-wide fruit abundance in tropical forest. *Biotropica*, 26(2), 160-171.
- Charpentier, M. J. E., Peignot, P., Hossaert-McKey, M., & Wickings, E. J. (2004). Changes in social interactions during adolescence in male mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, 63, 63-73.
- Charpentier, M. J. E., Peignot, P., Hossaert-McKey, M., & Wickings, E. J. (2007). Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. *Animal Behaviour*, 73(1), 37-45.
- Cheney, D. L. (1977). The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behavioral Ecology and Sociobiology*, 2(3), 303-318.
- CI. (2007). Eastern Afromontane hotspot. Retrieved December, 2008, from <http://www.biodiversityhotspots.org>
- Cipolletta, C., Spagnoletti, N., Todd, A., Robbins, M., Cohen, H., & Pacyna, S. (2007). Termite feeding by gorilla *Gorilla gorilla* at Bai Hokou, Central African Republic. *International Journal of Primatology*, 28(2), 457-476.
- Clutton-Brock, T. H. (1974). Primate social organisation and ecology. *Nature*, 250(5467), 539-542.
- Clutton-Brock, T. H. (1989). Female transfer and inbreeding avoidance in social mammals. *Nature*, 337(6202), 70-72.
- Clutton-Brock, T. H., & Harvey, P. H. (1976). Evolutionary rules and primates societies. In P.P.G. Bateson & R.A. Hinde (Eds.), *Growing points in Ethology* (pp. 195-237). Cambridge: Cambridge University Press.
- Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology London*, 183, 1-39.
- Clutton-Brock, T. H., Harvey, P. H., & Rudder, B. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, 269(5631), 797-800.
- Colyn, M. M., Gautier-Hion, A., & Thys van den Audenaerde, D. (1991). *Cercopithecus dryas* Schwarz 1993 and *C. solongo* Thys van den Audenaerde 1977 are the same species with age-related coat pattern. *Folia Primatologica*, 56, 167-170.
- Cooper Jr, W. E., Adams, C. S., & Dobie, J. L. (1983). Female color change in the keeled earless lizard, *Holbrookia propinqua*: Relationship to the reproductive cycle. *The Southwestern Naturalist*, 28(3), 275-280.
- Cordeiro, N. J. (1992). Behaviour of Blue monkeys (*Cercopithecus mitis*) in the presence of Crowned eagles (*Stephanoaetus coronatus*). *Folia Primatologica*, 59, 203-207.
- Cronin, J. E., & Sarich, V. M. (1976). Molecular evidence for dual origin of mangabeys among Old World monkeys. *Nature*, 260(5553), 700-702.

- Crook, J. H., & Gartlan, J. S. (1966). Evolution of primate societies. *Nature*, 210(5042), 1200-1203.
- Daegling, D. J., & Mc Graw, W. S. (2007). Functional morphology of the mangabey mandibular corpus: Relationship to dental specializations and feeding behavior. *American Journal of Physical Anthropology*, 134(1), 50-62.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- de A Moura, A. C. (2007). Primate group size and abundance in the Caatinga dry forest, northeastern Brazil. *International Journal of Primatology*, 28(6), 1279-1297.
- de Ruiter, J. R., & Geffen, E. (1998). Relatedness of matriline, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the royal Society of London*, 265, 79-87.
- de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, 50(5), 1375-1389.
- de Vries, H., Netto, W. J., & Hanegraaf, P. L. H. (1993). Matman: A Program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, 125(3/4), 157-175.
- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71(3), 585-592.
- de Waal, F. B. M. (1997). The Chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, 18(6), 375-386.
- de Waal, F. B. M., & Luttrell, L. M. (1986). The similarities principle underlying social bonding among female rhesus monkeys. *Folia Primatologica*, 46, 215-234.
- Deag, J. M., & Crook, J. H. (1971). Social behaviour and 'Agonistic Buffering' in the wild Barbary macaque, *Macaca sylvana* L. *Folia Primatologica*, 15(3-4), 183-200.
- Decker, B. S. (1995). Effects of habitat disturbance on the behavioral ecology and demographics of the Tana river red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology*, 15(5), 703-737.
- Defler, T. R. (1978). Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates*, 19(1), 153-167.
- Defler, T. R., & Pintor, D. (1985). Censusing primates by transect in a forest of known primate density. *International Journal of Primatology*, 6(3), 243-259.
- Deputte, B. L. (1991). Reproductive parameters of captive grey-cheeked mangabeys. *Folia Primatologica*, 57, 57-69.
- Deputte, B. L. (1992). Life history of captive gray-cheeked mangabeys: Physical and sexual development. *International Journal of Primatology*, 13(5), 509-531.
- Deschner, T., Heistermann, M., Hodges, K. J., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, 66(3), 551-560.
- Deschner, T., Heistermann, M., Hodges, K. J., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*, 46(2), 204-215.
- Dinesen, L., Lehmberg, T., Rahner, M. C., & Fjeldsø, J. (2001). Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. *Biological Conservation*, 99(2), 223-236.

- Disotell, T. R. (2000). The Molecular systematics of the *Cercopithecidae*. In P.F. Whitehead & C.J. Jolly (Eds.), *Old World monkeys* (pp. 29-56). Cambridge, UK: Cambridge University Press.
- Dixon, A. F. (1983). Observations on the evolution and behavioral significance of 'sexual skin' in female primates. *Advances in the study of Behavior.*, 13, 63-106.
- Dixon, A. F. (1998). *Primate sexuality*. New York: Oxford University Press.
- Dixon, A. F. (2002). Sexual selection by cryptic female choice and the evolution of primate sexuality. *Evolutionary Anthropology: Issues, News, and Reviews*, 11(S1), 195-199.
- Dixon, A. F., & Anderson, M. J. (2004). Effects of sexual selection upon sperm morphology and sexual skin morphology in Primates. *International Journal of Primatology*, 25, 1159-1171.
- Domb, L. G., & Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature London*, 410, 204-206.
- Droney, D. C., & Hock, M. B. (1998). Male sexual signals and female choice in *Drosophila grimshawi* (Diptera: Drosophilidae). *Journal of Insect Behavior*, 11(1), 59-71.
- Dunbar, R. I. M. (1980). Determinants and evolutionary consequences of dominance among female Gelada baboons. *Behavioral Ecology and Sociobiology*, 7(4), 253-265.
- Dunbur, R. I. M. (1988). *Primates social systems*. London: Chapman and Hall.
- EAM. (2002). Eastern Arc forests of Tanzania and Kenya. Retrieved December, 2008, from <http://www.easternarc.org>
- Ehardt, C. L. (1988a). Absence of strongly kin-preferential behavior by adult female sooty mangabeys (*Cercocebus atys*). *American Journal of Physical Anthropology*, 76(2), 233-243.
- Ehardt, C. L. (1988b). Affiliative behavior of adult female sooty mangabeys (*Cercocebus atys*). *American Journal of Primatology*, 15(2), 115-127.
- Ehardt, C. L. (2001). The endemic primates of the Udzungwa Mountains, Tanzania. *African Primates*, 4, 15-26.
- Ehardt, C. L., Butynski, T. M., & Struhsaker, T. T. (2008). *Cercocebus sanjei*. 2008 IUCN Red List of Threatened Species. Retrieved 22 January, 2009, from www.iucnredlist.org
- Ehardt, C. L., Jones, T., & Butynski, T. M. (2005). Protective status, ecology and strategies for improving conservation of *Cercocebus sanjei* in the Udzungwa Mountains, Tanzania. *International Journal of Primatology*, 26(3), 557-583.
- Elton, S. (2007). Environmental correlates of the Cercopithecoid radiations. *Folia Primatologica*, 78(5-6), 344.
- Engelhardt, A., Hodges, J. K., Niemitz, C., & Heistermann, M. (2005). Female sexual behavior, but not sex skin swelling, reliably indicates the timing of the fertile phase in wild long-tailed macaques (*Macaca fascicularis*). *Hormones and Behavior*, 47(2), 195-204.
- Erhart, E. M., & Overdorff, D. J. (2008). Spatial memory during foraging in Prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. *Folia Primatologica*, 79(4), 185.
- Fairbanks, L. A. (1980). Relationships among adult females in captive vervet monkeys: Testing a model of rank-related attractiveness. *Animal Behaviour*, 28(3), 853-859.

- Fashing, P., Mulindahabi, F., Gakima, J.-B., Masozera, M., Mununura, I., Plumptre, A. J., & Nguyen, N. (2007). Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe forest, Rwanda: Possible costs of large group size. *International Journal of Primatology*, 28(3), 529-550.
- Felton, A., Felton, A., Wood, J., & Lindenmayer, D. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: The importance of *Ficus* as a staple food resource. *International Journal of Primatology*, 29(2), 379-403.
- Fimbel, C. (1994). Ecological correlates of species success in modified habitats may be disturbance and site-specific: The primates of Tiwai Island. *Conservation Biology*, 8(1), 106-113.
- Fraser, Ó., & Plowman, A. (2007). Function of notification in *Papio hamadryas*. *International Journal of Primatology*, 28(6), 1439-1448.
- Freeland, W. J. (1980). Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination. *Ecology*, 61(6), 1297-1303.
- Freese, C. H., Heltne, P. G., Napoleon, C. R., & Whitesides, G. H. (1982). Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology*, 3(1), 53-90.
- Gautier-Hion, A., & Tutin, C. E. G. (1988). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatologica* 51 149–151.
- Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, 14(1), 205-220.
- Girolami, L., & Bielert, C. (1987). Female perineal swelling and its effect on male sexual arousal: an apparent sexual releaser in the chacma baboon (*Papio ursinus*). *International Journal of Primatology*, 8, 651-661.
- Goodall, J. (1986). *The Chimpanzees of Gombe*. Cambridge: Harvard University Press.
- Gordon, T. P., & Busse, C. D. (1984). Periannual swellings in female mangabeys during pregnancy. *American Journal of Primatology*, 6, 404-405.
- Gordon, T. P., Gust, D. A., Busse, C. D., & Wilson, M. E. (1991). Hormones and sexual behavior associated with postconception perineal swelling in the sooty mangabey (*Cercocebus torquatus atys*). *International Journal of Primatology*, 12(6), 585-597.
- Greenberg, C. H. (2001). Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *Forest Ecology and Management*, 148(1-3), 135-144.
- Greenwood, J. J. D., & Robinson, R. A. (2006). Principles of sampling. In W.J. Sunderland (Ed.), *Ecological census techniques* (2nd ed.). Cambridge: Cambridge University Press.
- Groves, C. P. (1978). Phylogenetic and population systematics of the Mangabeys (Primates: Cercopithecoidea). *Primates*, 19(1), 1-34.
- Groves, C. P. (1996). The nomenclature of the Tanzanian mangabey and the Siberut macaque. *Australian Primatology*, 10(4), 2-5.
- Groves, C. P. (2001). *Primate taxonomy*. Washington DC.: Smithsonian Institution Press.
- Groves, C. P. (2004). The what, why and how of primate taxonomy. *International Journal of Primatology*, 25(5), 1105-1126.
- Groves, C. P. (2005). Order Primates. In D.E. Wilson & D.M. Reeder (Eds.), *Mammal Species of the World* (3 ed., pp. 111-184). Baltimore: The Johns Hopkins University Press.

- Groves, C. P. (2006). Taxonomy and biogeography of the primates of western Uganda. In N.E. Newton-Fisher, H. Notman, J.D. Paterson & V. Reynolds (Eds.), *Primates of Western Uganda* (pp. 3-20).
- Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the diversity of African primates. *International Journal of Primatology*, 24(6), 1301-1357.
- Gumert, M. (2007). Grooming and infant handling interchange in *Macaca fascicularis* : The relationship between infant supply and grooming payment. *International Journal of Primatology*, 28(5), 1059-1074.
- Gumert, M., & Ho, M.-H. (2008). The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (*Macaca fascicularis*). *Primates*, 49(3), 176-185.
- Gust, D. A. (1994a). Alpha-male sooty mangabeys differentiate between females' fertile and their postconception maximal swellings. *International Journal of Primatology*, 15(2), 289-301.
- Gust, D. A. (1994b). A brief report on the social behavior of the crested mangabey (*Cercocebus galeritus galeritus*) with a comparison to the sooty mangabey (*C. torquatus atys*). *Primates*, 35(3), 375-383.
- Gust, D. A. (1995). Moving up the dominance hierarchy in young sooty mangabeys. *Animal Behaviour*, 50(1), 15-21.
- Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (*Cercocebus torquatus atys*). *American Journal of Primatology*, 22(4), 241-250.
- Gust, D. A., & Gordon, T. P. (1991a). Female rank instability in newly formed groups of familiar sooty mangabeys (*Cercocebus torquatus atys*). *Primates*, 32(4), 465-471.
- Gust, D. A., & Gordon, T. P. (1991b). Male age and reproductive behaviour in sooty mangabeys, *Cercocebus torquatus atys*. *Animal Behaviour*, 41(2), 277-283.
- Gust, D. A., & Gordon, T. P. (1994). The absence of a matrilineally based dominance system in sooty mangabeys, *Cercocebus torquatus atys*. *Animal Behaviour*, 47(3), 589-594.
- Gust, D. A., Gordon, T. P., & Gergits, W. (1995). Proximity at birth relates to a sire's tolerance of his offspring among sooty mangabeys. *Animal Behaviour*, 49(5), 1403-1405.
- Hadidian, J., & Bernstein, I. S. (1979). Female reproductive cycles and birth data from an Old World Monkey colony. *Primates*, 20(3), 429-442.
- Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7(1), 1-16.
- Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17-52.
- Hamilton, W. J. (1984). Significance of parental investment by primates to the evolution of male-female associations. In D.M. Taub (Ed.), *Primate paternalism* (pp. 303-335). New York: Van Nostrand Reinhold.
- Hanna, L. W. (1976). Potential water deficits in Uganda: An assessment of wet and dry seasons. *Transactions of the Institute of British Geographers, New Series*, 1(2), 190-202.
- Harcourt, A. H. (1992). Coalition and alliances: are primates more complex than non-primates? In A.H. Harcourt & F.B.M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 132-152). Oxford: Oxford University Press.

- Harvey, P. H., & May, R. M. (1989). Out for the sperm count. *Nature London*, 337(6207), 508-509.
- Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, 40(1), 47-59.
- Henzi, S. P., Barrett, L., Gaynor, D., Greeff, J., Weingrill, T., & Hill, R. A. (2003). Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Animal Behaviour*, 66(5), 931-938.
- Hill, W. C. O. (1969). *Primates. Comparative anatomy and taxonomy*. 6. *Catarrhini, Cercopithecoidea, Cynopithecinae*. (Vol. 6). Edinburgh: Edinburgh University Press.
- Hill, W. C. O. (1970). *Primates. Comparative anatomy and Taxonomy*. 8. *Catarrhini, Cercopithecoidea, Cynopithecinae: Papio, Mandrillus, Theropithecus* (Vol. 8). Edinburgh: Edinburgh University Press.
- Hill, W. C. O. (1974). *Primates. Comparative anatomy and taxonomy*. *Catarrhini, Cercopithecoidea, Cynopithecinae: Cercocebus, Macaca, Cynopithecus*. (Vol. 7). Edinburgh: Edinburgh University Press.
- Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, 11(1), 1-17.
- Hinde, R. A., & Rowell, T. E. (1962). Communication by postures and facial expressions of the rhesus monkey (*Macaca mulatta*). *Proceedings of the Royal Society of London*, 138, 1-21.
- Homewood, K. M. (1976). *Ecology and behaviour of the Tana mangabey (Cercocebus galeritus galeritus)*. Unpublished PhD dissertation, University college London, London.
- Homewood, K. M., & Rodgers, W. A. (1981). A previously undescribed mangabey from Southern Tanzania. *International Journal of Primatology*, 2(1), 47-55.
- Hoshino, J. (1985). Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo animal reserve, Cameroon. *Primates*, 26(3), 248-273.
- Hrady, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1(1), 13-40.
- Hrady, S. B. (1981). *The woman that never evolved*. Cambridge, Massachusetts: Harvard University Press.
- Hrady, S. B., & Whitten, P. L. (1987). Patterning of sexual activity. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 370-384). Chicago, Illinois: University of Chicago Press.
- Irwin, M. (2008). Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. *International Journal of Primatology*, 29(1), 95-115.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, 2(2), 143-155.
- Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (1990). Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behavioral Ecology and Sociobiology*, 27(5), 351-358.
- Isbell, L. A., Pruett, J. D., & Young, T. P. (1998). Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology*, 42(2), 123-133.

- Jameson, K. A., Appleby, M. C., & Freeman, L. C. (1999). Finding an appropriate order for a hierarchy based on probabilistic dominance. *Animal Behaviour*, 57(5), 991-998.
- Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, 48(3/4), 215-267.
- Johansson, B. G., & Jones, T. M. (2007). The role of chemical communication in mate choice. *Biological Reviews*, 82(2), 265-289.
- Johns, A. D., & Skorupa, J. (1987). Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*, 8(2), 157-191.
- Johnson, P. S., Shifley, S. R., & Rogers, R. (Eds.). (2002). *The ecology and silviculture of Oaks* (7 ed.). New York, USA: CABI Publishing.
- Jolly, C. J. (2007). Baboons, mandrills and mangabeys, Afro-Papionin socioecology in a phylogenetic perspective. In C.J. Campbell, A. Fuentes, K.C. Mackinnon, M. Panger & S.K. Bearder (Eds.), *Primates in Perspective* (pp. 240-251). NY: Oxford University Press.
- Jones, T., Ehardt, C. L., Butynski, T. M., Davenport, T. R. B., Mpunga, N. E., Machaga, S. J., & De Luca, D. W. (2005). The highland mangabey *Lophocebus kipunji*: A new species of African monkey. *Science*, 308(5725), 1161-1164.
- Jones, T., Laurent, S., Mselewa, F., & Mtui, A. (2006). Sanje mangabey *Cercocebus sanjei* kills an african crowned eagle *Stephanoaetus coronatus*. *Folia Primatologica*, 77, 357-363.
- Kahurananga, J. (1981). Population estimates, densities and biomass of large herbivores in Simanjiro Plains, Northern Tanzania. *African Journal of Ecology*, 19(3), 225-238.
- Kappeler, P. M. (2000). Primate males: History and theory. In P.M. Kappeler (Ed.), *Primate males* (Vol. 3-7). Cambridge: Cambridge University Press.
- Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23(4), 707-740.
- Kie, J. G., Baldwin, J. A., & Evans, C. J. (1996). CALHOME: A program for estimating animal home ranges. *Wildlife Society Bulletin*, 24(2), 342-344.
- Kingdon, J. S. (1997). *The Kingdon field guide to African mammals*. London: Academic Press.
- Kinnaird, M. F. (1990a). *Behavioral and demographic responses of to habitat by the Tana River crested mangabey (Cercocebus galeritus galeritus)*. Unpublished PhD dissertation, University of Florida, Gainesville, Florida.
- Kinnaird, M. F. (1990b). Pregnancy, gestation and parturition in free-ranging Tana River crested mangabeys (*Cercocebus galeritus galeritus*). *American Journal of Primatology*, 22(4), 285-289.
- Kuitunen, M., Rossi, E., & Stenroos, A. (1998). Do highways influence density of land birds? *Environmental Management*, 22(2), 297-302.
- Leigh, S. R., Setchell, J. M., & Buchanan, L. S. (2005). Ontogenetic bases of canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 127(3), 296-311.
- Leighton, M., & Leighton, D. R. (1982). The relationship of size of feeding aggregate to size of food patch: Howler Monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica*, 14(2), 81-90.
- Leinfelder, I., de Vries, H., Deleu, R., & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology*, 55(1), 25-42.

- Leonard, W. R., Robertson, M. L., Aiello, L. C., & Wheeler, P. (1996). On Diet, Energy Metabolism, and Brain Size in Human Evolution. *Current Anthropology*, 37(1), 125-129.
- Leong, K. M., Ortolani, A., Graham, L. H., & Savage, A. (2003). The use of low-frequency vocalizations in African elephant (*Loxodonta africana*) reproductive strategies. *Hormones and Behavior*, 43(4), 433-443.
- Lieberman, D., Lieberman, M., Peralta, R., & Hartshorn, G. S. (1996). Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica. *The Journal of Ecology*, 84(2), 137-152.
- Lovett, J. C. (1996). Elevational and latitudinal changes in tree association and diversity in the Eastern Arc Mountains of Tanzania. *Journal of Tropical Ecology*, 12, 629-650.
- Lovett, J. C., Marshall, A. R., & Jeff, C. (2006). Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology*, 44(4), 478-490.
- Lovett, J. C., & Wasser, S. K. (Eds.). (1993). *Biogeography and Ecology of the Rain forest of Eastern Africa*. Cambridge: Cambridge University Press.
- Maestriperi, D. (1998). The evolution of male-infant interactions in the tribe Papionini (Primates: *Cercopithecidae*). *Folia Primatologica*, 69, 247-251.
- Maestriperi, D., Leoni, M., Raza, S. S., Hirsch, E. J., & Whitham, J. C. (2005). Female copulation calls in Guinea baboons: Evidence for postcopulatory female choice? *International Journal of Primatology*, 26(4), 737-758.
- Manson, J. H. (1997). Primate consortships: A critical review. *Current Anthropology*, 38(3), 353-374.
- Manson, J. H., David Navarrete, C., Silk, J. B., & Perry, S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, 67(3), 493-500.
- Marshall, A. R. (2007). *Disturbance in the Udzungwas: Responses of monkeys and trees to forest degradation*. Unpublished PhD Thesis, University of York, York.
- Marshall, A. R., Topp-Jørgensen, J. E., Brink, H., & Fanning, E. (2005). Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. *International Journal of Primatology*, 26(1), 127-145.
- Marshall, A. R., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28(6), 1219-1235.
- Martin, P., & Bateson, P. (1993). *Measuring behaviour*. Cambridge: Cambridge University Press.
- Marvan, R., Stevens, J. M. G., Roeder, A. D., Mazura, I., Bruford, M. W., & de Ruiter, J. R. (2006). Male dominance rank, mating and reproductive success in captive Bonobos (*Pan paniscus*). *Folia Primatologica*, 77, 364-376.
- Mc Graw, W. S., & Fleagle, J. (2006). Biogeography and evolution of the *Cercocebus-Mandrillus* Clade: Evidence from the face. In *Primate Biogeography* (pp. 201-224).
- McArthur, J. W., Beitins, I. Z., Gorman, A., Collins, D. C., Preedy, J. R. K., & Graham, C. E. (1981). The interrelationship between sex skin swelling and the urinary excretion of LH, estrone, and pregnanediol by the cycling female chimpanzee. *American Journal of Primatology*, 1(3), 265-270.
- McDiarmid, R. W., Ricklefs, R. E., & Foster, M. S. (1977). Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. *Biotropica*, 9(1), 9-25.

- McGraw, W. S., & Fleagle, J. (2006). Biogeography and evolution of the *Cercocebus-Mandrillus* Clade: Evidence from the face. In *Primate Biogeography* (pp. 201-224).
- Melton, D. A. (1983). Population dynamics of waterbuck (*Kobus ellipsiprymnus*) in the Umfolozi Game Reserve. *African Journal of Ecology*, 21(2), 77-91.
- Michael, R. P., & Keverne, E. B. (1968). Pheromones in the communication of sexual status in primates. *Nature*, 218(5143), 746-749.
- Milton, K. (2006). Diet and Primate Evolution. *Scientific American Special Edition*, 16(2), 22-29.
- Mitani, J., Struhsaker, T. T., & Lwanga, J. (2000). Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: Implications for conservation and census methods. *International Journal of Primatology*, 21(2), 269-286.
- Mitani, M. (1989). *Cercocebus torquatus*: Adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. *Primates*, 30(3), 307-323.
- Moore, J., & Ali, R. (1984). Are dispersal and inbreeding avoidance related? *Animal Behaviour*, 32(1), 94-112.
- Muroyama, Y. (1991). Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). *Behaviour*, 119(3/4), 161-170.
- Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, 128(1/2), 103-119.
- Murray, C. (2007). Method for assigning categorical rank in female *Pan troglodytes schweinfurthii* via the frequency of approaches. *International Journal of Primatology*, 28(4), 853-864.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.
- Nadler, R. D. (1975). Periparturitional behaviour of a primiparous lowland gollila. *Primates*, 15, 55-73.
- Newmark, W. D. (1991). Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara mountains, Tanzania. *Conservation Biology*, 5(1), 67-78.
- Newmark, W. D. (1998). Forest area, fragmentation, and loss in the Eastern Arc Mountains: Implications for conservation of biological diversity. *Journal of East Africa Natural history*, 87, 29-39.
- Nikitopoulos, E., Arnhem, E., van Hooff, J. A. R. A. M., & Sterck, E. (2004). Influence of female copulation calls on male sexual behavior in aptive *Macaca fascicularis*. *International Journal of Primatology*, 25(3), 659-677.
- Norscia, I., Carrai, V., & Borgognini-Tarli, S. M. (2006). Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*, 27(4), 1001-1022.
- Nunn, C. L. (1999a). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, 58(2), 229-246.
- Nunn, C. L. (1999b). The number of males in primate social groups: A comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, 46(1), 1-13.

- Olupot, W., Chapman, C. A., Brown, C. H., & Waser, P. M. (1994). Mangabey (*Cercocebus albigena*) population density, group size, and ranging: A twenty-year comparison. *American Journal of Primatology*, 32(3), 197-205.
- Olupot, W., Chapman, C. A., Waser, P. M., & Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology*, 43(1), 65-78.
- Olupot, W., & Waser, P. M. (2001). Correlates of intergroup transfer in male grey-cheeked mangabeys. *International Journal of Primatology*, 22(2), 169-187.
- Onderdonk, D. A., & Chapman, C. A. (2000). Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21(4), 587-611.
- Ostro, L. E. T., Silver, S. C., Koontz, F. W., Young, T. P., & Horwich, R. H. (1999). Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America. *Biological Conservation*, 87(2), 181-190.
- Packer, C. (1985). Dispersal and inbreeding avoidance. *Animal Behaviour*, 33(2), 676-678.
- Pagel, M. (1994). The evolution of conspicuous oestrous advertisement in Old World monkeys. *Animal Behaviour*, 47(6), 1333-1341.
- Paoli, T., Palagi, E., Tacconi, G., & Borgognini-Tarli, S. M. (2006). Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). *American Journal of Primatology*, 68(4), 333-347.
- Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, 40(2), 167-182.
- Plavcan, M. J. (2001). Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology*, 116(S33), 25-53.
- Plumptre, A. J. (2000). Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*, 37(2), 356-368.
- Pocock, R. I. (1925). The external characters of the *Catarrhine* monkeys and apes. *Proceedings of Zoological Society of London*, 1479-1579.
- Rand, A. S. (1964). Ecological distribution in Anoline lizards of Puerto Rico. *Ecology*, 45(4), 745-752.
- Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Tai National Park. *American Journal of Primatology*, 56(3), 137-153.
- Reichert, K. E., Heistermann, M., Hodges, K. J., Boesch, C., & Hohman, G. (2002). What females tell males about their reproductive status: are morphological and behavioural cues reliable signals of ovulation in bonobos, *Pan paniscus*? *Ethology*, 108, 583-600.
- Reynolds, V. (1968). Kinship and the family in monkeys, apes and man. *Man*, 3(2), 209-223.
- Rodgers, W. A., & Homewood, K. M. (1982). Biological values and conservation prospects for the forests and primate populations of the Udzungwa Mountains, Tanzania. *Biological Conservation*, 24, 285-304.
- Rovero, F., Struhsaker, T. T., Marshall, A. R., Rinne, T., Pedersen, U., Butynski, T. M., Ehardt, C. L., *et al.* (2006). Abundance of diurnal primates in Mwanihana forest, Udzungwa mountains, Tanzania. *International Journal of Primatology*, 27(3), 675-697.

- Rowell, T. E. (1969). Long term changes in a population of Ugandan baboons. *Folia Primatologica*, 11, 241-254.
- Rowell, T. E., & Chalmers, N. R. (1970). Reproductive cycle of the mangabey *Cercocebus albigena*. *Folia Primatologica*, 12, 264-272.
- Sailer, L., Gaulin, S., Boster, J., & Kurland, J. (1985). Measuring the relationship between dietary quality and body size in primates. *Primates*, 26(1), 14-27.
- Saito, C. (1996). Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Animal Behaviour*, 51(5), 967-980.
- Saj, T. L., & Sicotte, P. (2007). Scramble competition among *Colobus vellerosus* at Boabeng-Fiema, Ghana. *International Journal of Primatology*, 28(2), 337-355.
- Setchell, J. M., & Dixon, A. F. (2001a). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior*, 39(3), 177-184.
- Setchell, J. M., & Dixon, A. F. (2001b). Circannual changes in the secondary sexual adornments of semifree-ranging male and female mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, 53(3), 109-121.
- Setchell, J. M., & Dixon, A. F. (2002). Developmental variables and dominance rank in adolescent male mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, 56(1), 9-25.
- Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixon, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 115(4), 349-360.
- Setchell, J. M., & Wickings, E. J. (2004a). Sexual swelling in mandrills (*Mandrillus sphinx*): a test of the reliable indicator hypothesis. *Behaviour Ecology*, 15(3), 438-445.
- Setchell, J. M., & Wickings, E. J. (2004b). Social and seasonal influences on the reproductive cycle in female mandrills (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 125(1), 73-84.
- Setchell, J. M., Wickings, E. J., & Knapp, L. A. (2006). Life history in male mandrills (*Mandrillus sphinx*): Physical development, dominance rank, and group association. *American Journal of Physical Anthropology*, 131(4), 498-510.
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671-698.
- Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, 28(3), 798-813.
- Shaikh, A. A., Celaya, C. L., Gomez, I., & Shaikh, S. A. (1982). Temporal relationships of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates*, 23, 444-452.
- Shultz, S. (2001). Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia Primatologica*, 72(4), 248.
- Silk, J. B. (1982). Altruism among female *Macaca radiata*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, 79(2/4), 162-188.
- Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine.
- Smuts, B. B., & Gubernick, D. J. (1992). Male-Infant relationships in nonhuman primates: Paternal investment or mating effort? In B.S. Hewlett (Ed.), *Father-Child Relations: Cultural and Biosocial Contexts* (pp. 1-23). New York: Aldine De Gruyter.

- Snaith, T., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, 59(2), 185-190.
- Stanford, C. B. (1995). The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour*, 49(3), 577-587.
- Stebenfeldt, G. H., & Hendrickx, A. G. (1973). Progesterone levels in the sooty mangabey (*Cercocebus atys*) during menstrual cycle, pregnancy and parturition. *Journal of Medical Primatology*, 2, 1-10.
- Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology*, 49(2), 100-110.
- Steklis, H., & Fox, R. (1988). Menstrual-cycle phase and sexual behavior in semi-free-ranging stump-tail macaques (*Macaca arctoides*). *International Journal of Primatology*, 9(5), 443-456.
- Sterck, E. (1999). Variation in langur social organization in relation to the socioecological model, human habitat alteration, and phylogenetic constraints. *Primates*, 40(1), 199-213.
- Stewart, K. J. (1977). The birth of a wild mountain gorilla, *Gorilla beringei*. *Primates*, 18, 965-976.
- Strier, K. B. (1992). Atelinae adaptations: Behavioral strategies and ecological constraints. *American Journal of Physical Anthropology*, 88(4), 515-524.
- Struhsaker, T. T. (1997). *Ecology of an African rainforest: Logging in Kibale and the conflict between conservation and exploitation*. Gainesville: University Press of Florida, USA.
- Struhsaker, T. T., Marshall, A. R., Detwiler, K., Siex, K., Ehardt, C. L., Lisbjerg, D. D., & Butynski, T. M. (2004). Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology*, 25(3), 615-658.
- T.M.A. (2008). Seasonal weather forecasts. *Tanzania Meteorological Agency Seasonal weather forecast for the country*. Retrieved September, 2008, from <http://www.meteo.go.tz/mwb/index.php>
- Teichroeb, J. A., Saj, T. L., Paterson, J. D., & Sicote, P. (2003). Effect of group size on activity budgets of *Colobus vellerosus* in Ghana. *International Journal of Primatology*, 24, 743-758.
- Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., *et al.* (2006). Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment. Retrieved 10 December, 2008, from <http://www.ruwpa.st-and.ac.uk/distance/>
- Thomas, S. C. (1991). Population densities and patterns of habitat use among anthropoid primates of the Ituri forest, Zaire. *Biotropica*, 23(1), 68-83.
- Tokuda, K., Simons, R. C., & Jensen, G. D. (1968). Sexual behavior in a captive group of pigtailed monkeys (*Macaca nemestrina*). *Primates*, 9(3), 283-294.
- Troisi, A., & Carosi, M. (1998). Female orgasm rate increases with male dominance in Japanese macaques. *Animal Behaviour*, 56(5), 1261-1266.
- Tutin, C. E. G. (1999). Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates*, 40(1), 249-265.

- Tutin, C. E. G., White, L. J. T., & Mackanga-Missandzou, A. (1997). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology*, 11(5), 1190-1203.
- van Hooff, J. A. R. A. M., & Wensing, J. A. B. (1987). Dominance and its behavioral measures in a captive wolf pack. In H.W. Frank (Ed.), *Man and Wolf* (pp. 219-252). Dordrecht, The Netherlands: Junk Publishers.
- van Noordwijk, M. A., & van Schaik, C. P. (1987). Competition among female long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, 35(2), 577-589.
- van Noordwijk, M. A., & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, 40(1), 105-130.
- van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87, 120-144.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R.A. Foley (Eds.), *Comparative socioecology: The behaviour ecology of humans and other animals* (pp. 241-269). Oxford: Blackwell.
- van Schaik, C. P., & Paul, A. (1996). Male care in primates: does it ever reflect paternity? *Evolutionary Anthropology*, 5(5), 152-156.
- van Schaik, C. P., & van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour*, 85, 91-117.
- van Schaik, C. P., & van Noordwijk, M. A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 105(1/2), 77-98.
- Ventura, R., Majoro, B., Koyama, N. F., Hardie, S., & Schino, G. (2006). Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding, and agonistic support. *American Journal of Primatology*, 68, 1138-1149.
- Vervaecke, H., de Vries, H., & van Elsacker, L. (2000). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). *International Journal of Primatology*, 21(1), 47-68.
- Wahungu, G. M. (1998). Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology*, 36(2), 159-173.
- Wakibara, J. V. (2005). Abundance and dispersion of some chimpanzee-dispersed fruiting plants at Mahale, Tanzania. *African Journal of Ecology*, 43(2), 107-113.
- Walker, S. E., Strasser, M. E., & Field, L. P. (2004). Reproductive parameters and life-history variables in captive golden-bellied mangabeys (*Cercocebus agilis chrysogaster*). *American Journal of Primatology*, 64(1), 123-131.
- Wallis, S. (1983). Sexual behavior and reproduction of *Cercocebus albigena johnstonii* in Kibale forest, western Uganda. *International Journal of Primatology*, 4(2), 153-166.
- Waser, P. M. (1977). Feeding, ranging, and group size in the mangabey *Cercocebus albigena*. In T.H. Clutton-Brock (Ed.), *Primate ecology* (pp. 183-222). NY: Academic press.
- Wasser, S. K. (1993). The socioecology of interspecific associations among the monkeys of Mwanihana rain forest, Tanzania: A biogeographic perspective. In J.C. Lovett & S.K. Wasser (Eds.), *Biogeography and Ecology of the Rain*

- forest of Eastern Africa*. (pp. 267-279). Cambridge: Cambridge University Press.
- Watts, D. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, 21(2), 189-210.
- Watts, D. (2000b). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, 21(2), 211-238.
- Weisbard, C., & Goy, R. W. (1976). Effect of parturition and group size composition on competitive drinking order in stumped macaques (*Macaca arctoides*). *Folia Primatologica*, 25, 95-121.
- White, L. J. T., & Edwards, A. (Eds.). (2000). *Conservation research in the African rain forests*. New York, USA: Wildlife Conservation Society.
- Whiten, A., & Rumsey, T. J. (1973). 'Agonistic buffering' in the wild barbary macaque, *Macaca sylvana* L. *Primates*, 14(4), 421-425.
- Whitesides, G. H., Oates, J. F., Green, S. M., & Kluberanz, R. P. (1988). Estimating primate densities from transects in a west African rain forest: A comparison of techniques. *The Journal of Animal Ecology*, 57(2), 345-367.
- Whitmore, T. C. (1990). *An introduction to tropical rain forests*. Oxford: Clarendon Press.
- Whitten, P. L., & Russell, E. (1996). Information content of sexual swellings and fecal steroids in sooty mangabeys (*Cercocebus torquatus atys*). *American Journal of Primatology*, 40(1), 67-82.
- Wickings, E. J., & Dixon, A. F. (1992). Development from birth to sexual maturity in a semifree-ranging colony of mandrills (*Mandrillus sphinx*) in Gabon. *Journal of reproductive fertility*, 95, 129-138.
- Wieczkowski, J. (2005a). Comprehensive conservation profile of Tana mangabeys. *International Journal of Primatology*, 26(3), 651-660.
- Wieczkowski, J. (2005b). Examination of increased annual range of a Tana mangabey (*Cercocebus galeritus*) group. *American Journal of Physical Anthropology*, 128(2), 381-388.
- Wildt, D. E., Doyle, L. L., Stone, S. C., & Harrison, R. M. (1977). Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during baboon reproductive cycle. *Primates*, 18, 261-270.
- Wilson, W. L., & Johns, A. D. (1982). Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in East Kalimantan, Indonesia. *Biological Conservation*, 24(3), 205-218.
- Wong, S. N. P., & Sicotte, P. (2007). Activity budget and ranging patterns of *Colobus vellerosus* in forest fragments in central Ghana. *Folia Primatologica*, 78(4), 245.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75(3/4), 262-300.
- WTO. (2006). *Yearbook of tourism statistics*. Madrid: World Tourism Organisation (WTO).
- Zinner, D. P., Schwibbe, M. H., & Kaumanns, W. (1994). Cycle synchrony and probability of conception in female hamadryas baboons *Papio hamadryas*. *Behavioral Ecology and Sociobiology*, 35(3), 175-183.
- Zinner, D. P., van Schaik, C. P., Nunn, C. L., & Kappeler, P. M. (2004). Sexual selection and exaggerated sexual swellings of female primates. In P.M.

Kappeler & C.P. van Schaik (Eds.), *Sexual Selection in Primates*: Cambridge University Press

Zuckerman, S. (1937). The duration and phases of the menstrual cycle in primates. . *Proceedings of Zoological society of London*, 107, 315-346.

