

**CONTINGENCY AND CONTEXT IN THE RELATIONSHIPS OF
FEMALE VERVET MONKEYS**

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A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

MASTER OF SCIENCE

Department of Psychology
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

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ABSTRACT

This study explored the organizing principles of female sociality in free-ranging vervet monkeys (*Chlorocebus aethiops*) inhabiting the Klein Karoo, South Africa. Females groomed more than males, grooming peaked at the end of the day and less grooming occurred during the mating season. Although females competed over food, they did not compete over grooming partners, rarely formed coalitions and did not trade grooming against other activities. Instead, they maintained grooming whilst trading between feeding and resting and feeding and moving. Despite seasonal shifts in food competition, grooming was not traded for tolerance and there was an upper limit to cohort size before clique size declined. Inter-population comparisons revealed no troop size effects on clique size, aggression and competition over high-ranking grooming partners. The rarity of coalitions suggests coalitions are unlikely to be a central component of female relationships.

ACKNOWLEDGEMENTS

First, thank you to my supervisors, Dr. Peter Henzi and Dr. Louise Barrett, for providing the wonderful opportunity to embark upon field research in South Africa. Having assisted other researchers with their field projects, I am particularly grateful to have had the opportunity to conduct my own field research. I am also grateful for the guidance I received and for the independence that was instilled in me during this research experience.

Thanks to Mark and Sarah Tompkins for allowing me to carry out my research at Samara Private Game Reserve. Thanks also to Dr. Parry Clarke, Dave McCaffrey, Petra McDougall, April Takahashi and Nicole Whale for their friendship and insightful discussions during my time in the field. Special thanks to Ria Boner for her assistance, friendship and support in the field. To Kitty and Richard Viljoen, thank you for your amazing hospitality and for creating a home away from home.

I am grateful to Ian Griffiths, Kurt Loewen, Patrick M'Gonigle, Peter Mynett and Paul Wolda for lifting my spirits during my time in Lethbridge. Finally, I truly appreciate the continuous support of my family and my dear friends Andrea Vaxvick, Becky Watson, Layla Watson, Lucy Pankhurst and Sarah Friesen.

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CHAPTER ONE

GENERAL INTRODUCTION

It has been argued that there is insufficient empirical evidence supporting the notion that certain crucial activities (e.g. grooming for support, coalitions) constitute appropriate organizing principles for primate sociality (Henzi & Barrett 1999, 2007) and that there is, at present, no conclusive evidence to support the assumed cognitive capacities (e.g. abstract representation, temporal projection) thought to underpin primate social engagement (Barrett & Henzi 2005, Barrett, Henzi & Dunbar, 2003, Roberts, 2002). Thus, although several theoretical models, aiming to ground the study of primate social cognition in its ecological and evolutionary context, have provided great advances in explaining female social relationships, alternative and possibly more realistic explanations of female sociality are now available.

Studies of primate sociality typically involve examination of grooming patterns, with factors such as dominance and competition used to explain variation in grooming interactions (Seyfarth, 1977). Grooming, however, cannot be understood without also considering the manner in and extent to which ecological demands and time budgeting conflicts structure the possibilities for social engagement.

One of the first models to ground the study of female sociality in its ecological context was proposed by Wrangham (1980). Wrangham's model identified food distribution as the primary factor underlying variation in the patterning of female social engagement, categorizing individuals as female-bonded or non-female-bonded according

to their patterns of resource competition. This dichotomous approach, involving the categorization of females, does not however fully capture the complexity of female social interactions. Additional models were subsequently developed to further define competition type, both within and between troops, the role of predation and other food related factors, such as abundance and depletion time (Isbell, 1991, van Schaik, 1989, Sterck, Watts & van Schaik, 1997).

Although the second-generation models recognize the role of ecology in the evolution of female social relationships and provide more detailed explanations of social interaction, females are still confined to categories and are given ambiguous labels (e.g. despotic, egalitarian) to define their social relationships and dominance interactions (Isbell & Young, 2002). Not all primates, however, can be readily compartmentalized into the prescribed categories and neither can they easily be labeled (Barrett & Henzi, 2006, Sterck *et al.*, 1997).

A further point of contention in primate sociality research is the suggestion that grooming is causally linked to coalition formation (Dunbar, 1988, van Schaik & van Noordwijk, 1988, Isbell, 1991). Specifically, females that groom one another are suggested to support one another during agonistic interactions, therefore mitigating the effects of resource competition (Seyfarth & Cheney, 1984, Silk, 1987). However, since an individual's need for support cannot be predetermined, it is suggested that individuals monitor their own grooming relationships and the grooming relations between other group members over time (Dunbar, 1998). Monitoring relationships in this manner is a demanding task requiring flexible cognitive assessment of one's social environment.

According to the ‘social brain’ hypothesis the relationship between grooming clique size, group size and neocortex size reflects the cognitive demands of mentally representing social bonds and alliances through time (Dunbar, 1998). This view of primate sociality and cognition extends neatly from the Machiavellian intelligence hypothesis, which also places emphasis on internal mental representations (Byrne & Whiten, 1988). Furthermore, by directly linking grooming to coalitions, it is implied that primates have the cognitive capacity to think ahead and therefore plan for the future. This proposition has been debated as there is currently limited evidence supporting the notion that monkeys are capable of contingency planning (Barrett *et al.*, 2003, Roberts, 2002).

Moreover, that grooming occurs in the absence of coalitionary aid, coupled with the overall rarity of coalitions among female-bonded primates, suggests coalitions are unlikely to be a central organizing feature of primate social groups and grooming is unlikely to function to secure coalitionary alliances (Barrett & Henzi, 2006, Henzi & Barrett, 1999, Henzi, Lycett & Weingrill, 1997b, Ron, Henzi & Motro, 1996, Silk, Alberts & Altmann, 2004). Coupled with the limited abilities of primates to plan for the future, alternative explanations of how females contend with within group competition and why females persist with grooming in the absence of coalitions are required.

Unlike the Machiavellian intelligence hypothesis, which emphasizes deception and cheat-detection strategies and the need for individuals to out compete one another, and the social brain hypothesis which similarly presents a view of primate cognition based on internal mental representations, a biological market approach has recently been offered as an alternative framework for understanding primate sociality (Henzi & Barrett, 1999, Noë, van Hooff & Hammerstein, 2001). In a biological market individual members

of a group are considered traders, exchanging commodities in a manner that maximizes their fitness. Specifically, trading decisions are contingent upon the dynamics of the local socio-ecological environment in which the availability of commodities and partner value fluctuates over time. Thus, although sociality is considered the driving force behind brain evolution, biological markets differ from the Machiavellian intelligence hypothesis in that it does not assume evolution has selected for the use of temporal tactical social strategies. Rather, it is the need to monitor fluctuations in commodities and the value of partners that is believed to have driven primate brain size and structure (Barrett *et al.*, 2003).

Like the Social Brain hypothesis, which emphasizes that being embedded in a social world has selected for greater intelligence, the Biological Market paradigm also recognizes primates as embedded in, and responding to, a continuously changing environment (Dunbar, 1998, Barrett & Henzi, 2001). However, given that primates face ecological problems, and these are suggested to be no different than those experienced by other mammals (Humphrey, 1976), the primary difference between a more cognitive approach to understanding sociality and the Biological Market paradigm lies in latter recognizing that an individual's response to their socio-ecological environment involves contingency and therefore variability (Barrett, 2009). Specifically, it has been suggested that social complexity is not the only force selecting for greater brain size among primates, but rather it is the fluctuations in the social and ecological environment over time that has played a key role in this process (Barrett, Henzi & Rendall, 2007). Assessing the contingent nature between an animal and their interaction with the environment is therefore key to understanding social engagement, and it is the

contingency of social engagement that must be acknowledged if we are to explore and further our understanding of the social complexities of primate groups.

Recognizing the dynamic nature of sociality and assessing its inherent complexities is likely to provide a more ecologically valid approach to understanding primate sociality and more broadly, primate social cognition. This has been the focus of primate socio-ecology for approximately the past 50 years. During this time much research has been conducted on female-bonded primates (Wrangham, 1980). In female-bonded societies, females remain in their natal group for life (female philopatric) and form strong social bonds. Females are able to capitalize on the predator detection benefits offered by group life but also face costs associated with intra-group competition over access to resources (Dunbar, 1988).

A females' ability to compete and access resources is influenced by her social rank. Rank not only affects the amount of effort a female exerts when locating food but also influences her spatial positioning within the group. Low ranking females, for example, exhibit greater foraging effort and are more likely to be dispersed, or on the periphery of the group, than higher-ranking females. Lower ranking females subsequently have less time available for social engagement and their spatial positioning within the group reduces affordances for social engagement (Henzi *et al.*, 1997b, van Schaik & van Noordwijk, 1988).

Viewing animals as embedded in a socio-ecological environment requires not only consideration of the effect of social rank, but also the effect of ecological and temporal factors, such as climate and variation in day length, on activity and socio-spatial

patterns. Climatic variables such as rainfall and temperature play a key role in seasonal changes in food availability with feeding time being structured not only by rank, but the availability, quality and distribution of food (Agetsuma, 1995, Clutton-Brock, 1977, Davidge, 1977, Deshmuck, 1984, Iwamoto & Dunbar, 1989, Lawes & Piper, 1992, Roberts & Dunbar, 1991, Rutherford, 1980).

Day length also structures individual activity patterns. As day length varies across the year the amount of time available for individuals to meet their needs (e.g. nutritional needs) also fluctuates across the year. Moreover, that the allocation of time to feeding determines the time remaining for non-feeding activities means activities such as social grooming may be constrained as day length decreases during the winter months (Altman, 1982, Dunbar, 1992). However, despite social, ecological and temporal demands, individuals do not appear to compromise the amount of time they allocate to social engagement and, where possible, try to sustain their grooming cliques (Dunbar & Dunbar, 1988, Dunbar & Sharman, 1984, Henzi *et al.*, 1997b, Iwamoto & Dunbar, 1989, Pazol & Cords, 2005).

Aims of the current study: The study of sociality among Old World monkeys inherently involves exploration of social grooming relations and the extent to which the time available for social interaction is structured by activities such as feeding, and socio-ecological factors such as day length, time of day, seasonality and dominance rank. An understanding of social relations not only requires assessment of such factors but also consideration of the fact that for female philopatric primates, such as vervets, being unable to leave the natal group and competing with relatives over resources provides an interesting quandary, raising questions on how females that compete with their relatives

and who face possible reproductive costs associated with group life, deal with within-group competition.

Given that coalitions are unlikely to be the primary means by which females mitigate the deleterious effects of competition on reproductive success and considering that the local environment in which an animal is situated not only structures, but also constrains action, the current study will aim to explore the ecological structuring of social opportunity and the patterning of sociality in two large groups of free-ranging vervet monkeys (*Chlorocebus aethiops*).

CHAPTER TWO

GENERAL METHODOLOGY

2.1 Study Animals

2.1.1 Taxonomic affiliation

As the largest group of African primates, the guenons are comprised of at least 23, and as many as 36 species, including vervets, which are distributed throughout sub-Saharan Africa (Groves, 2001, Grubb *et al.*, 2003). There has, however, long been some debate regarding the taxonomic classification of *Cercopithecine* monkeys (Enstam & Isbell, 2007, Tappen, 1960). Specifically, *C. aethiops* have been separated, based on morphological differences, from this species group and the genus *Cercopithecus*, such that they are now considered to have their own genus, *Chlorocebus* (Groves, 2001). Thus, the guenons, also including *Allenopithecus*, *Erythrocebus* and *Miopithecus*, are not a group belonging to a single genus. In fact, it was approximately ten million years ago that the guenon group (Cercopithecini) separated from the baboon, macaque, and mangabey group (Papionini: Cords, 1987).

Guenons are generally characterized as diurnal, small to medium bodied monkeys weighing an average of 3.6 kg for females and 5.9 kg for males (Haltenorth & Diller, 1988). Vervets (*C. aethiops*), specifically, have a silvery grey coat with a white band of fur across the brow area, black skin on their face, hands and feet and blue skin on their abdomen, which is covered by light grey-white fur. Males have brightly coloured

genitalia (blue scrotal area and a red penis) and are larger bodied than females. Males, on average, weigh 5.5 kg and females 4.1 kg (Cawthon Lang, 2006).

2.1.2 Distribution of Vervets

Vervets (*C. aethiops*) are widely distributed throughout Africa, inhabiting most countries on the continent and, following their introduction to the islands of St. Kitt's, Barbados, during the 17th and 18th century, they are also found in certain parts of the Caribbean (Chapman & Fedigan, 1984, Tappen, 1960). The fundamental difference between vervets and forest guenons is that the latter are generally bound by tree cover as a consequence, mostly, of anatomical adaptations to arboreality. That vervets are described as opportunists is derived from their ability to feed on a wide variety of foods and traverse a diverse range of habitats (Fedigan & Fedigan, 1988). With this flexibility, vervets are able to exploit less desirable habitats and overcome the demands of environmental change faced by species exhibiting habitat and nutritional specialization (Fedigan & Fedigan, 1988, Poche, 1976).

Also, despite their ability to reside in marginal habitats, vervet distribution is constrained by seasonal variation in food availability and, due to their territoriality, is restricted to areas of water availability, facing increased risk of mortality during periods of prolonged water absence (Fedigan & Fedigan, 1988, Struhsaker, 1967a, Wrangham, 1981). A further restriction, imposed by the risk of predation, is the availability of sleeping trees, which provide safety from predators during the night (Chapman & Fedigan, 1984, Fedigan & Fedigan, 1988, Nakawaga, 1999, Wahungu, 2001). Home

range size is variable, with the smallest average range reported for St. Kitts vervets (.06 km²) and the largest for vervets in Senegal (1.78 km²) (Harrison, 1983).

2.1.3 Ecology and Habitat

Vervets are habitat generalists, occupying a wide range of habitat types, including semi-desert environments, savannah, woodlands, swamps and urban areas (Fedigan & Fedigan, 1988). Although they show great adaptability, they exhibit a preference for riverine woodland and are more reliant on the availability of trees than patas monkeys (*Erythrocebus patas*), which are also semi-terrestrial guenons (Cords, 87, Fedigan & Fedigan, 1988, Strasser, 1992, Struhsaker, 1967b). As omnivores (Whitten, 1983), vervets feed on a wide variety of foods, including fruits, flowers, fungi, grasses, gum, leaves, shoots, insects, lizards and birds' eggs (Fedigan & Fedigan, 1988). Furthermore, one member of the vervet group, the Bale monkey (*Chlorocebus djamdjamensis*, Mekonnen, Bekele, Fashing, Hemson & Atickem, 2010), has been reported to eat mostly bamboo leaves. Such variety in diet can be attributed to seasonal variation in food availability and the ability to adapt to fluctuations in ecological resources (Harrison, 1984). Resource availability can influence vervet population density with as few as 9 and as many as 225 individuals reported in areas of limited or rich resources, respectively (Harrison, 1983).

2.1.4 Seasonal Breeding

South African vervets breed for approximately three months of the year, typically commencing towards the end of April. Gestation subsequently lasts, on average, 163 days

(Melnick & Pearl, 1987). Variation in resource availability, particularly food availability, has been suggested to play a role in vervet breeding, which occurs seasonally, around the time of year when food is most abundant. It is possible, in African guenons, that following the rainy season, increased food availability and diversity and changes in range size may reduce nutritional and energetic stress for the mother and infant and thus promote survival (Baldellou & Adan, 1997, Butynski, 1988, Melnick & Pearl, 1987). Births typically occur over a period of approximately three months spanning September, October and November, with few births occurring after the primary birthing season in December (Butynski, 1988).

2.1.5 Social Organization

Vervets live in multi-male, multi-female groups with an average of 25 animals in a group and an average sex ratio of 1:5 (Fedigan & Fedigan, 1988, Struhsaker, 1967b). Groups of as few as 5 and as many as 76 animals have, however, been reported (Fedigan & Fedigan, 1988). Whereas males reach sexual maturity at around five years of age, females are considered sexually mature around four years of age, having their first infant at approximately age five with inter-birth intervals ranging from 11 to 24 months (Cheney, Seyfarth, Andelman & Lee, 1988, Melnick & Pearl, 1987).

Unlike females, who typically remain in their natal troop, males emigrate between troops upon reaching sexual maturity and continue to transfer several times throughout their lifetime (Melnick & Pearl, 1987). During transfer males are vulnerable to the risk of predation and attack from other troop members. These costs may, however, be reduced if a male transfers with another male. In addition, inter-troop transfer reduces the risk of

males inter-breeding with their sexually mature female offspring and typically occurs during breeding season (Cheney & Seyfarth, 1983). Also, male dispersal patterns and the associated risk of mortality, related to the risk of predation and attack from other troop members, during inter-troop transfer, may, among other factors, contribute to the female-biased adult sex ratio (Henzi & Lucas, 1980).

Females acquire a position in the dominance hierarchy that is similar to their mothers rank. Maternal rank inheritance is possible because females are philopatric, typically remaining in their natal troop, with female relatives, for life. Thus, female offspring obtain a rank that is below their mothers' position in the hierarchy, which usually remains stable over time unless there are female deaths within the troop (Fairbanks & McGuire, 1985). In contrast, due to male emigration, maternal rank is not a reliable indicator of male dominance. Thus, within their multi-male, female-bonded troops, the female dominance hierarchy is characterised as linear and stable (Isbell & Pruett, 1998) whereas male dominance varies depending on the outcomes of agonistic interactions with other males.

2.2 Study Site

Data were collected on two troops of free ranging vervet monkeys at Samara Private Game Reserve, Eastern Cape, South Africa (32°22S, 24°52E). Samara, located in the Plains of Camdeboo, South-East of the town of Graaff Reinet, contains four of South Africa's seven biomes, including Grassland, Nama-Karoo, Valley thicket and Savannah (Rutherford & Westfall, 1986).

2.2.1 Climate and Seasonality

In the Karoo, the winter season typically ranges from May to September and the summer ranges from October to April (Dean & Milton, 1999). During the study period, mean monthly precipitation is approximately 15.07mm, with most rain falling over the summer (Figure 2.1). Mean monthly temperature is 18°C, with an average winter temperature of 5°C and an average summer temperature of 20°C (Figure 2.2). The average summer day length is 12.96 (hr, min) and the average winter day length is 10.76 (hr, min).

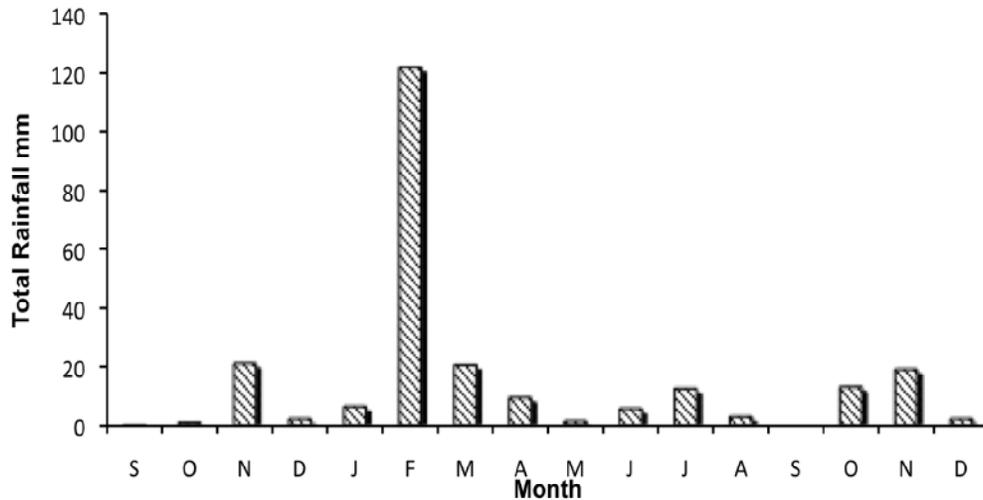


Figure 2.1. Total rainfall (mm) per month, for the town of Graaff Reinet, 33km from the study site, during the study period (only total values were available: September 2008-December 2009).

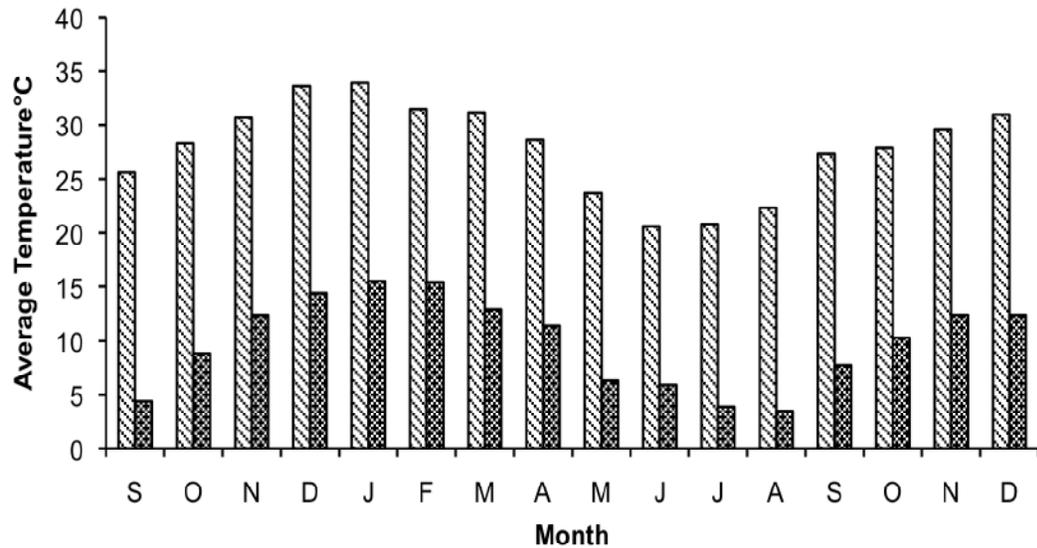


Figure 2.2. Mean (Cross hatch: Min., Diagonal: Max.) temperature values (°C), for the town of Graaff Reinet, 33km from the study site, across the months during the study period (September 2008-December 2009).

2.2.2 Fauna and Flora

A variety of mammal species are found at Samara and include large mammals such as Cape buffalo (*Bubalus bubalis*), eland (*Aurotragus oryx*), gemsbok (*Oryx gazella*), giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcelaphus caama*), kudu (*ragelaphus strepsiceros*), white rhino (*Ceratotherium simum*), black wildebeest (*Connochaetes gnou*), Burchell's zebra (*Equus quagga burchellii*) and Cape Mountain Zebra (*Equus zebra zebra*). Smaller ungulates include the common duiker (*Sylvicapra grimmia*), blue duiker (*Philantomba monticola*), springbok (*Antidorcas marsupialis*) and steenbok (*Raphicerus campestris*). Carnivores are represented by cheetah (*Acinonyx*

jubatus), caracal (*Caracal caracal*) and jackal (*Canis mesomelas*). Primates are represented by both vervet monkeys (*C. aethiops*) and baboons (*Papio hamadryas*).

Samara's primary biomes are grassland, Nama Karoo (Karoo bushland), valley thicket and savannah. Grassland biomes include sweet and sour grasses, which grow predominantly in summer rainfall areas. Nama Karoo consists of grasses and dwarf shrub land. As with the former biomes, savannah includes grasses, intermingled with dwarf shrubs (See Figure 2.3 for main food items). The study population at Samara mostly occupy valley thicket along streams although smaller groups use Karoo bushland in the vicinity of artificial waterholes. These areas include several tree species that vervets incorporate into their diet, including acacia (*Acacia karoo*), karee (*Rhus lancea*) and Peruvian pepper (*Schinus molle*). Peruvian pepper trees predominate each of the study troops sleep sites, which are located by the riverbed, providing access to water when the river flows or when catchments form following downpours. At times, water is very limited, resulting in intra and inter-troop competition (McDougall, Forshaw, Barrett & Henzi, 2010).



Figure 2.3. Top left: Peruvian pepper corns, Right: Succulent, Middle Left: Acacia flowers, Right: Dwarf Shrub Fruits, Bottom Left: Grass, Right: Succulent Flowers.

2.3 Study Troops

The two troops of vervets were located in adjacent territories (both ~25ha) along the Milk River (Figure 2.4), which only flows during times of heavy rain, leaving water catchments that are replenished following further rain. During the course of the study the River-bend Mob (RBM) utilized four sleep sites, located at different points along the river. The Riverside Troop (RST) utilized two sleep sites, also located along the river. RBM and RST shared one of their sleep sites following a period of low rainfall during the summer of 2008 (McDougall *et al.*, 2010). Although there were a couple of occasions when the two troops spent the night at the same sleep site, the two troops typically slept at separate sleep sites.

Although one of the troops (RST) had received some intermittent habituation for three months in 2007, the first two months (September, October 2008) of this study were spent habituating the animals in each of the two troops. This involved locating and following the animals on foot as they ranged throughout their territory. Data collection began in November 2008 when the animals ceased running away from the observer and could be followed $\leq 10\text{m}$ and identified using individual markings of sub-adult and adult males and females.

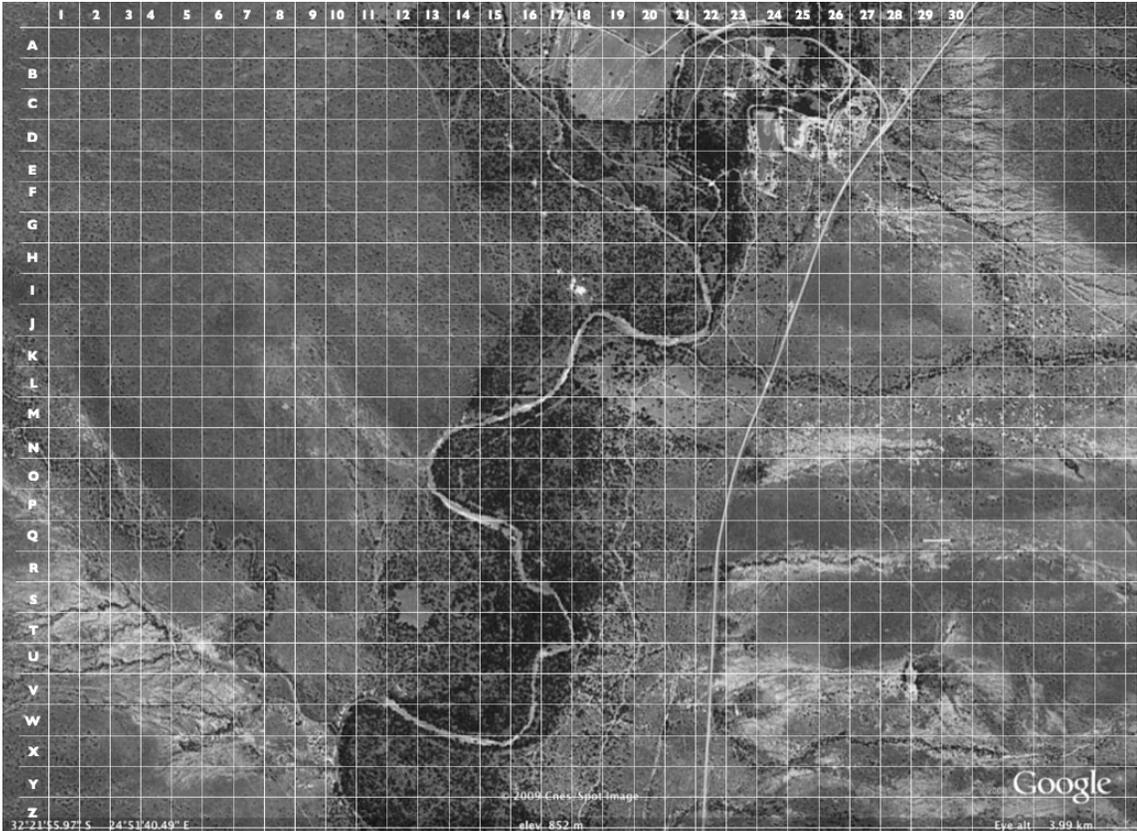


Figure 2.4. Aerial view of the study area running along side the Milk River. Aerial photograph courtesy of Google Earth.

2.3.1 Demographic Structure of Study Troops

The two troops, RBM and RST in this study are approximately two times larger than the average vervet troop reported in other field sites (Fedigan & Fedigan, 1988). Specifically, vervet troop sizes in this study consist of 72 and 48 individuals for RST and RBM, respectively. In contrast, vervet troops elsewhere consist, on average, of 25 individuals (Fedigan & Fedigan, 1988). Troop size and composition are presented in Table 2.1. The demographic structure of other vervet troops in South Africa is similar to that of the two troops in this study. Specifically, vervet troops are reported to consist of

more females than males (1:3.4) and to have a high number of infants and juveniles (12.3 individuals; Henzi & Lucas, 1980).

Table 2.1. Troop size, composition and sex ratio for the two study troops at the start of data collection.

	RBM	RST
Adult Males	11	12
Sub-Adult Males	0	2
Adult Females	13	19
Sub-Adult Females	2	5
Juveniles and Infants	22	31
Troop Size	48	69

Troop sizes varied throughout the study due to births, deaths and migrations, in and out of the troops. During the months of October and November 2008, 9 infants were born in RBM and 13 infants were born in RST. Between the months of October and December 2009, 10 infants were born in RBM and 7 infants were born in RST. The majority of births in RBM and RST with known dates occurred during the months of October (15 births) and November (12 births) in 2008 and 2009. Specifically, 80% of births in RBM occurred during October and 20% occurred during November. For RST, 38.89% of births occurred in October, 55.56% occurred in November and 5.56%

occurred in December. That the majority of births occurred over a two month period illustrates there is a birthing peak (Fedigan & Fedigan, 1988).

Data on immigrations into and out of the study troops were only available for the year of 2009. In 2009, 11 adult males and one adult female immigrated into RST. Of these immigrants, 7 males were observed to copulate with resident females during the study. In contrast, only one adult male immigrated into RBM during 2009 and was not observed to copulate with resident females during the study. Furthermore, five RBM males and four RST males, that were present from the start of the study in September 2008, left their troops during 2009. It is thought that these males emigrated into other troops as there was no sign of predation or other possible causes of death around the time of their departure. In contrast, two RST adult females and one sub-adult female, also present from the start of the study, were absent from their troop during 2009. That the females appeared to be healthy prior to their disappearance and fur and skull remains were found only days prior to the sub adults' disappearance, suggests predation was responsible for the loss of these females. The majority of individuals in RBM and RST left their troops at the peak of the breeding season during the month of May 2009 (Figure 2.5: excludes suspected predator related disappearances).

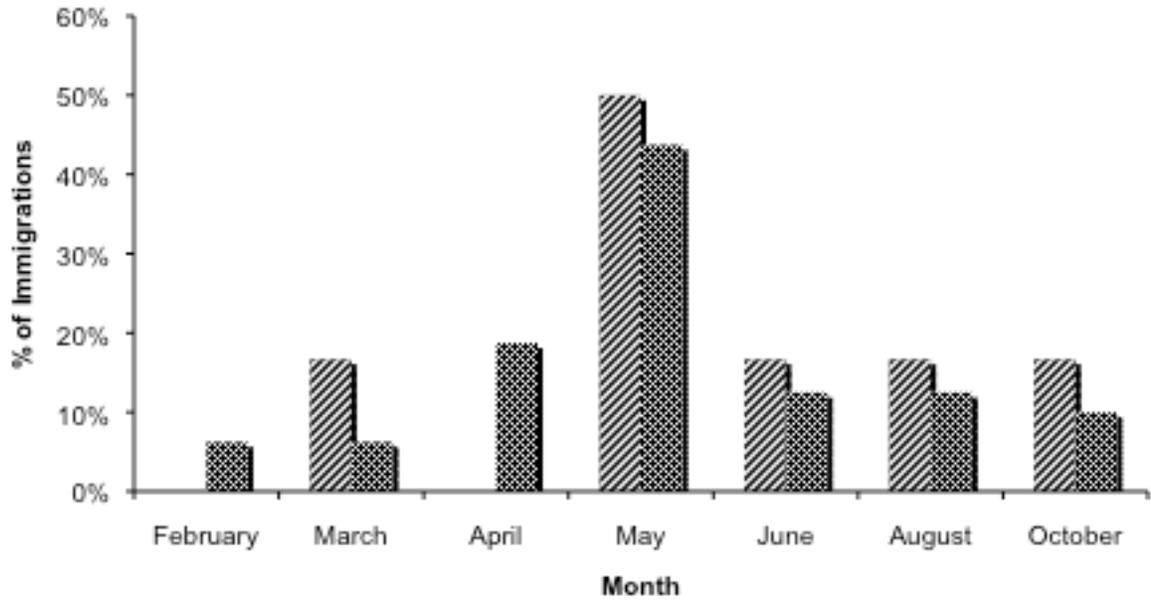


Figure 2.5. The percentage of immigrations during the months in which males and females were observed to leave their troops in 2009 (RST: Cross hatch, RBM: Diagonal).

2.4 Data Collection

Data collection began in November 2008 when the animals could be followed, after 8 weeks of habitation, at a distance of $\pm 10\text{m}$. All adults and sub-adults were identified using a variety of characteristics, including body size, facial features (e.g. brow width/length), tail length, coat colour and, more specifically, by any scars or wounds incurred on their face, body and, or tail (e.g. Figure 2.6).

The monkeys were followed on foot for 10 hours per day, weather permitting, at an eventual distance of 3-5m. To ensure data were collected evenly during the day, each day of data collection was divided into four equal time blocks, ranging from 05:00 – 18:30 and lasting 2 to 3.5 hours each.



Figure 2.6. The female on the left has a tear in the top edge of the left ear. Light white markings are present directly under both eyes with the right being more pronounced than the left. Also, her brow is straight. The female on the right has extensive white markings around the eye and chin area. Her brow is slightly furrowed.

2.4.1 Sampling Procedures

Data, including Focal Animal Sampling, Instantaneous Point Sampling, All Occurrence Sampling and *Ad libitum* Sampling (Altman, 1974) were collected using a Palm Tungsten™ E2 Handheld with Pendragon Forms Manager 5.1 (2005-2007, Pendragon Software Cooperation). No subject was focal sampled consecutively on a given day, while within a given month, an attempt was made to balance each of the subjects focals across time blocks and to follow both troops for an equal number of days. A minimum of 8hr 53min (8hr 53min-25hr 13min) of focal data were collected on a

single RST female and a minimum of 5hr 58min minutes (5hr 58min- 22hr 40min) of focal data were collected on a single RBM female (Table 2.2). For RST, 10 minute focal sampling of sub-adult and adult females began in November 2008 but, as of April 2009, habituation of the animals had improved such that the focal sample duration was increased to 16 minutes. For RBM, 10 minute focal sampling began in January 2009 and was also increased to 16 minutes in April 2009. Focal sampling for both troops continued until mid December 2009.

2.4.1.1 Focal Animal Sampling

Focal Sampling was used to continuously sample a focal animal for a predetermined amount of time. A focal sample provides a comprehensive record of all the acts a focal animal engages in and all the individuals the animal interacts with (Altman, 1974). The date, time, focal animal ID, general troop activity and location were all recorded at the start of each focal. If the animal was out of view for more than half the total duration of the focal sample, the sample was terminated. Furthermore, if a social interaction (i.e. allogrooming, aggression, infant interaction) occurred between two adult females, the focal sample was subsequently extended by 5 additional instantaneous scan samples, equivalent to approximately 10 minutes. Extending the focal sample provides information on the context in which social interactions continue and, or cease to continue. An ethogram (Table 2.3) was developed based on preliminary observations of the animals during the first 8 weeks of habituation.

Focal samples involved continuous sampling methods to capture the duration of the following individual states: resting, moving, foraging, drinking, autogrooming

(including scratching) and time out of view. Events were also recorded during focal samples and included the following social interactions: allogrooming, aggression, copulation and play (Table 2.4, Appendix A).

During a focal sample, proximity maintenance was measured by recording all approaches and withdrawals. Approach and withdrawal interactions were initiated either by the focal animal or a social partner and occurred whenever individuals came within (approach) or beyond (withdrawal) a two-meter radius of one another. As the focus was on female-female interactions, a two-meter radius was considered a sufficient distance to determine who was responsible for the maintenance and termination of proximity interactions.

2.4.1.2 Instantaneous Scan Sampling

Spatial relations were also monitored using nearest neighbour information. The ID and distance of all adult males, adult females, sub-adult males and sub-adult females and the distance of juveniles within a five-meter radius of the focal animal were recorded immediately prior to starting a focal sample, as well as every two minutes during the focal sample. Initially, when focal samples were ten minutes in duration, 6 nearest neighbour scans were recorded, then, once focal samples increased to 16 minutes, 9 scans were recorded.

Table 2.2. Hours (hr, min) of observation per month, per troop.

Month	Observation Hours RST	Observation Hours RBM
<i>2008</i>		
November	5hr	0hr
December	14hr 16min	0hr
<i>2009</i>		
January	23hr 43min	4hr
February	29hr 13	12hr 50min
March	27hr 11min	14hr 23min
April	29hr 23min	16hr 3min
May	33hr 18min	11hr 58min
June	19hr 35min	9hr 18min
July	47hr 15min	19hr 8min
August	26hr 21min	30hr 46min
September	36hr 36min	34hr 45min
October	34hr 43min	34hr 53min
November	52hr 3min	34hr 23
December	19hr 31min	13hr 3min
Total	398hr 8min	235hr 30min

2.4.1.3 Half Hour Troop Scans

Scan samples were taken at thirty minute intervals and included the ID, activity, location and nearest adult male and adult female neighbour of each visible animal scanned in a five minute period. Activity was recorded as falling in one of the following

nine categories: aggression, allogrooming, autogrooming, drinking, feeding, moving, playing, resting and other (see Table 2.3 for definitions). Locations were categorised as ground, open ground (no environmental substrate e.g. tree, shrub or rock, was ≤ 2 m of the animal), shrub and tree. Nearest neighbour distances ranged from contact to 20 m+ (0m, 1m, 2m, 3m, 5m, 10m, 15m, 20m, 20m+) and included a 'not visible' category. A total of 16268 scan samples were collected on both troops between November 2008 and January 2010.

2.4.1.4 *Ad Libitum Data Collection*

a. To determine the dominance of sub-adult and adult females in each of the two troops, a dominance matrix was generated for both troops based on the outcomes of *ad libitum* female-female dyadic agonistic events (Altmann, 1974). Females were subsequently arranged in the matrix according to wins and losses and the interactions were organized such that the number of reversals was minimized (Tables 2.5 and 2.6).

b. A daily census of all sub-adult and adult males and females was recorded, as was any information related to injury, predation events and birth dates.

2.4.2 *Data Analysis*

Analyses were conducted using JMP 8 software program and SPSS 18 software program. Where appropriate, statistical significance (alpha level) was set at $p = 0.05$. See 'Statistical Notes' in each data chapter for further details.

Table 2.3. Definitions of the behaviours used during each phase of the study.

Behaviour	Definitions
<i>General:</i>	
Autogrooming	Involves an animal combing through its fur with its hands and/or mouth. A new grooming bout is recorded after the animal ceases grooming for five seconds. Also includes scratching - rough movement of hands or feet across the fur. A new scratching bout is recorded after the animal ceases scratching for five seconds.
Resting	The animal is stationary, typically in a sitting or lying position but occasionally also standing.
Moving	The animal is moving, typically on the ground, in trees or shrubs, on all four limbs.
Feeding	Actively searching for or consuming food items.
Out of View	The animal is not within the sight of the observer.
<i>Proximity Maintenance</i>	
Neighbours	Consists of sub-adults and adults within a 5m radius of the focal animal. The number of juveniles was also recorded.
Approach	Involves the animal moving to within 2m of another animal.
Leave	The animal moves more than 2m away from another.

Social

Allogrooming

Involves one individual grooming the recipient with its hands and/or mouth. An animal can solicit allogrooming by exposing an area of its body, usually by stretching or presenting its hindquarters, to their social partner. Refusal occurs if solicitation is ignored. In addition, a new grooming episode is recorded after a five second break in grooming and changes in the direction of grooming can occur when partners switch roles between groomer and groomee.

Aggression

Involves both physical and non-physical agonistic interactions. The former includes biting, swiping and grabbing and the latter involves chasing, supplants, displacements, eyelid threats, lunges and vocal threats.

Bite - aggressor clenches their teeth on to part of the recipients' body. The recipient's skin may or may not be pierced.

Swipe - aggressor reaches out in a swift motion towards the recipient. Contact is typically not made with the recipient.

Grab - Aggressor reaches out and using their hand/s clasps on to part of the body and, or fur of the recipient.

Chase - aggressor moves directly towards the recipient and continues to do so as the recipient moves away.

Supplant - aggressor takes the spatial location of, and engages in the activity of another animal.

Displacement - change of location following movement by the aggressor.

Aggression

Cont'd.

Eye-lid threat – the pink area of the eye-lid is exposed as the animal raises their brow.

Vocal threat – aggressor directs a vocalization towards the recipient.

Coalitions can also occur whereby a third party joins one of the animals already involved in the social interaction.

Participation can be passive (stands in proximity to one of the partners) or active (physical or non-physical aggression). The recipient of aggression can respond with physical and non-physical counter attacks or may retreat by walking or running away.

Copulation

Males or females can initiate copulation. Females initiate copulation by presenting their hindquarters to the male. The male solicits copulation by placing his hand/s on the females' hindquarters. During copulation the male clasps the females hindquarters with his feet and thrusts. The copulation can be completed, interrupted by a third party, or resisted by the female.

Females refuse solicitations by directing aggression (non/physical) towards the male. Males can refuse solicitations by ignoring and or walking away from the female.

Table 2.5. RST adult and sub-adult female dominance matrix.

		Wins																								
		Sm	Me	PJ	Iz	Al	Wi	Do	He	El	Cl	Um	Ni	Ru	Te	Xa	Gl	Vv	Zi	Li	Je	Fe	Safi	Ki		
Losses	Sm	■	14	2	3		9	14	2	1	3	3	4	9	5		4			2	2	9	2	3	91	
	Me	3	■	5	13		9	6	4	2	4	5	3	2	5		2			12	4	7	12	8	4	107
	PJ			■	13	1	9	16	9	2	4	4	7	8	4	4	1	1		11	9	10	12	5	8	138
	Iz	1	2	4	■	6	7	23	9	3	2	4	4	7	5	3	6	1		9	7	4	21	2	10	133
	Al					■	4	1	3			6	1	9	4	1	2			2	2				3	38
	Wi		1				■	2	3	2	2	9	2	5	1	6	3			5	9	4	13		2	68
	Do		1		1	2	2	■	10	1		9	14	10	6	1	3	2		13	17	5	11		1	103
	He						1		■	3	2	13	7	14	6	12	3	2		10	13	13	13		14	125
	El									■	4	2	3	1	6				1		2	3			2	24
	Cl										■	8	5	2	3	3			1	2	3	4	9	1		41
	Um							1				■	6	4	1	1			2	5	6	2	1		2	30
	Ni		1							2	1	1	■	6	7	1	2	3		9	3	12	8		6	57
	Ru		1	1										■	6	2	3	5		7	16	7	14		9	69
	Te											3			■	9	4	7		20	20	5	12		16	93
	Xa		1				2						1			■	2	1		6	4	2			2	17
	Gl														1		■				3	5	1		4	13
	Vv																	■				3	4		1	8
	Zi																		■		2	9	3		2	16
	Li																			■	32	18			24	74
	Je																				■	8	1		3	12
Fe										1		1	1					2	7		■			14	14	
Safi																	1					■		1	1	
Ki													1					1	1	1	1			■	0	
	4	7	5	1	2	5	0	1	2	2	8	2	5	0	0	1	3	10	1	1	1	0	0	0		

Note. 'Al' last seen on 25 April 2009, 'Fe', 'Ni', 'Zi' and 'Safi' were sub-adults at the start of the study.

Table 2.6. RBM adult and sub-adult female dominance matrix.

Wins

	Am	Sa	Fa	Lo	Mi	Pe	Ka	Ts	Va	Ds	Gi	Oc	Ro	Sc	Ho	
Am		12	3	10	5	6	2		7	2	9	6	3	5		70
Sa	1		3	12	10	6	1	10	1	7	6	12	12		15	95
Fa				3		6	1	2	2	2	1	1	1			19
Lo		1			4	2		1		2	3	4			5	21
Mi						5	2	5	2	10	5	5	1		11	46
Pe				2			3	1			2	1	1		4	12
Ka										1						1
Ts					1					2	2	2	1	3	5	15
Va											1					1
Ds												6	8	1	7	22
Gi							2		3				4		9	13
Oc		1		2	2					2				1		1
Ro										1	1				5	5
Sc										1					2	2
Ho												2				0
	1	2	0	4	3	0	2	0	3	4	1	2	0	0	0	

Losses

Note. 'Ds' and 'Ho' were sub-adults at the start of the study.

CHAPTER THREE

SOCIO-ECOLOGICAL CONSTRAINTS ON TIME BUDGETS

3.1 The Importance of Time Budgeting

The division of time and energy between activities has implications for an animal's survival and reproduction (Watts, 1988). Specifically, feeding provides energy for reproduction, travelling and social interaction, whilst resting allows for the conservation of energy (Herbers, 1981, Korstjens, Lehmann & Dunbar, 2010, Muruthi, Altmann & Altmann, 1991). Thus, when an animal's time budget is constrained, perhaps as a consequence of group size, variation in day length or increased energetic demands, the stability of social relationships and individual fitness may be compromised (Dunbar, 1988). Fitness is broadly determined by an animal's ability to forage and avoid predation and disease (van Schaik, van Noordwijk, Boer & Tonkelaar, 1983, Krebs & Davies, 1993). Specifically, for males, lifetime reproductive success is related to obtaining food, maintaining safety and foremost, accessing mates (Wrangham, 1980). In contrast, female reproductive success is characterized by a high-investment reproductive strategy that depends primarily on birth rate, infant survival and reproductive lifespan and is limited mostly by ecological resources (Gaulin & Sailer, 1985, p.112, van Noordwijk & van Schaik, 1987). Thus, the socio-ecological constraints experienced by the two sexes should also be reflected in their time budgets and patterns of association.

3.2 Costs and Benefits of Group Life

It is the case for most diurnal primate species that group life enhances reproductive success by virtue of resource defense and reduced predation risk (Krebs & Davies, 1993, van Schaik, 1983, Terborgh & Jansen, 1986, Wrangham, 1980). There are, however, costs associated with sociality. The primary cost is related to competition for access to limited resources (Krebs & Davies, 1993, Ron *et al.*, 1996, Terborgh & Janson, 1986, Walters & Seyfarth, 1987). Competition can be direct (contest competition) or, perhaps more commonly, indirect (scramble competition) and is influenced, in part, by the availability and distribution of resources (Janson & van Schaik, 1988, van Schaik & van Noordwijk, 1988, Sterck *et al.*, 1997). Contest competition is related to dominance such that when high-ranking individuals monopolize food resources, the feeding success of lower-ranking individuals is potentially compromised. In contrast, scramble competition is related to group size whereby an individual's ability to access resources is influenced by depletion previously incurred by other group members (van Schaik & van Noordwijk, 1988, Sterck *et al.*, 1997).

There are a variety of resources over which individuals may compete. These include competition over safe spatial positions, food, water and mates (Cowlshaw, 1997, Krebs & Davies, 1993, Ron *et al.*, 1996, van Schaik & van Noordwijk, 1988, Terborgh & Janson, 1986, Walters & Seyfarth, 1987). Males may compete against one another for access to reproductive females and females may compete against one another for access to ecological resources, such as food (Dunbar, 1988, Wrangham, 1980). Thus, although predator avoidance and inter-group resource defense are, amongst other factors,

important forces selecting for group living, individuals living within a group also incur costs (Hamilton, 1971, Krebs & Davies, 1993).

3.3 Feeding Competition

In mammals, it is the differential reproductive effort of males and females that makes females more vulnerable to feeding competition (Dunbar, 1988, Trivers, 1972). Feeding competition is dependent on group size, food patch size and the density and dispersal of food resources (Wrangham, 1980, van Schaik & van Noordwijk, 1986, Whitten, 1983). Depending on its severity and an individual's social rank, resource competition can potentially reduce a female's reproductive success (Isbell, 1991, Whitten, 1983). Competition also has social consequences, which are dependent on the form it takes. When scramble competition, associated with low quality dispersed resources, is prevalent, individuals do not compete directly with one another for access to resources. However, when contest competition, associated with high quality clumped resources, is prevalent, individuals exert their dominance and compete directly with one another by engaging in agonistic interactions (Pazol & Cords, 2005, Sterck *et al.*, 1997). Females should therefore benefit from adjusting their behaviour or developing strategies to minimize the impact of intra-group contest competition and, where possible, maximize their reproductive advantage over other females (van Noordwijk & van Schaik, 1987).

According to Isbell (1991), individuals can reduce feeding competition by foraging on dispersed rather than clumped foods. Subordinates could also forage for food items that are less likely to be competed for (e.g. lower quality foods). Doing so, however, requires individuals to forage for longer so as to compensate for the lower

nutritional content of the foods they are eating (Agetsuma, 1995, 1998, Dunbar, 1992). Alternatively, depending on the species, individuals could minimize competition by using a social and, or locational strategy such as emigrating into a smaller group or splitting off with other individuals to create their own group (van Noordwijk & van Schaik, 1987, Isbell & van Vuren, 1996).

For female philopatric primate species, such as vervets, movement of females between troops is somewhat restricted and emigration, or fission, is likely to be an act of last resort, especially if smaller groups are at greater risk from predators or competition from neighbouring groups (Cowlshaw, 1997, Isbell & van Vuren, 1996, van Noordwijk & van Schaik, 1987, Wrangham, 1980). Thus, in the presence of cost-effective resources, females should remain in their natal groups and attempt to minimize the risk of resource competition while maximizing feeding efficiency. Doing so is important because if a female can maximize her feeding efficiency there will potentially be more time available for engagement in other fitness-enhancing activities, such as social interaction.

3.4 The Effects of Rank on Dispersion and Time Budgets

Rank-related behaviour patterns are likely to emerge when female reproductive success is limited by the availability of resources, such as food. Specifically, we expect inequalities in resource holding potential to be expressed during feeding when food resources are clumped and therefore monopolizable (Pruetz & Isbell, 2000, Whitten, 1983). The extent to which a female can defend resources then determines her dominance rank (Post, Hausfater & McCuskey, 1980, Pruetz & Isbell, 2000). Thus, competition for food is expected to produce two intersecting effects, including increased effort on behalf

of low ranking females to locate food and second, low ranking females being more likely than higher-ranking females to be dispersed or on the periphery of the group (Murray, Mane & Pusey, 2007, van Noordwijk & van Schaik, 1987, Pazol & Cords, 2005, Ron *et al.*, 1996, van Schaik & van Noodwijk, 1988). Both of these factors will potentially result in lower ranking females having less time available for social engagement and greater dispersal will reduce the affordances for social engagement (Henzi *et al.*, 1997b, van Schaik & van Noordwijk, 1988).

Since the spatial arrangement of individuals can influence the occurrence and outcome of social interactions and social interactions are determined by rank, variation in social dispersal patterns should emerge between females of varying rank (Post *et al.*, 1980, Sterck *et al.*, 1997, Whitten, 1983). This could be particularly important for species such as vervets as the extent to which an individual benefits from group life is determined, in part, by his or her social rank. For example, in a variety of primate species, high-ranking females expend less energy when foraging and have a higher nutritional intake of food than low-ranking females (van Noordwijk & van Schaik, 1987). Also, compared to subordinate females, high-ranking females are able to forage more efficiently as they have priority access to resources and are less likely to be disturbed during foraging (Deag, 1977, Post *et al.*, 1980, Murray, Eberly & Pusey, 2006, Whitten, 1983). It is also the case that the feeding efficiency of high-ranking females is related to their ability to monopolize resources and displace lower ranking females (Post *et al.*, 1980).

Increased foraging time, however, is associated with a reduction in time spent resting and may also reduce the time available for affiliative social interactions (Barrett,

Halliday & Henzi, 2006, Bronikowski & Altmann, 1996, Pazol & Cords, 2005, van Schaik & van Noordwijk, 1988). Thus, longer periods of foraging constrain the amount of time an individual has available for non-feeding activities. In particular, if the time available for grooming is reduced, social cohesion may be compromised (Dunbar, 1992, Seyfarth, 1977, but see Barrett *et al.*, 2006). It seems, however, that despite social (and ecological) demands, individuals do not always compromise the amount of time they allocate to social engagement and, where possible, try to sustain their grooming cliques (Dunbar & Dunbar, 1988, Dunbar & Sharman, 1984, Henzi *et al.*, 1997b, Iwamoto & Dunbar, 1989, Pazol & Cords, 2005).

3.5 Managing Feeding Competition

According to Koenig (2002), subordinate females are able to minimize feeding interruption by foraging away from other individuals. In long-tailed macaques (*Macaca fascicularis*) females minimize the costs of feeding competition by dispersing from the main group during foraging (van Noordwijk & van Schaik, 1987). In Japanese macaques (*Macaca fuscata*) dominance effects are mitigated when inter-individual distances between high and low-ranking females are large or above a particular tolerance level (Furuichi, 1983). In blue monkeys (*Cercopithecus mitis stuhlmanni*) females responded to limited food availability by varying the food resources they consumed and by spending less time in proximity to other individuals during feeding than non-feeding activities (Pazol & Cords, 2005). Also, in vervets (*C. aethiops*) low-ranking females avoid competition by feeding in separate feeding trees away from high-ranking females

(Whitten, 1983). Such examples demonstrate that feeding competition affects social structure as reflected by the dispersal patterns of females (Koenig, 2002).

That feeding behaviour and inter-individual spatial arrangement vary when food resources are limited and feeding competition is prevalent has reinforced the idea that females are responding to the dynamics of their socio-ecological environment by developing strategies, such as avoidance, that help mitigate the impact and costs of feeding competition (Isbell & van Vuren, 1996, Pazol & Cords, 2005). It is, however, plausible that the changes in feeding activity and proximity are an unavoidable consequence of feeding competition such that the behaviour patterns emerging in this context reflect the possibility that individuals have no other option but to forage away from other individuals or to feed on alternative foods (Murray *et al.*, 2007, Whitten, 1983). That is, if low ranking females are displaced when feeding on clumped foods they may have to content themselves by feeding on dispersed foods. Differentiating between strategies and unavoidable consequences is therefore necessary when interpreting feeding behaviour.

Since, in primate species such as vervets, social interactions are determined by rank (Post *et al.*, 1980) and dispersal can potentially compromise an individual's safety against predation (Ron *et al.*, 1996, van Schaik & van Noordwijk, 1988), females should adjust their association patterns such that the costs of feeding competition are counterbalanced by the risk of predation (van Noordwijk & van Schaik, 1987). That the costs and benefits of living within a group vary according to the spatial distribution of individuals within a group suggests low-ranking females may also benefit from

increasing their inter-individual distance from higher-ranking individuals whilst maintaining proximity to similar ranking females (Hall & Fedigan, 1987).

3.6 Sex Differences in Time Budgets

Sex differences in time budgets occur for a variety of reasons and in females variation in time budgets can be attributed to a female's reproductive condition. For example, the metabolic demands of pregnancy and lactation affect the feeding behaviour of females such that the proportion of time spent feeding is higher among pregnant and lactating females than non-mothers and is also higher during pregnancy than lactation (Post *et al.*, 1980). Females also increase their consumption of protein-rich foods and in some cases females with infants reduce their activity levels, reflected by increased resting, perhaps as a means of coping with the energetic demands of lactation (Barrett *et al.*, 2006, Nakawaga, 2000). In addition, as infants are an attractive resource, the presence of infants may result in mothers being the recipients of more affiliative interactions, such as grooming and embracing, than non-mothers (Henzi & Barrett, 2002, Slater, Schaffner & Aureli, 2007).

In contrast, male time budgets are expected to differ from female time budgets because males do not experience the same energetic demands as females (i.e. lactation and gestation). Thus, whereas feeding activity may constrain a female's budget, males may be more constrained by the demands of mating and predator detection (Nakawaga, 2000). This sex difference can, to some extent, be attributed to the fitness of males being related to his ability to access mates and the fitness of females being related to her ability to maximize the time she spends feeding (Schoener, 1971). That sex differences in

feeding and resting (including vigilance) are more pronounced during the mating season and that males compete for access to mates, lends support to the notion that the fitness of males and females is determined by different socio-ecological factors, as reflected by seasonal variation in their time budgets (Henzi & Lawes, 1987, Nakawaga, 2000).

3.7 Environmental Factors and Time Budgets

Viewing animals as embedded in a socio-ecological environment requires not only consideration of the effect of social rank, but also the effect of ecological and temporal factors such as climate and variation in day length, on activity and socio-spatial patterns (Baldellou & Adan, 1997, Bernstein, 1982, Harrison, 1985, Lawes & Piper, 1992). In the context of my analyses, what is important are the indirect effects of temperature and rainfall because of the role they play in seasonal changes in food availability (Clutton-Brock, 1977, Deshmuck, 1984, Roberts & Dunbar, 1991, Rutherford, 1980). Feeding activity is related to food availability such that when food is plentiful feeding time increases (*Cercopithecus sabeus*: Harrison, 1985) and when it is scarce foraging time increases (*Papio ursinus*: Davidge, 1977). Besides food availability, it is also the case that the amount, quality and distribution of food play a role in the variation of behaviour patterns (Agetsuma, 1995, Davidge, 1977, Iwamoto & Dunbar, 1989, Lawes & Piper, 1992). Resting, for example, is not only a function of temperature but also of the need to digest the foods they have been feeding on (Korstjens *et al.*, 2010, Lawes & Piper, 1992, Schmidt-Nielsen, 1964).

Temporal factors such as variation in day length can also constrain time budgets (Lawes & Piper, 1992). Specifically, the length of the active period is determined by day

length and therefore frames the time available to animals in which to meet their needs (Dunbar, 1988, Hill, Barrett, Gaynor, Weingrill, Dixon, Payne & Henzi, 2003). The shorter day lengths associated with high latitude winters may constrain feeding (Lawes & Piper, 1992). Since the allocation of time to feeding determines the time remaining for non-feeding activities, social grooming may be further constrained by this increase in feeding (Altman, 1982, Dunbar, 1992). In contrast, the increase in day length during summer allows for greater behavioural flexibility, reflected by variation in foraging strategies, and may result in an excess of time that, in some cases, has been used for increased resting, rather than social engagement (Bronikowski & Altmann, 1996). Resting is necessary for recuperation and digestion (enforced resting) and once these needs are met, resting is considered to reflect free time (Herbers, 1981, Korstjens *et al.*, 2010). Thus, resting is also shaped by ecological constraints and should not be simply viewed as an activity that occurs when all other needs are met.

3.8 Aims

My broad aim in this chapter, following the general trends outlined above, is to explore the time budgets and association patterns of free-ranging adult vervet monkeys (*C. aethiops*) in two troops to determine the extent to which temporal factors, such as time of day, and seasonality and social factors, such as dominance rank, structure the time available for social interaction to females and, as a comparison, to males. The extent of my analyses is limited by the relatively small size of the scan data set, which makes broad scale partitioning problematic. Nevertheless, the primary point of the analyses is to

establish a broad context in which to situate the more detailed analyses of female social engagement that are presented in the next chapter.

METHOD

3.9 Subjects

Data were collected from November 2008 to January 2010 on sub-adult and adult males and females in two troops (RBM, RST) of free-ranging vervet monkeys. RST consisted of 23 adult and sub-adult females and 18 adult and sub-adult males. The second troop, RBM, consisted of 14 adult and sub-adult females and 10 adult males. Individuals with a limited total number of scan samples (i.e. the least habituated animals) were, however, excluded from data analysis. Thus, for RST, data analyzed here came from 18 females (14 adults, 4 sub-adults) and 11 males (9 adults, 2 sub-adults) while, for RBM, data came from 10 females (9 adults, 1 sub-adult) and 6 adult males.

3.9.1 Social Rank

Dominance hierarchies, based on decided agonistic interactions, were constructed for males and females in each troop (Chapter 2). Each individual was assigned a numerical rank position based on the ratio of aggression given to that received. Then, for the purpose of rank-related analyses, individuals were split as equally as possible between three rank categories (high, medium, low) according to their numerical rank value. Whereas, in the next chapter, I derive cardinal ranks for each female for analyses.

This categorization of ranks allows me to use the scan data most efficiently, given that there is wide variation in the representation of different individuals in the scan samples.

3.10 Data Collection

3.10.1 Half Hour Troop Scans

Scan samples (Altman, 1974) were taken on all visible animals at thirty minute intervals to generate estimates of the overall proportion of time allocated to the recorded activities. Activity states were recorded and categorized as **feeding**, **moving**, **social** (grooming) and **resting** (as defined in Chapter 2). These behaviours constitute the main mutually exclusive activity categories used in primate time budget analyses, including vervets (Baldellou, 1997, Dunbar, 1988, Harrison, 1985, Hill *et al.*, 2003).

Scans were taken from early morning, when the animals came down from their sleep trees, until the evening when they returned to their sleep trees (between 5:00-18:30). Point samples were taken for all visible animals over a five-minute period. Each point sample identified the animal and recorded its activity and the ID and distance of all adult and subadult males and females. No individual was observed more than once in any five-minute scan period.

A total of 13,638 scan point samples of male and female activity was collected for both troops across the year. Differences in the level of habituation between troops resulted in an unequal number of scans (RBM: 4603, RST: 9035). Data were collected using a Palm Tungsten™ E2 Handheld with Pendragon Forms Manager 5.1 (2005-2007, Pendragon Software Cooperation).

3.10.2 Day Length

Systematic scan samples make possible the estimation of the allocation of time to activities across a given period and can thus be used to illustrate daily, monthly or even annual variation in behavioural patterns within and between populations of a given species (Baldellou & Adan, 1997). While activity patterns are usually reported as a percentage of some predetermined total, this method ignores variation in day length, which differs across study sites and is more pronounced at higher latitudes (Hill *et al.*, 2004). As day length at Samara varied from 7.57-15.69hrs, I corrected for the time available to the animals by converting the proportion of scan samples allocated to different activities into minutes. As day length is a fixed attribute of latitude, a day length calculator (Retrieved from <http://www.jgiesen.de/astro/astroJS/decEoT/index.htm>) was used to provide an estimate of the average day length for each of the designated seasons (Mating, Pregnancy, Post Gestation Dependent and Post Gestation Non-Dependent – See below). Seasonal day length was determined by averaging the first and last day of each season. Scan sample proportions were thus multiplied by the average day length (in minutes) for the corresponding season to give an approximate estimate of time in minutes.

3.10.3 Diurnal Variation

Due to an uneven distribution of scan samples across each active hour of the day, average diurnal activity patterns were based on the division of scan samples into four time blocks (Block 1. 5:00-8:29, Block 2. 8:30-11:59, Block 3. 12:00-15:29, Block 4. 15:30-18:30). Mean ($\pm SD$) proportions of scan samples were subsequently calculated

for resting, moving, feeding and social (allogrooming) interaction across the four time blocks.

3.10.4 Seasons

Although previous research has explored seasonal variation in behaviour, including changes in ranging behaviour, fluctuations in diet as reflected by food items consumed, and foraging strategies (Fedigan & Fedigan, 1988, Harrison, 1983, Kavanagh, 1978), other temporal variations, such as breeding seasonality, have mostly been ignored (but see Baldellou, 1997). Breeding seasonality alters the social dynamics of primate groups and is contingent upon local ecological conditions, with birthing season typically occurring when food resources are plentiful (Butynski, 1988). I therefore divided the year into broad reproductive seasons to explore variation in vervet activity patterns across the year. These female-centered periods were: the Mating, Pregnancy, Post-Gestation Dependent and Post-Gestation Non-dependent seasons. The dates for each season are specific to each female and are derived from the date of her infant's birth in 2008 and 2009. The dates that bounded the period over which individuals were observed copulating defined their specific mating season. For males, and females who did not give birth, seasons were based on the average dates of all other individuals.

Weather conditions are outlined for each season and are summarized in Table 3.1 and Table 3.2. As rainfall influences vegetation growth and provides an indirect measure of food availability (Deshmukh, 1984, Rutherford, 1980) seasons proceeding the months that receive the most amount of rain, typically spanning the summer months, are considered food plentiful seasons and include the Post-Gestation Dependent and Post-

Gestation Non-Dependent season. In contrast, food-scarce seasons occur during the winter when rainfall is lower and encompasses the Mating and Pregnancy season. The seasons are defined as follows:

Mating (April-May): Commenced late April (21 April) when the majority of copulations were observed and ended, on average, in May (18 May) when the number of copulations declined to levels approximately equal to the non-mating season. Females were observed to solicit and refuse copulations and were generally pursued by males. Day length ranged from 14.13hr at the start of the season to 15.64hr at the end of the season. Minimum and maximum temperature values (Table 3.1) and mean rainfall values (Table 3.2) are presented below.

Pregnancy (May-October/November): The period of time between the end of the mating season and the start of the post-gestation dependent season in late October, early November. As female's progress through pregnancy, lasting approximately 163 days, their weight and energetic demands increase. Day length ranged from 15.69hr at the start of the season to 9.51hr at the end of the season. Minimum and maximum temperature values (Table 3.1) and mean rainfall values (Table 3.2) are presented below.

Post-Gestation Dependent Season (October/November-December/January): This commenced when the first infant was born. In 2008 this occurred, for most individuals, by mid November and ended mid January 2009. In 2009 this occurred, for most individuals, late October and ended late December 2009. During this period infants were spending more time on than off their mothers and had not yet been observed to feed independently. In 2008, day length ranged from 8.62hr at the start of the season to 7.96hr

at the end of the season. In 2009 average seasonal day length ranged from 9.45hr at the start of the season to 7.57hr at the end of the season. Minimum and maximum temperature values (Table 3.1) and mean rainfall values (Table 3.2) are presented below.

Post-Gestation Non-Dependent Season (January – April): This season lasted from late January 2009 until April 21st 2009 and late January 2010. Infants spent more time off than on their mothers and had started to feed independently of their mothers. Infants were, on average, 15 days old when they were first seen off their mothers, 37 days old when they were first seen to forage on their own and 45 days old when they were observed to be off their mothers more than they were on their mothers (weaning data was only available for infants born in 2009). In 2008-2009 average seasonal day length ranged from 8hr at the start of the season to 14.06hr at the end of the season. In 2009-2010 average seasonal day length ranged from 7.58hr at the start of the season to 8.88hr when data collection ended on January 31, 2010. Minimum and maximum temperature values (Table 3.1) and mean rainfall values (Table 3.2) are presented below.

Table 3.1. Daily mean (°c) and range (°c) for minimum and maximum seasonal temperatures (*data ceased to be collected on 31.1.10).

Season	Minimum Temperature		Maximum Temperature	
	Mean	Range	Mean	Range
PG Dependent 08	14.31	8.0 - 21.2	32.3	21.5 - 38.3
PG Non Dependent 08-09	14.1	2.8 - 24.0	32.3	17.1 - 39.3
Mating 09	8.4	0.7 - 17.3	23.8	18.8 - 28.1
Pregnancy 09	5.74	-3.7 - 18.1	23.3	11.6 - 34.6
PG Dependent 09	12.3	8.3 - 18.7	30.2	21.0 - 38.0
PG Non Dependent 00-10*	16.5	12.1 - 20.9	33.9	26.3 - 38.9

Table 3.2. Daily mean, range and total seasonal rainfall (mm) across the study period

(*data ceased to be collected on 31.1.10).

Season	Daily Mean	Daily Range	Season Total
PG Dependent 08	0.79	0 – 13.72	22.13
PG Non Dependent 08-09	1.30	0 – 22.61	153.92
Mating 09	0.26	0 – 0.29	7.11
Pregnancy 09	0.30	0 – 7.62	34.80
PG Dependent 09	0.82	0 – 11.43	21.35
PG Non Dependent 00-10*	2.43	0 – 10.92	41.16

3.11 Statistical Notes

Descriptive statistics were based on log-transformed proportions of scan samples to correct for the uneven distribution of samples across months and seasons. Diurnal data was, however, limited and therefore calculated as proportions of scan samples across time blocks.

RESULTS

3.12 Seasonal Effects

3.12.1 Descriptives: Activity by Season and Sex

Overall, RST spent more time (minutes) engaged in feeding and generally more time engaged in social activity, across all seasons (mating, pregnancy, PG dependent, PG non-dependent), than RBM. RBM, in contrast, generally spent more time resting and generally less time moving than RST across all seasons (Table 3.3). For both troops, females spent more time engaged in feeding and social activities, across all seasons, than males. Males, in contrast, spent more time resting and moving across all seasons than females (Table 3.3).

Table 3.3. Proportion of time allocated to each behaviour state, by sex and troop, across seasons.

		Mating		Pregnancy		PG Dependent		PG Non Dependent	
		M	F	M	F	M	F	M	F
RST	Feeding	2.50	2.66	2.57	2.61	2.50	2.46	2.45	2.53
	Social	1.12	1.97	1.49	1.79	0.99	1.83	1.43	2.00
	Resting	2.45	2.20	2.54	2.44	2.61	2.62	2.61	2.52
	Moving	2.22	2.01	2.22	2.22	2.36	2.26	2.22	2.15
RBM	Feeding	2.45	2.61	2.50	2.61	2.35	2.41	2.33	2.47
	Social	0.77	1.65	1.81	1.32	1.24	1.57	1.76	1.96
	Resting	2.50	2.13	2.62	2.48	2.67	2.65	2.69	2.57
	Moving	2.16	2.10	1.85	2.18	2.40	2.32	2.08	2.14

3.12.2 Descriptives: Activity by Season and Rank

3.12.2.1 Social: In all seasons, low-ranking RST females spent the least amount of time engaged in social interactions. Medium and high-ranking females allocated more time to social engagement during the mating and PG non-dependent seasons. Low-ranking females, however, spent the least amount of time engaged in social interactions during the mating season, increasing their allocation of time to social engagement during the PG non-dependent season. In RBM, high-ranking females generally spent the least amount of time engaged in social interactions compared to low and medium-ranking females. High-ranking females spent more time engaged in social interactions during the PG dependent season than the other seasons whereas low and medium-ranking females spent more time engaged in social interactions during the PG non-dependent season compared to the other seasons.

3.12.2.2 Feeding: Low-ranking females in RST spent the most time feeding across all seasons compared to medium and high-ranking females in their troop. RST females of all ranks spent more time feeding during the mating and pregnancy seasons and the least amount of time spent feeding during the PG non-dependent season. In RBM, there were no clear rank related patterns of feeding in females. However, like RST, RBM's feeding varied seasonally with more feeding generally occurring in the mating and pregnancy season than the PG dependent and PG non-dependent seasons.

3.12.2.3 Moving: Females in both troops and of all ranks moved the most during the PG dependent season. Compared to low-ranking RST females, medium and high-ranking RST females spent less time moving during the mating season than the other

seasons. In contrast, low-ranking females were more active during the PG dependent season than the other seasons. In RBM, females of all ranks spent more time moving during the PG dependent season.

3.12.2.4 Resting: In both troops, females of all ranks spent the least amount of time resting during the mating season compared to the other seasons and more time resting during the PG dependent season, with low-ranking females resting the most compared to medium and high-ranking females. All results are presented in Table 3.4.

Table 3.4. Mean amount of time (minutes) RST and RBM females spent engaged in each activity by season and rank (*limited data - value based on one individual).

		RST			RBM		
		Low	Medium	High	Low	Medium	High
Social	Mating	1.56	2.14	2.03	1.69	1.60	1.65
	Pregnancy	1.71	1.89	1.78	1.79	1.87	1.77
	PG Dep.	1.62	1.95	1.95	0.1*	1.86	1.85
	PG Non-Dep.	1.83	2.13	1.99	2.04	2.18	1.66
Feeding	Mating	2.72	2.62	2.68	2.56	2.55	2.69
	Pregnancy	2.64	2.55	2.63	2.67	2.53	2.62
	PG Dep.	2.53	2.40	2.45	2.04	2.52	2.46
	PG Non-Dep.	2.57	2.51	2.53	2.54	2.34	2.53
Moving	Mating	2.08	2.04	1.90	2.06	2.20	2.09
	Pregnancy	2.13	2.26	2.26	2.14	2.24	2.16
	PG Dep.	2.17	2.32	2.28	2.41	2.25	2.33
	PG Non-Dep.	2.13	2.16	2.14	2.11	2.15	2.16
Resting	Mating	2.19	2.21	2.20	2.38	2.28	1.82
	Pregnancy	2.47	2.45	2.41	2.46	2.51	2.46
	PG Dep.	2.64	2.60	2.62	2.79	2.62	2.63
	PG Non-Dep.	2.53	2.48	2.55	2.52	2.61	2.57

3.12.3 Descriptives: Activity, by Month, Across Seasons

3.12.3.1 Social: RST females spent more time grooming during the months spanning the PG dependent and PG non-dependent seasons and engaged in less grooming during the months spanning the mating and pregnancy season. RBM females generally spent more time grooming during the months spanning the PG dependent and PG non-dependent seasons. Time spent grooming decreased during the mating season, showing more variability during pregnancy but remaining lower overall than the PG dependent and PG non-dependent seasons. The time allocated to grooming by RST males remained constant earlier on in the year, spanning the end of the PG dependent season and the PG non-dependent season, increasing slightly at the beginning of the mating season before decreasing towards the end of the mating season, through to the pregnancy season and start of the PG dependent seasons. RBM males generally spent more time grooming during the PG dependent and PG non-dependent seasons. Less time was spent grooming during June (middle of the mating season), September (middle of the pregnancy season) and December (middle of the PG dependent season). Overall, males in both troops generally spent less time engaged in grooming, across all months, than females. See Figure 3.1.

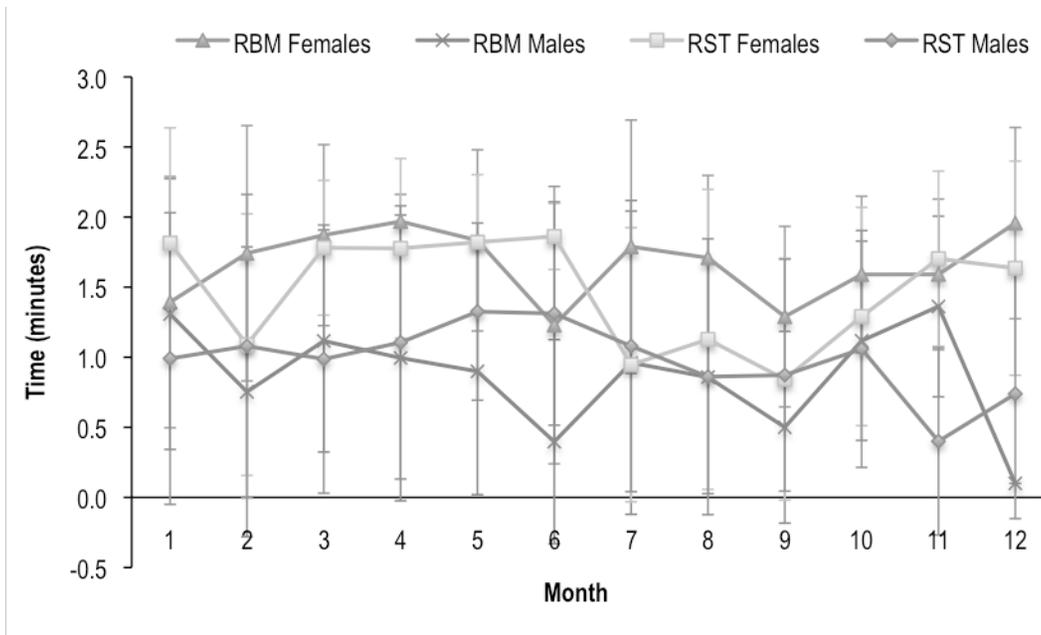


Figure 3.1. Mean (\pm SD) amount of time (minutes) spent grooming, per month, by males and females in each troop, across the study period (November 2008 – January 2010) with season (Oct-Jan: PG Dependent, Jan-May: PG Non-Dependent, May-July: Mating, July-Oct: Pregnancy).

3.12.3.2 Feeding: The amount of time RST and RBM females spent feeding remained constant across the year. However, for RBM females, time spent feeding decreased during the mating season before increasing again during the months spanning the pregnancy season. The amount of time RST males spent feeding generally remained constant across the year, increasingly slightly during the months spanning the pregnancy season. The amount of time RBM males spent feeding declined earlier on in the year, with the least amount of time spent feeding during the middle of the mating season. Time spent feeding increase towards the end of the mating season and remained constant towards the end of the year during the months spanning the pregnancy and PG dependent

season. Overall, females generally spent more time feeding across the year. See Figure 3.2.

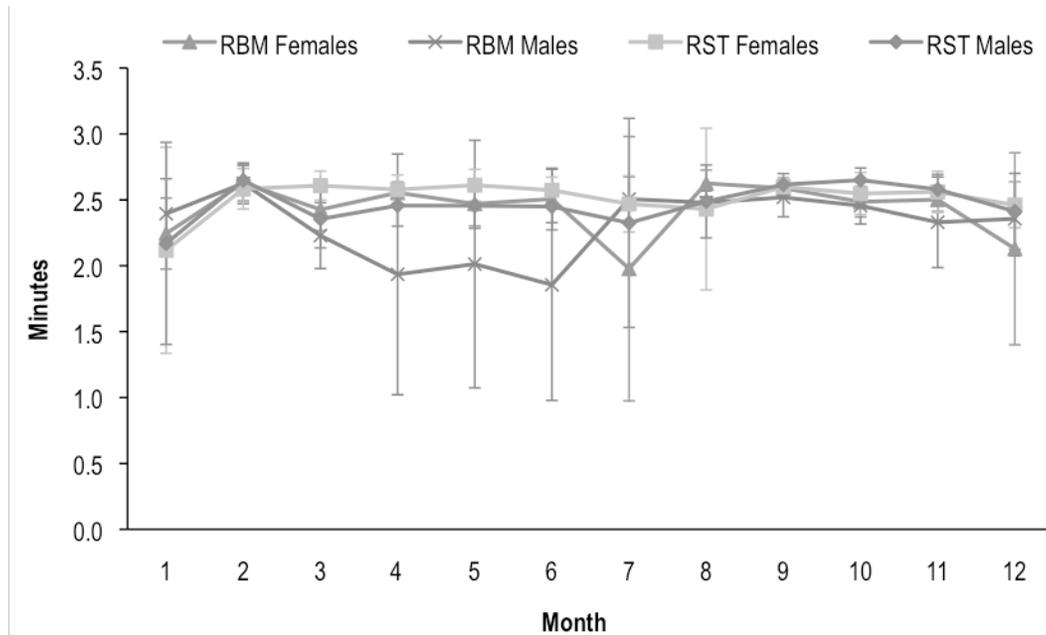


Figure 3.2. Mean (\pm SD) amount of time (minutes) spent feeding per month, by males and females in each troop, across the study period (November 2008 – January 2010).

3.12.3.3 Moving: The amount of time RST females spent moving remained constant early on in the year, decreasing towards the end of the mating season / beginning of the pregnancy season before increasing again and remaining constant across the rest of the year. The amount of time RBM females spent moving increased during the PG non-dependent season before decreasing during the mating season and gradually increasing over the course of the pregnancy season, leveling off from the middle of the pregnancy and through the PG dependent season. The amount of time RST males spent moving remained constant earlier in the year, decreasing between the end of the mating season and the start of the pregnancy season before increasing again during the pregnancy

season and remaining constant through to the end of the year. The amount of time RBM males spent moving declined during the first three months of the year before increasing from the middle of the PG non-dependent season until the start of the mating season. Time spent moving decreased across the mating season until the start of the pregnancy season and then increased across the pregnancy and PG dependent seasons. See Figure 3.3.

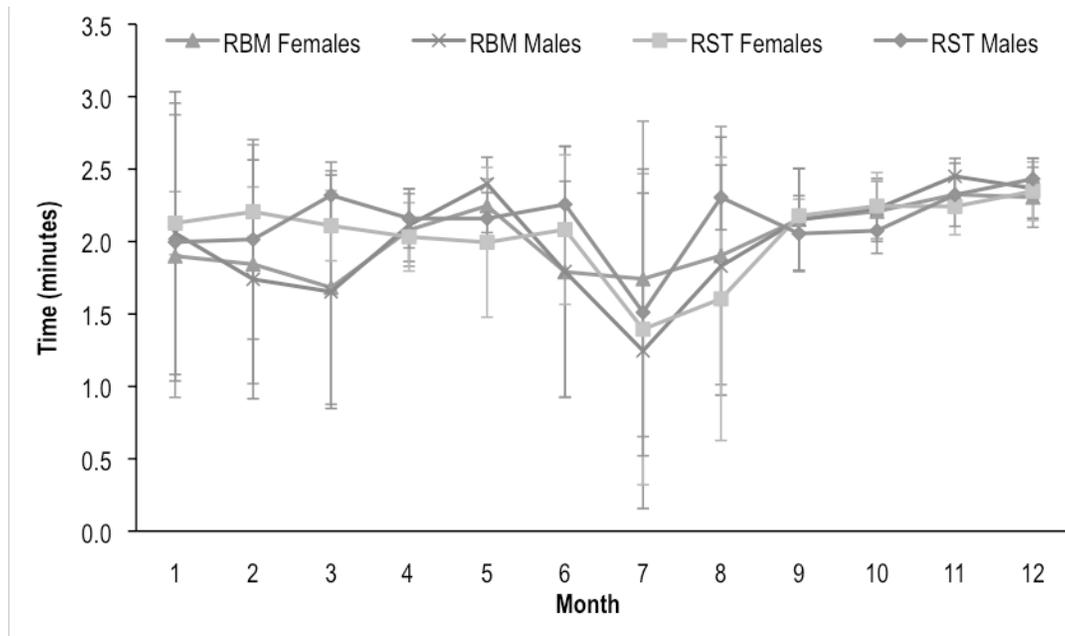


Figure 3.3. Mean (\pm SD) amount of time (minutes) spent moving per month, by males and females in each troop, across the study period (November 2008 – January 2010).

3.12.3.4 Resting: The time that RST females allocated to resting decreased gradually across the PG non-dependent season before gradually increasing during the months spanning the mating, pregnancy and PG dependent seasons. Although RBM exhibited a similar pattern of resting to RST females there were several months, including

February, June and August in which RBM females decreased the amount of time spent resting. The amount of time RST males spent resting decreased gradually through the months spanning the PG non-dependent, mating and pregnancy seasons and then increased gradually from August until the end of the year. The amount of time RBM males spent resting peaked during the middle of the mating season (June), spending the least amount of time resting at the beginning of the pregnancy season (July), gradually increasing the amount of time they spent resting through the remainder of the pregnancy season until the end of the year. See Figure 3.4.

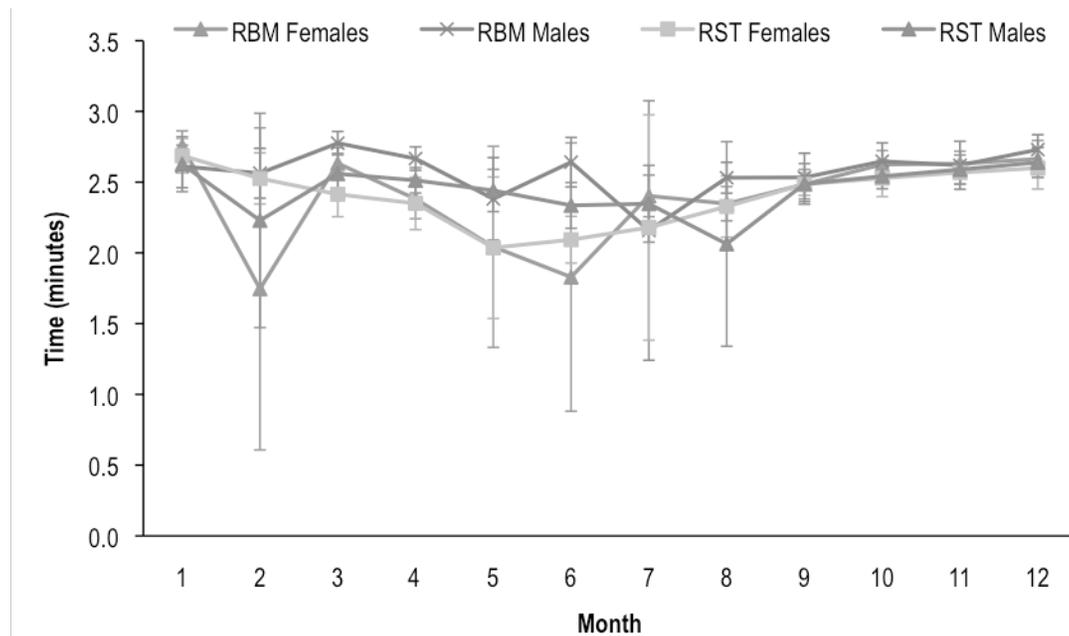


Figure 3.4. Mean (\pm SD) amount of time (minutes) spent resting per month, by males and females in each troop, across the study period (November 2008 – January 2010).

3.12.4 Generalized Linear Model Results for Allocation of Effort to Grooming

To determine the predictors of time spent grooming across the year, I constructed a GLMM with the summed minutes (log-transformed) spent grooming by each subject as the dependent variable and ID (within troop) as the random effect. *Season*, *Troop*, *Sex*, *Season*Sex*, *Rank*Season* and *Reproductive Status* (mother/non-mother) were entered as fixed effects and the time spent *Moving*, *Resting* and *Foraging* as covariates. The results are presented in Table 3.5 and indicate that in addition to the expected interrelationships among the activity categories, only *Season* and *Sex* were significant predictors of grooming time (Whole model Adj. $R^2=0.38$, $N=167$), although *Rank*Season* approached conventional levels of significance. Figure 3.5 indicates that males groomed less than females and that grooming was lowest during the mating season.

Table 3.5. Fixed effect outcomes in relation to time allocated to grooming.

Source	Nparm	DF	DFDen	F Ratio	P
Season	3	3	104.2	5.4295	<0.01*
Rank Category	2	2	25.19	1.0008	0.38
Sex	1	1	40.58	40.9381	<0.001*
Troop	1	1	112.3	0.3051	0.58
LogFeedMin	1	1	117.3	10.7169	<0.05*
LogMoveMin	1	1	92.73	7.2121	<0.01*
LogRestMin	1	1	146	6.8472	<0.01*
Mother/Non-Mother	1	1	45.82	0.1418	0.7
Rank Category*Season	6	6	85.38	1.9986	0.07
Sex*Season	3	3	99.15	1.8275	0.14

Note. Significant effects are indicated by P*.

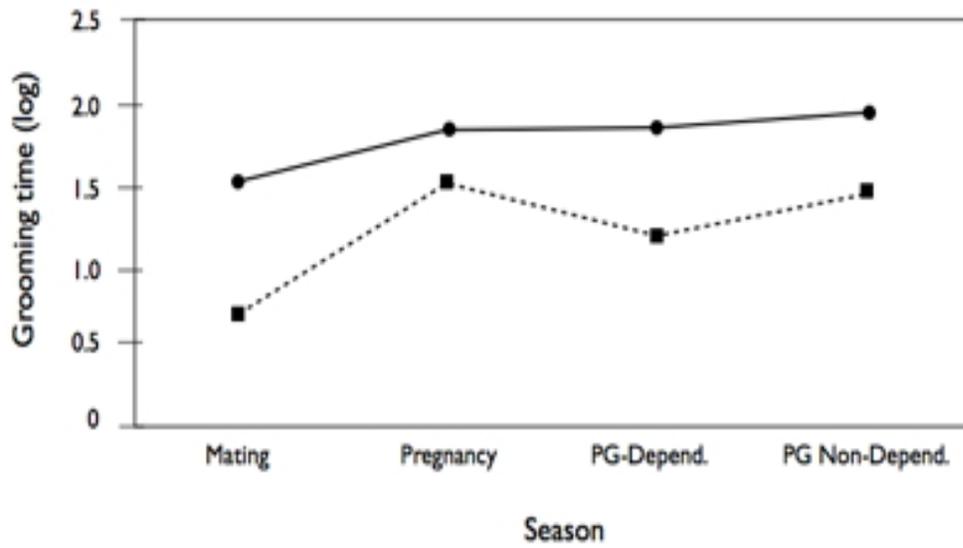


Figure 3.5. LS means plot of male (dashed line) and female (solid line) allocation of time to grooming across the functionally defined seasons. The seasons are arranged chronologically.

3.12.5 Descriptives: Nearest Neighbours, by Month, Across Seasons

Mean (\pm *SD*) monthly female nearest neighbour distance peaked at 5.8m (\pm 3.6) and 5.6m (\pm 3.4), for RBM and RST respectively, during the mating season. In contrast, females were closest to their neighbours during the PG Dependent season when their mean monthly female nearest neighbour distance reached 3.6m (\pm 3.3) and 4.1m (3.2), for RBM and RST respectively. See Figure 3.6.

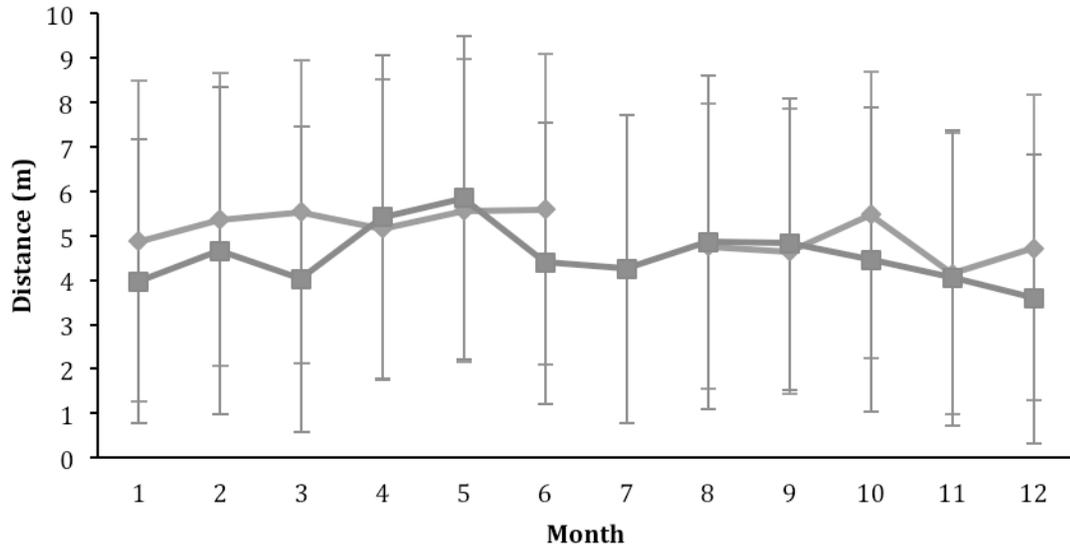


Figure 3.6. Average distance (meters, \pm SD) of the nearest female neighbour (Squares: RBM, Triangles: RST) across the study period (November 2008 – January 2010. Month 7 was represented by a single RST value and was subsequently omitted from the figure).

3.12.6 Nearest Neighbour Model

The effect of season on nearest female neighbour distance was investigated by constructing a model to examine *Season, Troop, Sex, Activity, Rank, Sex*Season, Activity*Rank, Activity*Sex and Sex*Rank* on neighbour distance, with *ID* (within troop) entered as a random effect. The results are presented in Table 3.6 and indicate significant main effects for Sex, Season and Activity, and significant interaction effects for Sex*Season and Activity*Rank. The amount of explained variance of the whole model (Adj. $R^2=0.09$, $N=6419$) was low however. The primary difference between the sexes was a lower mean distance to females by males during the mating season (Males: 5.45m; Females: 7.08m). The small distances separating females during grooming explained the

main effect for Activity and Tukey's HSD indicates that the distances to nearest female neighbours while Feeding (5.8m), Resting (5.03m) or Moving (6.6m) were all significantly different to one another.

Table 3.6. Fixed effect outcomes in relation to seasonal differences in nearest female neighbour distances.

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Troop	1	1	33.21	1.7837	0.19
Sex	1	1	85.98	26.4082	<.0001*
Season	3	3	6044	13.1884	<.0001*
Rank	2	2	38.99	0.5150	0.6
Activity	3	3	6392	146.0214	<.0001*
Sex*Season	3	3	5940	5.5908	<0.001*
Activity*Rank	6	6	6387	0.5952	0.73
Activity*Sex	3	3	6392	24.7393	<.0001*
Sex*Rank	2	2	24.22	2.5134	0.1

Note. Significant effects are indicated by P*.

3.12.7 Trade-offs Between Activities Model

To determine whether grooming time was traded against the other activities, I followed the approach of Dunbar and Sharman (1984) and simply generated pairwise

correlations for all four activity states (*Feeding, Moving, Resting, Social*). The results are presented in Table 3.7 and indicate that the strongest trade-off is between feeding and resting and feeding and moving. The trade-off between grooming and resting approaches conventional levels of significance.

Table 3.7. Pairwise correlations between the four activity states.

Variable	By-Variable	Correlation	N	P
LogFeedMin	LogGroomMin	0.06	167	0.41
LogMoveMin	LogGroomMin	-0.15	167	0.05*
LogMoveMin	LogFeedMin	-0.39	167	<.0001*
LogRestMin	LogGroomMin	-0.12	167	0.09
LogRestMin	LogFeedMin	-0.46	167	<.0001*
LogRestMin	LogMoveMin	0.05	167	0.5

Note. Data come from each adult's summed seasonal value. Significant effects are indicated by P*.

3.13 Diurnal Activity Patterns

3.13.1 Diurnal Activity Descriptives

3.13.1.1 Feeding: although RBM males fed consistently across the day, feeding was generally highest for RST males and females and RBM females during the morning

and decreased by the afternoon. Whereas feeding increased towards the end of the day in RBM females, feeding leveled off towards the end of the day in RST males and females. Overall, females engaged in feeding more than males across the day (Figure 3.7).

3.13.1.2 Moving: For RST, males and females both travelled more during the morning, decreasing by early afternoon and remaining constant towards the end of the day. Females travelled slightly more than males across the day. For RBM, males travelled slightly more than females across the day. Males travelled consistently across the day whereas females travelled more during the early morning before decreasing by early afternoon and then increasing slightly towards the end of the day (Figure 3.8).

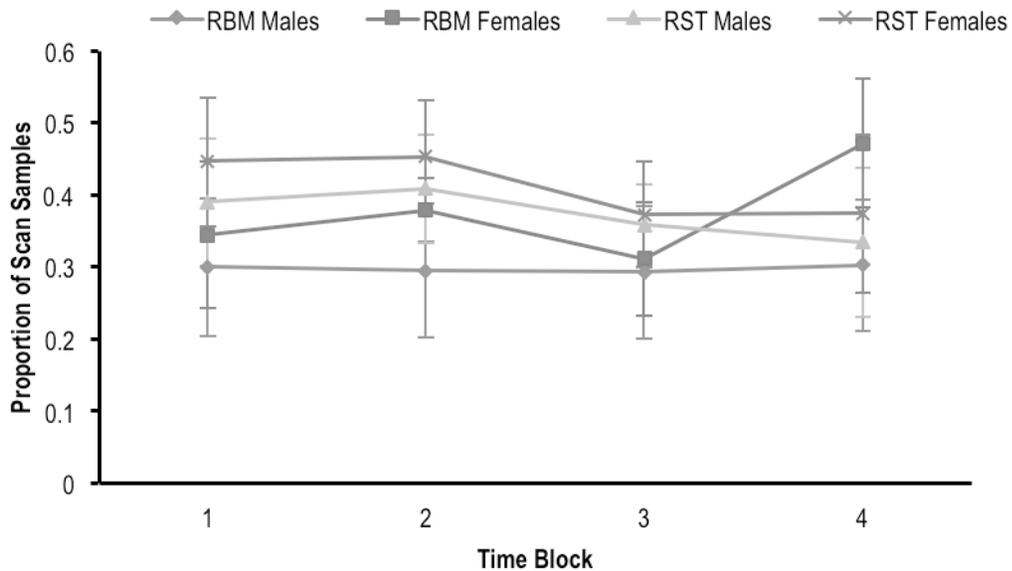


Figure 3.7. Mean proportion of feeding scan samples (\pm SD) across four time blocks (1: 5:00-8:29, 2: 8:30-11:59, 3: 12:00-15:29, 4: 15:30-18:30).

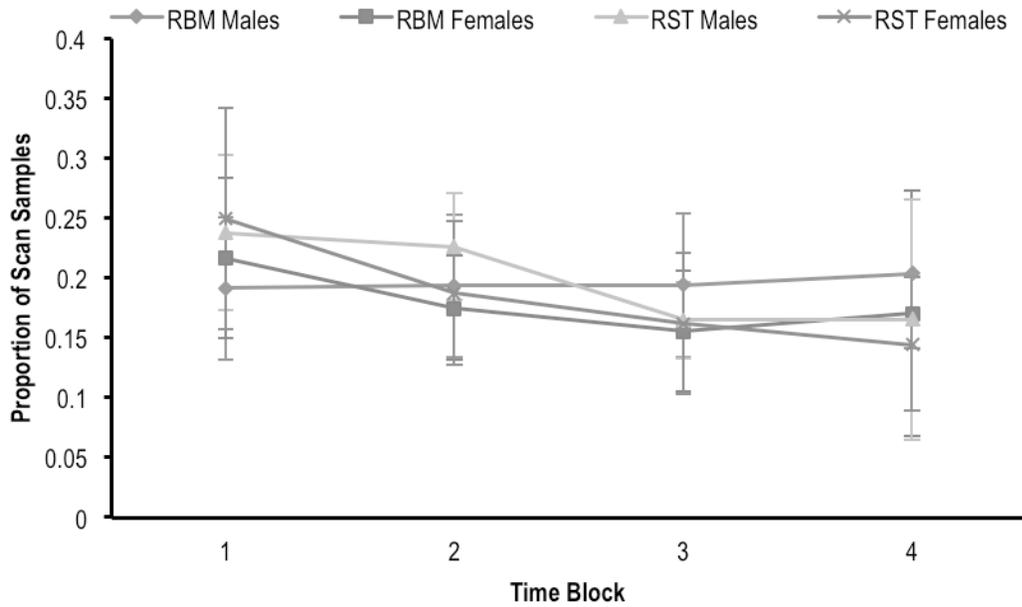


Figure 3.8. Mean proportion of moving scan samples (\pm SD) across four time blocks (1: 5:00-8:29, 2: 8:30-11:59, 3: 12:00-15:29, 4: 15:30-18:30).

3.13.1.3 Grooming: In RST, males and females engaged in more grooming in the afternoon with grooming peaking during the last two time blocks of the day. RBM females steadily increased their grooming across the morning, peaking during the afternoon before decreasing at the end of the day. RBM males groomed the least with little variation in grooming across the day. Overall, females spent more time grooming than males (Figure 3.9).

3.13.1.4 Resting: In RST, females rested the least in the morning, peaking during early afternoon before decreasing slightly towards the end of the day. RST males exhibited little change in resting during early and late morning. Like females, resting in males peaked during the early afternoon, decreasingly slightly towards the end of the day. Overall, resting was higher later in the day. In RBM, males exhibited little variation in

resting but rested more than RBM females across the day. RBM females exhibited a pattern of resting similar to RST with resting remaining constant early in the morning, peaking by early afternoon before decreasing at the end of the day (Figure 3.10).

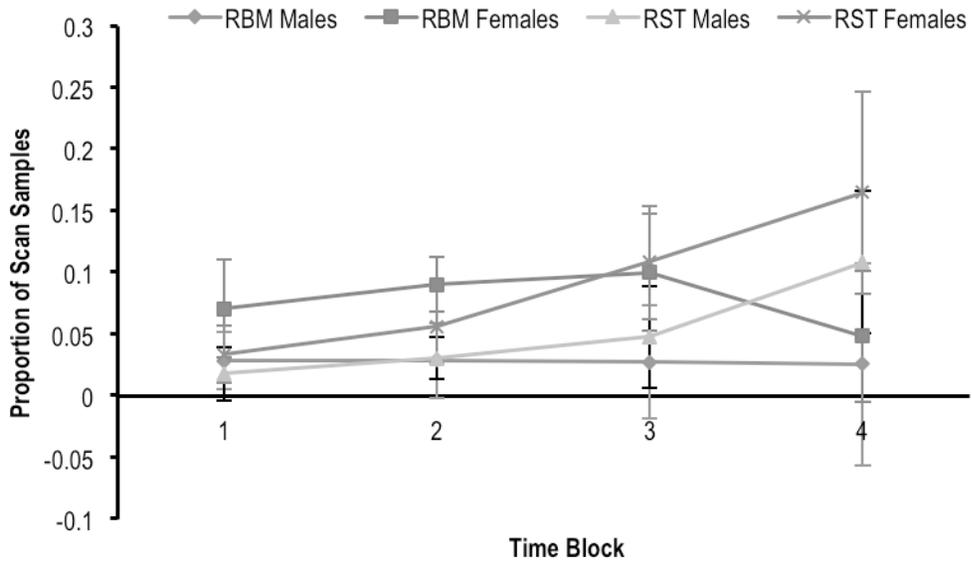


Figure 3.9. Mean proportion of grooming scan samples (\pm SD) across four time blocks (1: 5:00-8:29, 2: 8:30-11:59, 3: 12:00-15:29, 4: 15:30-18:30).

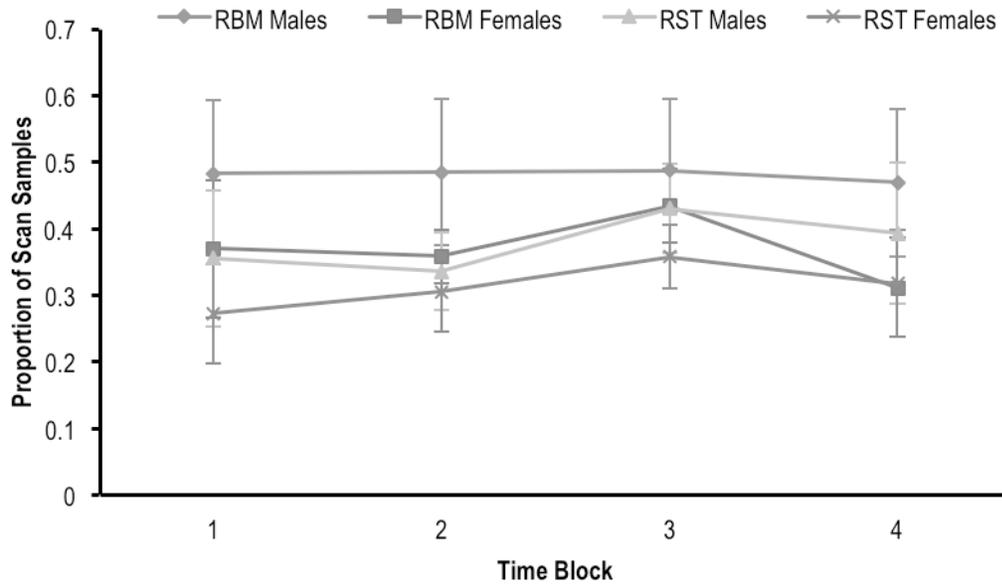


Figure 3.10. Mean proportion of resting scan samples (\pm SD) across four time blocks (1: 5:00-8:29, 2: 8:30-11:59, 3: 12:00-15:29, 4: 15:30-18:30).

3.13.2 Diurnal Activity Model

The effect of time of day on activity was investigated by constructing a model to examine *Time Block*, *Troop* and *Sex* on the proportion of time females spent grooming. Each subject had a single set of values for each time block. The resultant model was significant ($F_{7,172}=12.1$, $p<0.001$, Adj. $R^2=0.33$). Both *Time Block* ($F_3=17.04$, $p<0.001$) and *Sex* were significant ($F_1=33.77$, $p<0.001$), as was *troop* ($F_1=4.7$, $p<0.05$). The interaction of *Sex* and *Time Block* was not ($F_3=0.65$, $p=0.58$). Examination of the means indicates that females spent more time grooming than males and that grooming time increased during the day, with most occurring in time block 4. To determine the effects of relative rank, I re-ran the model for females only, adding *Rank* and *Rank*Time Block* as effects. The model was significant ($F_{6,105}=8.08$, $p<0.001$, Adj. $R^2=0.28$). There were

significant main effects for Rank ($F_2=4.8$, $p<0.05$), where mid-ranking females spent more time grooming than high and low-ranking females, and Time Block ($F_3=35.8$, $p<0.001$) but not for Troop ($F_1=0.94$, $p=0.33$) nor for the interaction of Rank and Time Block ($F_2=1.5$, $p=0.22$).

3.13.3 Diurnal Neighbour Model

The effect of time of day on the distance of nearest neighbours was investigated by constructing a full factorial model to examine *Time Block*, *Troop* and *Rank*. As male associations with females are strongly affected by the mating season (see above), I used only the data for females, with ID entered as a random effect. The results (Whole model Adj. $R^2=0.02$) indicate the absence of any significant fixed effects (Table 3.8).

Table 3.8. Fixed effect outcomes in relation to diurnal differences in nearest female neighbour distances.

Source	Nparm	DF	DFDen	F Ratio	P
Troop	1	1	44.81	0.0218	0.88
Time Block	3	3	2644	1.9776	0.11
Troop*Time Block	3	3	2644	1.1052	0.34
Rank	2	2	30.83	2.0916	0.14
Troop*Rank	2	2	30.83	0.3867	0.68
Time Block*Rank	6	6	2658	1.8300	0.08
Troop*Time Block*Rank	6	6	2658	1.4024	0.21

DISCUSSION

3.14 Summary of Findings

The data indicate two findings of general relevance. The first is that female rank manifests little of the predicted effects on the structuring of activity and, particularly, on the availability of time for grooming and the closeness of other females. There is no obvious explanation for the finding from the diurnal analysis that mid-ranking females spent more time grooming. This finding is made more problematic by the fact that there is no seasonal effect for rank and grooming.

The second is that there are no troop size effects, since it is predicted that females in larger groups within the same population or habitat should have less time available to them for socializing, especially during a drought, which was the case during my study (McDougall *et al.*, 2010). From the perspective of my objectives, the conclusion has to be that females in these two cohorts experience no systematic bias in their ability to devote time to grooming. Allocation of time to activities, according to Dunbar and Sharman (1984), involves trading time between activities with priority being given to time spent feeding. In light of the trade-off findings, the vervets in the current study appear to have traded feeding time off against moving and resting, thereby leaving grooming time buffered against daily time constraints.

For the rest, the finding that females spent more time grooming than males, across all seasons, is a common finding for Old-World monkeys (Isbell & Young, 1993). Unlike the males in RST, it is surprising that the males in RBM did not spend more time grooming during the mating season when they were in closer proximity to females. Similarly, we expect to see seasonal differences, especially at this latitude in a semi-desert environment, and this is the case here although it is primarily due to a reduction in allocation to social time during the mating season. Diurnal differences are manifest mainly as an increased allocation of time, by females, to grooming in the last quarter of the day.

3.15 Allocation of Effort to Grooming

Season and sex were significant predictors of grooming time. Males were groomed less than females and grooming was lowest during the mating season. That

females spent more time grooming than males is consistent with previous findings on sex differences in grooming behaviour, especially in female philopatric primate species, such as vervets, where females remain in their natal troop for life and are therefore related to one another (Melnick & Pearl, 1987). That grooming was lowest during the mating season could be attributed to individuals allocating more time to other activities, including males competing with other males over access to females, males transferring in and out of troops, individuals pursuing/resisting matings and other forms of sexual activity. As a result of increased mating behaviour and males pursuing potential mates, females may experience greater interruption of ongoing activities, including grooming. Also, that males were observed to engage in agonistic interactions, mostly with other males, and exhibited heightened vigilance suggests grooming may have been lower for males due to potentially more time spent engaged in male-male competition.

3.16 Nearest Neighbours

Sex, season and activity significantly affected nearest neighbor distance. Specifically sex interacted with season such that males were closer to females during the mating season. That males were closer to females during the mating season is possibly indicative of male mating strategies as they attempt to access females during their most fertile time of the year. In contrast, females were generally observed to be in closer proximity to other females during grooming. This finding may reflect the tendency of females to groom females more than they groom males and also their tendency to generally associate with kin more than non-kin, which in the case of vervets is more likely to consist of females than males because females remain in their natal troop for life

whereas males leave their troop upon reaching sexual maturity (Melnick & Pearl, 1987). Also, if females are exchanging grooming for tolerance, females are likely to be in closer proximity with one another during grooming, especially if the trade between grooming and tolerance is immediate (Barrett & Henzi, 2001). More detailed analyses are, however, required to determine whether biological market effects played a role in structuring female activity and spatial arrangement.

3.17 Seasonality

The absence of sharp seasonal differences in activity is interesting considering the study animals live in a seasonal habitat where food availability, climate and day length fluctuate throughout the year and such factors have previously been associated with changes in activity patterns (Baldellou & Adan, 1997, Bernstein, 1982, Harrison, 1985, Lawes & Piper, 1992). It is, however, likely that the absence of seasonal differences are a result of the limited amount of data collected during the study. Data limitations in the current study are a consequence of the unusually large troop sizes.

3.18 Trade-Offs Between Activities Model

To determine whether grooming time was traded against other activities, I followed the approach of Dunbar and Sharman (1984). The results indicate that grooming was maintained at the expense of other activities and the strongest trade-off occurred between feeding and resting and feeding and moving suggesting feeding is a high priority activity over resting and moving. The latter finding is not too surprising considering the possible ecological demands placed upon animals living in troops that are three times

greater than the average vervet troop size (van Schaik, 1983, Wrangham, 1980). Thus, in order for females to fulfill their nutritional needs, they may be required to devote more time to feeding and hence trade feeding against other activities. Specifically, animals in large troops have been shown to alter their foraging and travelling behaviour in response to socio-ecological demands, suggesting group size, among other factors, may play a key role in determining patterns of feeding behaviour (Sterck *et al.*, 1997).

Also, females in large troops may need to trade feeding against other activities because they may have to contend with feeding competition, which has been shown to be dependent, amongst other factors, on group size (Wrangham, 1980, van Schaik & van Noordwijk, 1986, Whitten, 1983). Furthermore, feeding is likely to be a high priority activity because the metabolic demands endured by females during pregnancy and lactation affect their feeding behaviour such that the proportion of time spent feeding is higher among pregnant and lactating females than non-mothers and is also higher during pregnancy than lactation (Post *et al.*, 1980).

3.19 Diurnal Effects

That most grooming in RST occurred during the last time block of the day could be attributed to individuals gathering in, or being in the vicinity of, their sleep site. Individuals were observed to eventually gather at their sleep site towards the end of the day whereas individuals dispersed throughout the day and in the case of RST, fragmented into two groups. Dispersal and fragmentation occurred almost immediately after individuals left their sleep site in the morning. It was not uncommon for individuals to subsequently be located on opposite sides of the river throughout the day. Thus,

reconvening at the sleep site may have increased individual accessibility to potential grooming partners, especially if individuals were grooming members of the sub-troop that would have otherwise been fragmented from the rest of the troop throughout the day. Also, although nearest neighbour distance did not vary, it is possible that the ID of neighbours could have varied across the day. Spatial affordances associated with reconvening at the sleep site may therefore have improved partner accessibility and promoted increased grooming towards the end of the day. In contrast, the females in RBM exhibited a decrease in grooming and an increase in feeding during the last time block of the day. Feeding may have been higher towards the end of the day because this is the time when RBM would typically be in their main territory having potentially frequented the water source earlier in the day. That the water source was furthest away from RBM's main territory and RBM, unlike RST, never slept at the water source (except for one instance) could have meant that RBM females fed later in the day when they were likely to be in their main territory.

There were also significant main effects for rank, where mid-ranking females spent more time grooming than high and low-ranking females. It is possible that low-ranking females, due to the constraints of their rank, spent more time engaged in other activities, such as feeding, and therefore had less time available for grooming and high-ranking females, because of their rank related benefits, may be in better physical condition than lower ranking individuals and do not require as much grooming in order to remove ectoparasites and dirt and thus maintain a healthy coat. Closer inspection of the results, however, suggest that alternative factors could be affecting grooming since rank was found not to have a significant effect in the allocation of time to grooming analysis.

3.20 Future Research

3.20.1 Diurnal Behavioural Patterns: That most grooming occurred during the last time block of the day could be attributed to the spatial affordances associated with RST individuals reconvening at their sleep site. Specifically, when individuals are in proximity to one another they are afforded the opportunity to interact (Barrett *et al.*, 2007). Thus, to ascertain whether individuals were grooming specific partners, that may have only been spatially available upon returning to the sleep site, or simply those individuals that were nearest neighbours throughout the day, future studies may benefit from determining which individuals are grooming one another by assessing the ID of grooming partners. That is, nearest neighbours may not necessarily be preferred grooming partners. Instead, preferred grooming partners may be dispersed throughout the day when individuals cross the river and split into sub troops during foraging.

Alternatively, it is possible that a greater variety of food resources are available outside of the sleep site such that when individuals wake in the morning they concentrate their efforts on foraging throughout the day and spend more time grooming upon returning to their sleep site. To determine whether a greater variety of food resources are indeed available in different areas of the animals' territory relative to their sleep site, a census of food items would need to be conducted. Specifically, since the amount, quality and distribution of food play a key role in the variation of behaviour patterns it may be useful to transect areas within a given territory to determine the amount and type of foods available to the animals.

Although food items were recorded during focal animal sampling, the data were not analysed. Peruvian pepper trees were, however, plentiful at the sleep sites and when

individuals foraged in this area they predominantly consumed peppercorns and dug for food items on the ground. Moreover, pepper trees, the largest tree in the animals' home range, may have provided safety from predators, during grooming, when individuals are more likely to direct their attention towards their grooming partner than their surrounding environment. Thus, the structure of the environment, coupled with the distribution of food resources and the availability of particular partners, may have contributed to the increase in grooming towards the end of the day when individuals reconvened at their sleep sites.

Moreover, the sampling constraints of the current study demonstrate the importance of collecting a greater amount of data in order to thoroughly test diurnal, seasonal and rank related patterns of behaviour. Future studies should therefore aim to increase the validity of the research by collecting data over longer periods of time so as to capture annual differences in seasonal changes in behaviour and to also have the ability to conduct more detailed diurnal analyses. This is particularly important for study populations, such as Samara, where there are large study troops, which due to the large number of study animals require a greater amount of data collection. For example, in the current study a total of 9641 scan samples were collected over approximately 13 months on two troops containing 48 (RBM) and 69 (RST) animals. In contrast, Baldellou and Adan (1997) were able to collect a relatively large number of scan samples (9295 scans) in a shorter period of time (8 months) by observing a single troop of vervets consisting of 18-23 individuals. Increasing the validity of ones findings is, however, important and although studying a single troop may result in a greater amount of data, it is also important to increase the validity and therefore generalizability of the results by

collecting data on more than one troop. Increasing the validity of ones research is likely to require a longer study period, as demonstrated by the limitations of the current study, which involved two unusually large study troops.

3.20.2 Activity Trade-Offs: Future research could also focus on sex differences in trade-offs between activities. The current findings suggest feeding is a high priority activity and that females trade feeding off against other activities, including resting. This result is not surprising given that females are considered the ecological sex. Also, grooming is not traded against any other activity. Comparing males and females will demonstrate basic sex differences in activity trade-offs and more specifically provide insight into which activities are high or low priority. From this, it may be possible to explore the socio-ecological demands experienced by males and females. Trade-offs could also be explored across seasons to determine how variation in resource availability (e.g. food) affects activity patterns.

3.21 Summary and Conclusions

The aims of this chapter were to explore time budgets and association patterns of free ranging adult vervet monkeys and to establish the broad context in which to situate the more detailed analyses of female social engagement. The current findings illustrate that females do not trade grooming against other activities. Instead, individuals maintain grooming whilst trading between feeding and resting and feeding and moving. The results also suggest that males and females were not differentially affected by their local ecology. Furthermore, the absence of sharp differences across season and day

demonstrate the need for a greater amount of data collection, especially when studying animals in unusually large troops. Collecting data on more than one troop, over a longer period of time, would not only improve the ecological validity of ones research but also increase the generalizability of ones results.

CHAPTER 4

COHORT SIZE AND THE STRUCTURE OF FEMALE SOCIALITY

4.1 Grooming

An understanding of primate sociality requires exploration of grooming, a behaviour that has long been recognised for its role in primate social relationships (Watson, 1908, Yerkes, 1933, Zuckerman, 1932). Grooming, a common form of affiliation, occurs among a variety of primate species and is predominantly observed in female-bonded Old World monkeys (Dunbar, 1991, Oki & Maeda, 1973). In female-bonded primates, such as vervets (*C. aethiops*), females remain in their natal group and form highly differentiated relationships with closely related females (Melnick & Pearl, 1987). These relationships are defined, in part, by patterns of social grooming (Wrangham, 1980). Grooming is mostly observed among female members of a group and has several functions that are of biological and social importance to primates (Dunbar & Dunbar, 1975, Kummer, 1968, McKenna, 1978).

Grooming is thought to have originally evolved for hygienic purposes whereby the recipient of grooming receives direct fitness benefits as the groomer searches through and removes ectoparasites and dirt from their pelage. Grooming, in this context, is advantageous for the recipient as it helps mitigate parasite infestation, reduce the risk of disease and thus maintains a healthy condition (Barton, 1985, Hutchins & Barash, 1976, McKenna, 1978, Struhsaker, 1967b). However, that time invested in grooming exceeds the amount necessary for skin care alludes to the possibility that hygiene is not the only

function grooming serves (Dunbar & Sharman, 1984, Goosen, 1981, Oki & Maeda, 1973).

Grooming has also been reported to have calming and tension reducing effects. Specifically, grooming has been linked to the release of β -endorphins and has been shown to modulate the recipients' physiological state, as reflected by a decrease in heart rate (Boccia, Reite & Ladenslager, 1989, Keverne, Martensz & Tuite, 1989, Oki & Maeda, 1973, Terry, 1970). In addition to its hedonic benefits, the indirect fitness benefits of grooming relate broadly to sociality and specifically to group cohesion and the service and maintenance of relationships (Dunbar, 1988, 1991, McKenna, 1978, Silk, Alberts & Altmann, 2003). Servicing and maintaining social relationships is paramount for females since deterioration of group cohesion may ensue if the demands of living in a group compromise an individual's ability to invest in their relationships (Dunbar, 1988, 1992).

4.2 Group Life

Maintaining group cohesion is important for female-bonded primates because it allows them to capitalise on the benefits that group life offers. Benefits primarily include detection of predators, cooperative resource defense and the ability to usurp resources during inter-group encounters (Dunbar, 1988, Wrangham, 1980). These benefits, however, are balanced against the costs of group life. One of the main demands of residing in a cohesive social group is competition between group members, including kin, over access to resources (Krebs & Davies, 1993, Ron *et al.*, 1996, Terborgh & Janson, 1986, Walters & Seyfarth, 1987). As the ecological sex, females predominantly compete over food, a resource that significantly contributes to their reproductive success (Gaulin

& Sailer, 1985). Thus, feeding competition, if severe, may affect a female's physical condition and therefore compromise individual fitness (Dunbar, 1988). The benefits, however, of cooperating with kin against individuals in other groups for access to feeding sites are thought to outweigh the costs of intra-group competition (Wrangham, 1980).

That alliances between females enhance their ability to procure resources, and grooming services these key relationships, has led to the assertion that grooming plays a central role in female social relationships and provides a useful index for the status of social relationships (Oki & Maeda, 1973, Sambrook, Whitten & Strum, 1995). The structure of these relationships are, however, widely variable and are influenced, amongst other factors, by socio-ecological factors including group size, kinship, rank, age, sex and resource competition (Dunbar, 1991, 1992, Seyfarth, 1977, 1980, Vervaecke, de Vries & van Elsaker, 2000).

4.3 Structure of Social Interactions

Demographic factors, such as group size, affect the distribution of social interactions, such as grooming, on both a quantitative and qualitative level. Specifically, groups that grow beyond the optimal size at which the environment can ecologically support them are vulnerable to the risk of ecological stress. Ecologically stressed groups attempt to maintain levels of feeding activity but exhibit a reduction in resting and social activity and become increasingly fragmented, which can potentially compromise group cohesion (Dunbar, 1991, 1992).

Group cohesion is affected by group spread, which increases as a function of group size and resource distribution (Henzi, Lycett & Piper, 1997a). As group size grows

females are confronted with the challenge of locating dispersed grooming partners, thereby making it increasingly difficult to groom all other female members of the group and thus maintain social bonds. When group size demands place social constraints upon females, grooming bout length is reduced, allowing grooming diversity to be maintained. If, however, constraints ensue, females may resort to reducing their number of grooming partners, resulting in smaller and less diverse grooming cliques (Henzi *et al.*, 1997b).

Social interactions are also affected by time budget constraints (Dunbar & Dunbar, 1988). However, even when confronted with such constraints females maintain grooming relationships with their primary partners and it is only when faced with severe constraints that social time is compromised. That females attempt to maintain grooming relations and allocate a large proportion of their time budget to this activity indicates grooming is of biological importance to these females (Henzi & Barrett, 1999).

In addition to group size and budget demands, rank also plays a role in structuring female social relationships. Seyfarth (1977), for example, proposed a model on attraction and competition to explain why higher-ranking females receive more grooming than they give and why grooming between females of adjacent rank occurs more often than expected. The premise for this model pertains to female attraction towards high-ranking female grooming partners, which, due to competition, results in closely ranked females grooming one another. Attraction to high-ranking females is, however, based on the assumption that females who groom one another also support one another and since high-ranking females have priority access to resources and a rank related advantage during agonistic interactions, they are expected to be preferred partners (Struhsaker, 1967b, Whitten, 1983, Wrangham, 1981).

Supporting evidence for Seyfarth's (1977) model relates to a behavioural study, also by Seyfarth (1980), on a group of free-ranging vervet monkeys (*C. aethiops*) and an experimental study involving playback experiments on the same population of vervet monkeys (Seyfarth & Cheney, 1984). Seyfarth (1980) demonstrated that grooming was linked to alliance formation and females competed for, and directed more grooming towards, higher-ranking females. It was also suggested that unrelated females who have previously groomed one another are more inclined to come to one another's aid (Seyfarth & Cheney, 1984). These studies have, however, been criticised for several reasons. First, in a reanalysis of Seyfarth's (1980) data the association between grooming and support was found not to be direct and individuals in the playback experiments (Seyfarth & Cheney, 1984) were reported to have behaved more responsively (i.e. gazed in the direction of the loudspeaker) to the calling monkey they had previously groomed, but did not, as the model predicts, exchange grooming for direct support (Hemelrijk, 1990, Henzi & Barrett, 1999).

Further evidence supporting Seyfarth's (1977) model is, however, equivocal. For example, although in a meta-analysis of 14 different primate species Schino (2001) reported competition for grooming partners significantly affects the distribution of grooming, there was no evidence that grooming was exchanged for support during agonistic interactions. Similarly, in a study on the social function of grooming bonobos (*Pan paniscus*) preferred to groom high-ranking individuals and exchanged grooming for support but did not compete for access to high-ranking individuals (Vervaecke, de Vries & van Elsacker, 2000). De Waal and Luttrell (1986), in a study on Rhesus macaques (*Macaca mulatta*), also provided mixed support regarding rank related grooming and the

exchange of grooming for support, concluding that the relationship between these social factors is not as simple as Seyfarth's (1977) model predicts. Additional research on macaques (*Macaca radiata*) indicates females tend not to compete for access to high-ranking females and rarely support the females who groom them the most (Silk, 1982). Likewise, Fairbanks (1980) was unable to demonstrate reciprocation of grooming and support in captive groups of vervet monkeys (*C. aethiops*).

According to Henzi *et al.*, (2003) even when female hamadrayas baboons (*Papio hamadrayas ursinus*) were not restricted in their access to partners they rarely engaged in coalitions, did not compete for grooming partners and high-ranking females gave, as well as received, the most grooming. Moreover, Chacma baboons (*P. hamadrayas ursinus*) maintain grooming relations even in the absence of resource competition (Henzi *et al.*, 1997b). Collectively, these findings provide little to no support for Seyfarth's (1977) grooming for support model.

4.4 Biological Markets

In light of the paucity of evidence pertaining to the role of grooming in coalition formation, the social function of grooming, a behaviour commonly observed in female-bonded primates, is brought into question. The direct hygienic benefits of grooming, coupled with an individual's inability to groom all of their body, has led to the suggestion that grooming is a commodity that can be exchanged or interchanged for access to other commodities (Barton, 1985, Henzi & Barrett, 1999).

Seyfarth (1977) incorporated the principles of exchange into his model, suggesting grooming could be exchanged for coalitionary support. Although indicative of

a biological market approach, Seyfarth's model does not consider fluctuations in resource availability or partner value and therefore presents a fixed view of social engagement that does not adhere to biological market principles (Henzi *et al.*, 2003). Grooming will therefore be incorporated into a biological market framework, formalised by Noë and Hammerstein (1995), to further our understanding of cooperation and how this affiliative behaviour can be traded for commodities other than coalitionary aid.

The biological market approach was developed in response to the shortcomings of models on intraspecific cooperation that are based on the repeated two-player Prisoner's Dilemma. This paradigm, although initially useful for understanding cooperation between unrelated individuals, is limited as individuals only have the choice of interacting with one other individual (cooperating) or forgoing interaction (defecting) with their partner all together (Axelrod & Hamilton, 1981, Noë & Hammerstein, 1995). In reality, however, individuals in social groups are not restricted to one partner but have the option to interact with a variety of individuals and are able to exert some choice over the partners they cooperate with (Barrett, Henzi, Weingrill, Lycett & Hill, 1999).

According to Noë and Hammerstein (1994) interactions involving the exchange of commodities between animals are similar to traders in human markets. Thus, in primates, for example, the social group is considered a market place and the individuals in that group are traders that have the potential to exchange or interchange commodities. Trade is determined by competition for resources and the supply and demand for resources (commodities) set the price at which they can be traded for. Fluctuations in individual behaviour are therefore indicative of changes within the market place.

Grooming, a suggested commodity, that can be exchanged for itself or interchanged for other commodities has been studied, in a biological market context, in a variety of primate species (*P. cynocephalus ursinus*: Barrett *et al.*, 1999, *C. aethiops*: Fruteau, Voelkl, van Damme & Noë, 2009, *Erythrocebus patas*, *Macaca fascicularis*: Gumert, 2007b, *Erythrocebus patas*: Muroyama, 1994, *Ateles geoffroyi yucatanensis*: Slater, Schaffner & Aureli, 2005, *Pan paniscus*: Stevens, Vervaecke, de Vries & van Elsacker, 2005). For example, in a study on female Chacma baboons (*P. cynocephalus ursinus*), the biological market paradigm was used to determine whether contest competition and dominance influences the exchange or interchange of grooming (commodity) for grooming or other services respectively (Barrett *et al.*, 1999). Where female dyads were closely ranked, time spent grooming was closely matched. Time matching in grooming also occurred in troops that, due to low levels of competition, were unable to interchange commodities. In contrast, there was some evidence suggesting that when competition was high time matching in grooming was reduced such that lower ranking females spent more time grooming than higher-ranking females.

Rank, therefore, sets the power differential between traders and plays a role in determining the nature of exchanges that can occur between individuals (Henzi & Barrett, 1999). Specifically, since high-ranking females have priority access to resources and low-ranking females are restricted in their access to resources, commodity interchange is likely to occur between females of distant rank (Wrangham, 1981, Barrett *et al.*, 2002). One example of interchange is grooming by a lower-ranking female for tolerance of a higher-ranking female (Barrett *et al.*, 1999, Barrett *et al.*, 2002). In contrast, adjacently ranked females, having similar resource holding potentials, are unable to interchange

resources and therefore exhibit reciprocal patterns of grooming (Barrett *et al.*, 1999). Female chacma baboons (*P. cynocephalus ursinus*) that engage in reciprocal grooming match the amount of time their partner invests in grooming by engaging reciprocally in discrete grooming episodes within a single bout. Breaking grooming bouts up into episodes by turn taking helps, according to the ‘parcelling’ model, to reduce the risk of defection and promotes cooperation and therefore reciprocal grooming (Barrett & Henzi, 2006, Barrett, Henzi, Weingrill, Lycett & Hill, 2000, Connor, 1995).

More recently a biological market framework was used to explain patterns of grooming among free-ranging vervet monkeys in a feeding context (Fruteau *et al.*, 2009). This study involved experimental manipulation of food availability by two low-ranking females. Grooming directed towards these females was found to be dependent on food availability with more grooming received by food providers when only one female gave the other group member access to food. That is, when food is plentiful the price paid for this commodity is lowered as reflected by a reduction in grooming directed towards the food providers.

A biological market framework has also been used to explore the relationship between grooming and tolerance (Barrett *et al.*, 2002). Specifically, following an increase in food availability high-ranking female Chacma baboons (*P. cynocephalus ursinus*) directed less aggression towards lower-ranking females and engaged in more reciprocal bouts of grooming. That is, a reduction in competition associated with an increase in resource availability reduces the dominance gradient between distantly ranked females and thereby increases the reciprocal nature of their social interactions.

4.5 Aims and Predictions

Collectively, studies on female sociality demonstrate that competition over access to resources is likely to structure female social interactions, reflected, in part, by patterns of social grooming (Barrett *et al.*, 2002, Fruteau *et al.*, 2009, Henzi *et al.*, 2003). Social grooming is a key component of Seyfarth's (1977) grooming for support model, which although receiving mixed support, has played a key role in the development of primate grooming models and recognises the importance of exchange, a key component of the biological market paradigm (Noë & Hammerstein, 1994, Schino, 2001). Thus far, however, the majority of research utilising a biological market framework has been conducted on baboon and macaque species and a few New world monkeys (e.g. Barrett *et al.*, 2000, Frank & Silk, 2009, Gumert, 2007b, Henzi & Barrett, 2002, Slater *et al.*, 2007). Further exploration of the biological market paradigm is therefore required in a greater variety of primate species.

In the current study, the assumptions of Seyfarth's (1977) grooming for support model will be tested in the two study troops at Samara (see Chapter 2) and compared to several other free-ranging vervet populations based on data available in the literature (see below). Collectively, the relationship between dominance rank, spatial association and grooming allocation will be assessed to determine how cohort size affects the dynamics of female social relationships. In addition, a biological market paradigm will be applied to further develop our understanding of how female vervets respond to local circumstances and how this, in turn, structures social relationships. Application of the two approaches will provide great insight into the driving forces shaping competitive interactions and thereby the structure of female sociality.

4.5.1 Dominance Hierarchies: In female philopatric primate species such as vervets, females are closely ranked to their mothers, compete with other females over access to resources and because of rank differences, have differential access to resources (Fedigan & Fedigan, 1980, Melnick & Pearl, 1987, Wrangham, 1981). Females, based on the outcomes of competitive interactions, can therefore be placed within a dominance hierarchy, which in vervets is organized linearly and depending on the steepness of the hierarchy, the outcome of agonistic interactions can be predicted quite consistently (Isbell & Pruett, 1998, Melnick & Pearl, 1987). A dominance hierarchy will be constructed for each of the study troops at Samara and the strength of agonistic relations will be determined by assessing the steepness of the hierarchy. It is expected that female dominance will be characterised by linear hierarchies in both troops.

4.5.2 Aggression: Rates and contexts of aggression will be assessed in the two study troops at Samara and compared to the three Amboseli vervet troops reported in Seyfarth (1980). As the ecological sex, females compete for access to resources and in vervets, like other female-bonded primate species, competition occurs over access to food and female grooming partners (Gaulin & Sailer, 1985, Pruett & Isbell, 2000, Seyfarth, 1980). According to Seyfarth (1980), grooming competition occurs between females because females who groom one another also provide coalitionary support to one another and since high-ranking females have priority access to resources and a rank related advantage during agonistic interactions, they are expected to be preferred partners (Struhsaker, 1967b, Whitten, 1983, Wrangham, 1981). If coalitions are indeed beneficial,

allowing females to procure resources, females are predicted, following Seyfarth (1980), to compete over access to grooming partners.

However, if, as reported in other primate species, coalitions are rare and females continue to groom in the absence of coalitions, alternative factors are likely to structure female social relationships (Barrett & Henzi, 2006, Henzi *et al.*, 2003, Silk *et al.*, 1999). That females compete for access to resources and the structure of female relationships fluctuate in accordance with changes in the local environment suggests ecological factors, such as seasonal variation in food availability, may affect rates of aggression (Barrett *et al.*, 2002, Barrett & Henzi, 2006, Pruett & Isbell, 2000). Monthly rates of aggression will be assessed in the two study troops to determine whether females i. engage in feeding related aggression and ii. exhibit temporal variation in aggression. If females do indeed respond to changes in local circumstances, such as seasonal fluctuations in food availability, and compete for access to food resources, rates of aggression are predicted to vary across the year, peaking during the dry (winter) season when food is typically less readily available. Furthermore, that group size has been suggested to affect intra-troop competition means larger troops, such as the two study troops at Samara, will experience greater time budget demands and more resource competition, as reflected by food-related agonism, than the smaller troops at Amboseli (Dunbar, 1991, 1992).

An understanding of primate sociality also requires exploration of grooming, a behaviour that has long been recognised for its role in primate social relationships (Watson, 1908, Yerkes, 1933, Zuckerman, 1932). Social relationships are structured, in part, by dominance, producing rank related variation in patterns of grooming (Barrett *et al.*, 1999, Singh, Krishna & Singh, 2006). Specifically, rank related differences in

grooming are determined, in part, by the steepness of the dominance hierarchy and thereby the strength of dominance relations (de Vries, Stevens & Vervaecke, 2006). According to Seyfarth (1977), female vervets exhibit rank related attraction towards female grooming partners, competing for access to high-ranking grooming partners because their ability to procure resources and win disputes makes them valuable coalition partners.

4.5.3 Grooming Competition: In the current study, I explored whether females compete for access to high-ranking grooming partners by assessing the effect of rank on the distribution of female grooming in two free-ranging vervet troops at Samara and in three free-ranging troops at Amboseli. Following Seyfarth (1977) high-ranking females are predicted to receive more grooming than low-ranking females and the ratio of grooming received to grooming given is expected to be greater for high-ranking than low-ranking females as the former will give less grooming than the latter. That is, there will be a rank related difference in the absolute amount of female grooming.

4.5.4 Grooming and Rank: The effect of rank on grooming will be explored in two free-ranging vervet troops at Samara and in three free-ranging troops at Amboseli. If, as has been reported in other female-bonded primate species, vervet females can be placed in a linear dominance hierarchy, indicative of their ability to procure resources, grooming is predicted to be directed up the hierarchy such that as rank increases, the amount of grooming given should decrease and the amount of grooming received should increase (Melnick & Pearl, 1987, Seyfarth, 1980). Specifically, rank effects on grooming

are expected to be greater at Samara, where troop sizes are larger and therefore more likely to experience greater competition, than the smaller troops at Amboseli.

4.5.5 Rank Distance and Grooming: The effect of rank distance on grooming will also be explored in the two study troops at Samara and in three vervet troops at Amboseli. If, following Seyfarth (1977), grooming and coalition formation are inter-related and females groom those females that could potentially provide valuable coalitionary support (i.e. high ranking females), grooming should be directed up the hierarchy as a means of securing support. However, because of dominance effects, females will be restricted in who they can groom and will therefore allocate more grooming towards individuals that are closer in rank to themselves.

4.5.6 Clique Size: Grooming clique size will be assessed in three vervet populations, including two free-ranging vervet troops at Samara, three free-ranging troops at Amboseli and two free-ranging troops at Loskop. Inter-troop differences will be explored in the Samara population. It is predicted that there will be a difference in clique size between troops that differ in cohort size. Specifically, individuals in larger troops are expected, due to increased competition and greater time budget constraints, to groom fewer females and therefore have smaller clique sizes than females in smaller troops (Dunbar, 1997, Henzi *et al.*, 1997, Nakamichi and Shizawa 2003). Thus, female grooming clique size at Samara will be smaller than the size of the troop's female cohort and the mean clique size will be smaller in the larger cohort.

4.5.7 Rank and Clique Size: The effect of rank on grooming clique size will also be explored in three vervet populations: Samara, Amboesli and Loskop. According to Seyfarth (1977), attraction towards high-ranking females promotes competition among females, but because of rank related constraints, lower-ranking females are limited in who they can groom. Unlike low-ranking females, high-ranking females are least constrained in their grooming activity because of their inherent rank related benefits. A rank related difference in clique size is expected such that there will be a positive relationship between rank and grooming cliques size. Higher-ranking females are predicted to have larger grooming cliques than lower-ranking females.

4.5.8 Grooming Clique Size, Cohort Size and Social Time: The current study also aims to explore the relationship between grooming clique size and female cohort size in relation to available social time. Patterns of grooming have been shown to vary with group size such that when group size increases grooming diversity decreases (Dunbar, 1991, Silk, Seyfarth & Cheney, 1999). Thus, although grooming plays an important role in the formation and maintenance of social relationships and females will attempt to service their social relationships by grooming other female members of the group, increases in group size, and therefore the number of potential grooming partners, have been suggested to place time budget constraints upon females such that they are unable to groom all females and are required to redistribute their grooming or, in some cases, cap their grooming cliques size (Dunbar, 1992, Henzi *et al.*, 1997b). In the current study the effect of cohort size on grooming clique size and social time is of particular interest due to the unusually large troop sizes in the Samara vervet population. Grooming diversity in

Samara troops will be compared with smaller vervet troops in the Amboseli and Loskop populations. It is predicted that females will cap their grooming clique size as cohort size increases beyond an optimal size such that females are unable, due to time constraints, groom all females. Also, as cohort size increases, allocation of social time to each female is expected to decrease, again due to time constraints. Thus, females in the Samara population, with their unusually large troops, will have smaller grooming clique sizes compared to vervet populations at Amboseli and Loskop. Similarly, the amount of social time available to each female is also expected to vary as a function of cohort size. It is predicted as cohort size increases time available to other clique members decreases.

4.5.9 Number of Nearest Neighbours: That group spread increases as a function of group size, potentially impeding an individual's ability to access social partners, and the size of the study troops at Samara are above average, makes these vervets a particularly interesting population to study. Specifically, the extent to which individuals are dispersed can, because of spatial constraints, impede an individuals' ability to access social partners (Henzi *et al.*, 1997a). Thus, the number of female neighbours will be assessed to determine whether a female's ability to access social partners is constrained by group spread or if partners are readily accessible, as indicated by the presence of nearest neighbours.

4.5.10 Number of Nearest Neighbours and Rank: If, according to Seyfarth (1977), high-ranking females are preferred partners they may be expected to have more female neighbours than lower-ranking females. I will therefore assess the possible relationship

between rank and the number of neighbours in each of the study troops at Samara. It is predicted that there will be a linear relationship between female rank and the number of nearest female neighbours.

4.5.11 Nearest Neighbour and Rank: Nearest neighbours may vary as a function of rank related competition. According to the biological market paradigm, resource competition not only structures female association patterns but determines, based on the competitive regime, whether resources are exchanged or interchanged (Barrett *et al.*, 1999). For example, although grooming can be exchanged reciprocally, it can also be interchanged, because of rank related differences in resource holding potential, for access to other resources (e.g. food, infants or tolerance, Barrett *et al.*, 1999, Barrett *et al.*, 2002, Henzi & Barrett, 2002). If grooming is interchanged, females are expected to interact with females that are not of similar rank to themselves (Henzi *et al.*, 2003). Thus, if competition is structuring female relations, nearest neighbours should not be similarly ranked. In contrast, when there is little to no competition, females exchange grooming for itself among similarly ranked females (Henzi *et al.*, 2003). In the absence of competition nearest neighbours are predicted to be of similar rank.

4.5.12 Nearest Neighbour and Rank Distance: According to Seyfarth (1977) dominance and rank structure female social relationships, suggesting, in the Priority of Access (POA) model, that females are attracted to high-ranking females as coalition partners because they have priority of access to resources thereby making a valuable coalition partner. Rank related attraction towards females is suggested to promote

competition, overt or covert, between females for access to high-ranking females. Passive competition creates inhibition among lower-ranking females (Henzi *et al.*, 2003). That is, lower-ranking females avoid higher-ranking females and thereby the other females that are in proximity to the high-ranking females (Hall & Fedigan, 1997). Thus, due to rank related competitive exclusion and female inhibition, females, under the POA model, are expected to spend more time in proximity to similarly ranked females. If this is the case, female neighbours should be of a similar rank to one another.

4.5.13 The Possible Role of Trade in Structuring Grooming Associations will be explored to determine whether realized grooming associations, in the absence of rank-effects, are a consequence of tactical partner choice by females, or whether they reflect mechanical constraints such as greater spatial dispersion and time budget asynchrony (Henzi *et al.*, 1997b). According to the biological market theory, partner choice is trade related, fluctuating in accordance with the competitive regime, which is set by the state of the local market as determined by current circumstances (e.g. food availability, Henzi *et al.*, 2003). Thus, when individuals are competing for access to resources, commodities (i.e. grooming) can be traded in exchange for access to other commodities (i.e. tolerance at feeding sites. Barrett *et al.*, 2002). Due to the rank related benefits of being a high-ranking female (e.g. better able to procure resources than lower-ranking females), lower-ranking females, during times of competition, are expected to trade grooming with higher-ranking females for access to resources. Greater rank discrepancies are therefore expected between female grooming partners during times of resource competition such

that as rank discrepancy increases, the discrepancy in grooming between partners also increases.

METHOD

4.6 Dominance

I used the matrix of all recorded agonistic encounters (Table 2.5, 2.6) to calculate normalized David's scores (NDS) for each female (Stevens *et al.*, 2005). NDS is a ranking method that provides an estimate of rank (based on repeated dyadic interactions) that can be subjected to parametric testing and allow comparisons of groups of different sizes, while also being considered a more reliable estimator of rank (Gammell, de Vries, Jennings, Carlin & Hayden, 2002, Stevens *et al.*, 2005, de Vries, 1998). Specifically, NDS calculations are based on the number of wins and losses between individuals during agonistic encounters and normalization of these scores is necessary to correct for variability in the number of inter-dyadic interactions. Higher rank is signaled by larger David's scores (Table 4.1). NormDS is calculated, for each individual, i , using the following formula:

$$DS = w + w^{(2)} - l - l^{(2)}$$

where w is the sum of i 's wins, l is the sum of i 's losses, $w^{(2)}$ is the sum of wins by those individuals defeated by i , $l^{(2)}$ is the sum of the losses of players to whom i lost.

Normalization of DS is required to determine the steepness of the hierarchies.

Normalization involves applying the following formula to DS:

$$\{DS + \text{MaxDS}(N) / N = \{DS + N(N-1)/2\} / N$$

where $\text{MaxDS}(N)$ represents the highest possible DS an individual can obtain in their group of N individuals.

4.7 Grooming

4.7.1 Distributions: I constructed grooming matrices for RBM and RST females, using the duration of grooming given and grooming received, during focal animal samples. Total amounts of grooming given and received by each female are presented in descending rank order (RBM: Table 4.2, RST: Table 4.3). One female from RST was excluded from all analyses involving grooming durations because her values were anomalous, as indicated by Mahalanobis distances. All female-female grooming bouts were dyadic.

4.7.2 Grooming Solicitations: The number of female-female grooming bouts that commenced with solicitation by one of the grooming partners was calculated as a percentage for each troop from focal animal sampling grooming data. Number of refusals was also calculated.

4.7.3 *Grooming Given and Received*: Female-female grooming bouts from focal animal samples were used to calculate the total amount of grooming (minutes: seconds) given and received by each female in RBM (Figure 4.3) and RST (Figure 4.4).

4.7.4 *Clique Size*: The allocation of each female's grooming to other members of the troop was used to determine the number of grooming partners each female has and, thereby, the size of her grooming clique, which was defined as the inclusive number of females she either groomed or from whom she received grooming, plus herself (Henzi *et al.*, 2003).

4.8 Spatial Associations

In order to test the null model that grooming associations were a consequence primarily of general spatial association, I used scan data to determine nearest female neighbour identities. In order to maximize the independence of the two data sets, only the nearest neighbours of foraging females were extracted from the scan data.

4.9 Comparative Data

I used published data on female cohorts in three vervet troops at Amboseli, Kenya (AMB-A: $N \sim 29$, $N_{\text{females}} = 8$; AMB-B: $N \sim 17$, $N_{\text{females}} = 7$ and AMB-C: $N \sim 30$, $N_{\text{females}} = 8$. Seyfarth, 1980) to calculate NDS and determine clique sizes in order to assess the effects of cohort size and rank on the allocated amounts and structure of grooming. The size of grooming cliques in each of two vervet troops at Loskop Nature Reserve, Mpumalanga (Picnic: $N = 15$, $N_{\text{females}} = 4$; Donga: $N = 15$, $N_{\text{females}} = 6$. A. Barrett, 2010, unpublished data),

together with time budget allocations to female grooming, were also available for comparison.

4.10 Statistical Notes

All proportions were Arcsine-transformed before analysis in order to improve the fit to the normal distribution. All curves were fitted using CurveExpert Professional v.1.1.1.

RESULTS

4.11 Dominance Hierarchies

Rank at Samara was transitive and well described by a linear fit for both troops ($NDS_{RBM} = 12.505 - 0.536 * \text{Ordinal rank}$, $N=15$, $R^2=0.93$; $p<0.001$; $NDS_{RST} = 18.754 - 0.648 * \text{Ordinal rank}$; $N=23$; $R^2=0.98$; $p<0.001$). This was also the case for the three troops at Amboseli ($NDS_{AMB-A} = 7.79 - 0.954 * \text{Ordinal rank}$, $N=8$, $R^2=0.99$, $p<0.001$; $NDS_{AMB-B} = 6.807 - 0.952 * \text{Ordinal rank}$, $N=7$, $R^2=0.98$, $p<0.001$; $NDS_{AMB-C} = 7.925 - 0.98 * \text{Ordinal rank}$, $N=8$, $R^2=0.99$, $p<0.001$).

To test for differences in the slopes of these regressions, both between troops and study sites, I ran a series of ANCOVA analyses, using a full factorial design with ordinal rank (OR) and either troop identity (ID) or study site (SS) as covariates.

i. I first tested the homogeneity of all five regression slopes. The whole model was significant ($F_{9,51}=515.23, p<0.001$), as was the ORxID interaction term ($F_{1,4}=13.25, p<0.001$), indicating a lack of homogeneity.

ii. I then used the same procedure to test for differences between troops at the two sites separately. The full model for each site was significant (Samara: $F_{3,34}=486.4, p<0.001$; Amboseli: $F_{5,17}=436.4, p<0.001$). The ORxID interaction was significant at Samara ($F_{1,1}=6.97, p<0.05$) but not at Amboseli ($F_{1,2}=0.28, p=0.75$).

iii. Last, I used the pooled data for each site to assess the steepness of the slopes of the hierarchies at the two sites. The whole model was significant ($F_{3,57}=353.58, p<0.001$) as was the interaction term ID*SS ($F_{1,1}=4.97, p<0.05$), indicating that hierarchies were steeper at Amboseli (Figure 4.1).

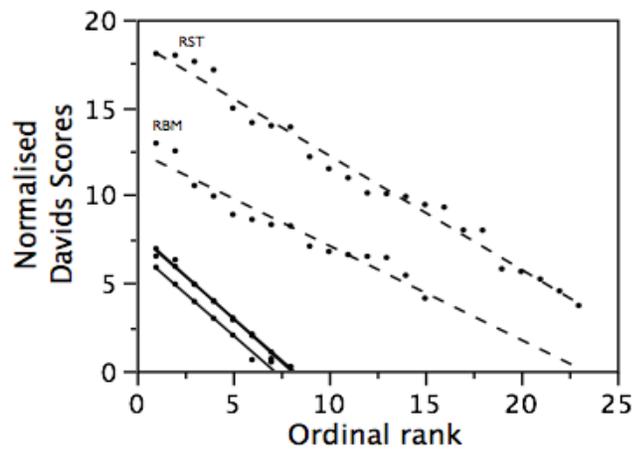


Figure 4.1. Dominance hierarchies for Samara (dashed lines) and Amboseli (solid lines).

Note that the lines for AMB-A and AMB-C overlap).

4.12 Aggression

Whereas I used all observed aggressive encounters to construct dominance hierarchies, I assessed the rate and contexts of aggression using 225 instances of female-female (FF) aggression collected over 224.4 hours of focal data from RBM (1.00 instance/hour) and 383 instances over 375.6 hours from RST (1.02 instances/hour). Most aggression was related to competition for food ($N_{\text{RBM}}=117$, 52.00%; $N_{\text{RST}}=207$, 54.04%), suggesting that coalitions might be advantageous to females. However, female-female coalitions against female targets accounted for only 1.33% of all aggression in RBM ($N=3$) and 0.78% in RST ($N=3$). There were correspondingly very few instances of aggression over access to grooming partners ($N_{\text{RBM}}=3$, 1.33%; $N_{\text{RST}}=3$, 0.78%). In contrast, estimated data from Seyfarth (1980) indicate a higher rate of aggression (~3.62 instances/hour). This is an over-estimate because data from ‘sequence’ samples were added to those collected during focal samples), of which relatively little was related to food (6.3%), while more was associated with access to grooming partners (10.53%). Quantitative data on coalition frequency are not provided by Seyfarth (1980) although he does indicate that 70% of female-female coalitions were directed against males. A more recent publication (Wittig, Crockford, Seyfarth & Cheney, 2007) alludes to a figure of 3% in total, which suggests that female coalitions against other females are a feature of 0.9% of female-female aggression. This is very similar to the mean value for the two Samara troops (1.05%).

Aggression was not evenly distributed across the year, being uncommon from January to April and most frequent from August to October (Figure 4.2). Monthly rates were very similar for the two troops ($r=0.89$, $N=12$, $p<0.0001$) and a matched-pairs t -test

indicated that RST had a consistently higher monthly rate of aggression (t -Ratio (11)=1.81, $p<0.05$).

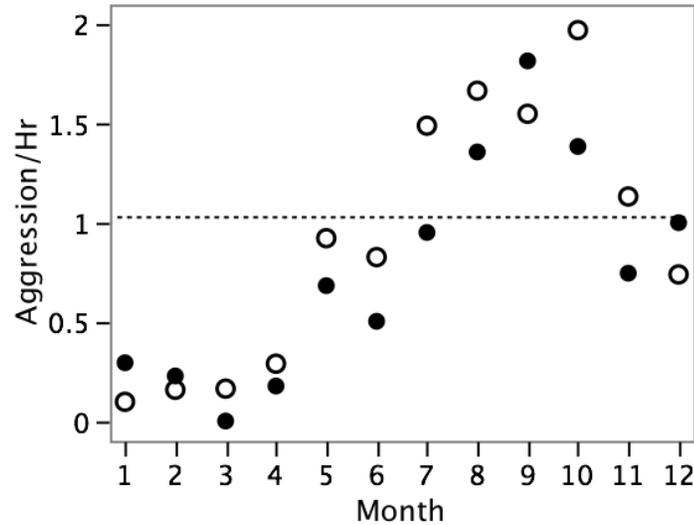


Figure 4.2. Monthly rates of female-female aggression (RBM: solid circles; RST: open circles). The dashed line indicates the approximate overall mean for both troops (1.01 aggressive encounters/hr).

4.13 Grooming Allocation.

4.13.1 Rank Effects: The matrices of the allocation of time to grooming partners are provided for RBM and RST in Tables 4.2 and 4.3 (see Appendix B and Figures 4.3, 4.4). Pairwise correlations for the different components of grooming in relation to rank as well as between the amount of grooming received by each female in relation to that given are provided for both Samara study troops and the three Amboseli troops (Table 4.4).

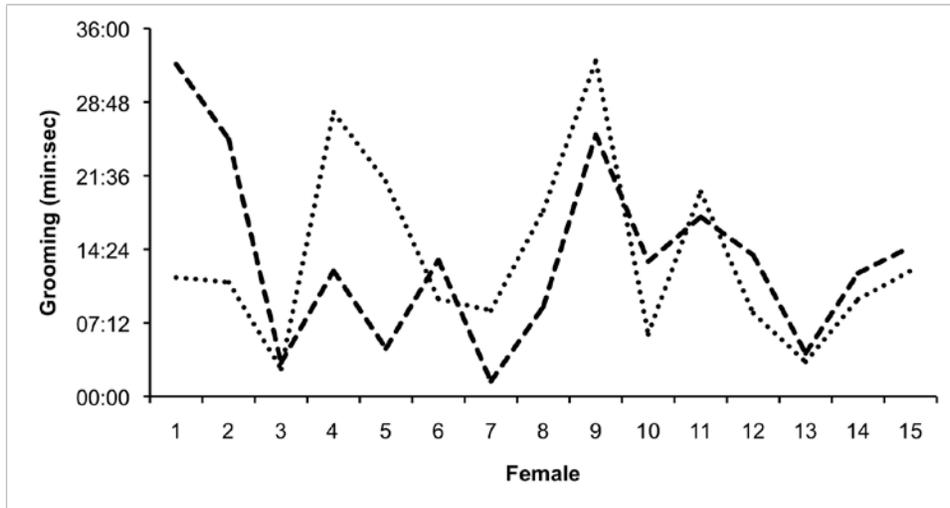


Figure 4.3. Total amount of grooming given (dotted line) and received (dashed line) by each focal female in RBM (1: highest ranking female, descending in order of rank).

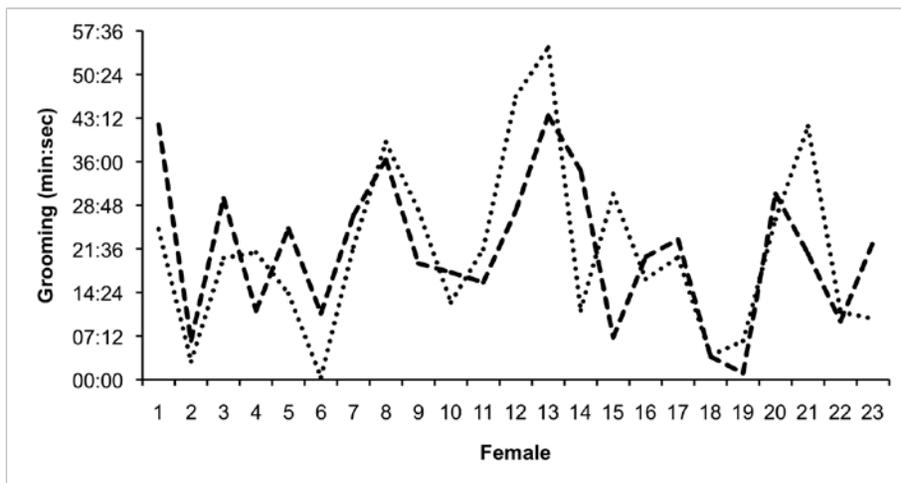


Figure 4.4. Overall amount of grooming given (dotted line) and received (dashed line) by each focal female in RST (1: highest ranking female, descending in order of rank).

Table 4.4. Pairwise correlations between the normalized David's score and three measures of grooming duration as well as between the amounts of grooming received and given. One extreme outlier was excluded from the analysis for RST (Mahalanobis Distance=4.55). Data for Amboseli (AMB) were extracted from Table I (Dominance interactions) and Table II (Grooming distributions) in Seyfarth (1980).

Troop	DS: Grooming received/given	DS: Grooming given	DS: Grooming received	Grooming received:Grooming given
RBM	r=0.32; N=15; p=0.24	r=0.18; N=15; p=0.94	r=0.33; N=15; p=0.22	r=0.33; N=15; p=0.22
RST	r=0.21; N=22; p=0.33	r=0.003; N=22; p=0.98	r=0.23; N=22; p=0.29	r=0.57; N=22; p=0.005*
AMB-A	r=0.66; N=8; p=0.07	r=0.86; N=8; p=0.006*	r=0.82; N=8; p=0.01	r=0.73; N=8; p=0.037*
AMB-B	r=0.41; N=7; p=0.35	r=0.09; N=7; p=0.84	r=0.8; N=7; p=0.027*	r=0.25; N=7; p=0.58
AMB-C	r=0.63; N=8; p=0.09	r=0.4; N=8; p=0.31	r=0.76; N=8; p=0.026*	r=0.15; N=8; p=0.12

4.13.2 Rank Distance Effects: While there is little indication of overt competition for access to grooming partners at Samara, it remains possible that there is covert competition (Henzi *et al.*, 2003). If so, Seyfarth's (1977) model, together with his data from the three Amboseli troops, predicts that female grooming will generally be restricted to those close in rank. We then expect the relative allocation of grooming to be negatively correlated with rank distance. I correlated the rank difference (RD) between each female and her grooming partners with the proportion of her grooming allocated to them. I found no relationship for RBM ($N_{\text{dyads}}=94$; $r=-0.1$; $p=0.3$) or RST ($N_{\text{dyads}}=110$; $r=-0.004$; $p=0.6$). At Amboseli, the correlation reached significance for two troops (AMB-A: $N_{\text{dyads}}=56$; $r=-0.56$; $p<0.001$; AMB-C: $N_{\text{dyads}}=56$; $r=-0.28$; $p<0.05$) while it approached conventional significance for the third (AMB-B: $N_{\text{dyads}}=42$; $r=-0.26$; $p=0.09$). The results are illustrated in Figure 4.5. To deal with the variable, repeated contribution of individual females, I analysed each site separately (because of the absolute differences in NDS size) with proportion of grooming as the DV. For Samara, I entered target female identity within troop as a random effect. RD and Troop were then entered as fixed effects in a full factorial model. The results indicate that neither main effect nor their interaction reached significance at Samara (Table 4.5). For Amboseli, given the fact that all possible dyads were represented, and because a mixed model failed to converge, I did not include any random effects but ran the full factorial described for Samara. The data for Amboseli indicate a significant negative relationship between RD and proportion of the target female's grooming, while neither Troop nor the RD*Troop interaction reached significance (Table 4.6).

Table 4.5. Comparison of proportion of grooming at Samara in relation to the rank difference between partners.

Parameter Estimates					
Term	Estimate	Std Error	DFDen	t Ratio	Prob>t
Intercept	0.176	0.0243	77.95	7.19	P<0.001
RD	-0.005	0.006	119.6	-0.89	P=0.37
Troop	-0.011	0.014	25.41	-0.76	P=0.45
Troop*RD	-0.004	0.006	119.6	-0.67	P=0.51
Fixed Effect Tests					
Source	Nparm	DF	DFDen	F Ratio	Prob>F
RD	1	1	119.6	0.7975	P=0.37
Troop	1	1	25.41	0.5745	P=0.45
Troop*RD	1	1	119.6	0.4472	P=0.51

Table 4.6. Comparison of proportion of grooming at Amboseli in relation to the rank difference between partners.

Parameter Estimates					
Term	Estimate	Std Error	t Ratio	Prob>t	
Intercept	0.2228885	0.016	13.15	P<0.001	
RD	-0.025811	0.005	-4.82	P<0.001	
Troop[AMB-A]	-0.005433	0.0117	-0.46	P=0.64	
Troop[AMB-B]	0.0104085	0.0127	0.81	P=0.42	
(RD-2.8)*Troop[AMB-A]	-0.012725	0.007	-1.77	P=0.08	
(RD-2.8)*Troop[AMB-B]	0.0040411	0.008	0.49	P=0.63	
Fixed Effect Tests					
Source	Nparm	DF	Sum of Squares	F Ratio	Prob>F
RD	1	1	0.25487374	23.2770	P<0.001
Troop	2	2	0.00726312	0.3317	P=0.73
RD*Troop	2	2	0.03946554	1.8021	P=0.17

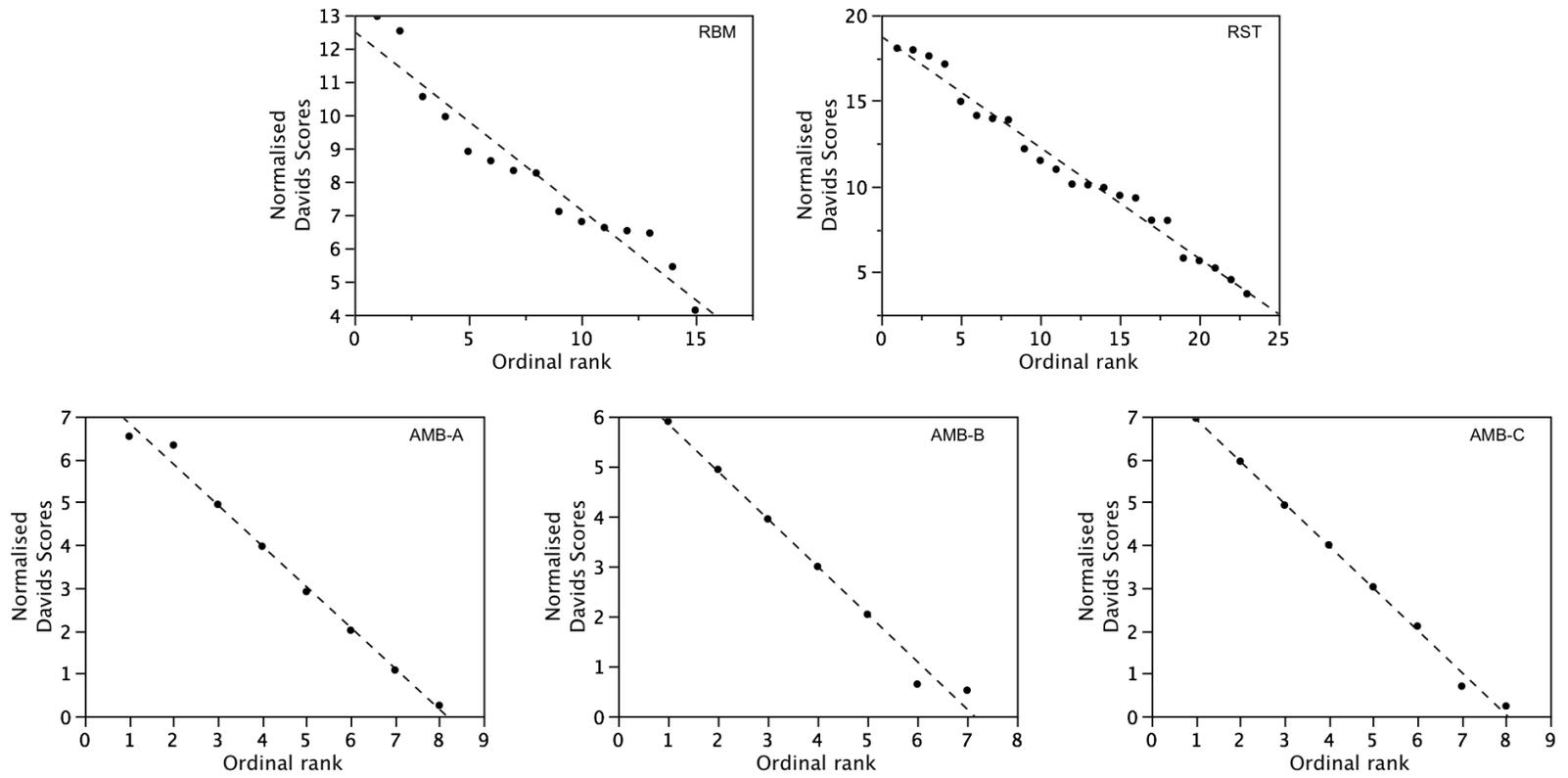


Figure 4.5. Normalized David's Score hierarchies for RBM, RST, AMB-A, AMB-B and AMB-C.

4.13.3 Grooming Solicitations and Refusals: Of all the observed grooming bouts between adult and sub-adult females in RBM 37% commenced following solicitation and 24% of those solicitations were refused. Of those refusals, 100% involved non-adjacently ranked females. For RST, 43% of grooming bouts commenced following solicitation and 24% of those solicitations were refused. Of those refusals 4.2% involved adjacently ranked females and 95.8% involved non-adjacently ranked females.

4.13.4 Grooming Clique Size: The Poisson distribution provided the best fit to the number of grooming partners in both troops (Kolmogorov Test: $D_{\text{RBM}}=0.096$, $p=1.0$; $D_{\text{RST}}=0.13$, $p=0.51$). The mean number of grooming partners for each female was 6.26 for RBM (Range: 2-10; Figure 4.6a) and 5.32 for RST (Range: 1-12; Figure 4.6b). Troop values were not significantly different (Wilcoxon test: $Z=-1.28$; $N_{\text{RBM}}=15$, $N_{\text{RST}}=23$, $p=0.2$). All females groomed one another in the three Amboseli troops (clique sizes: AMB-A=8; AMB-B=7; AMB-C=8), as did all females in the Picnic troop at Loskop (clique size=4). The mean clique size for the Donga troop at Loskop was 5.0 (+/-0.89 *SD*).

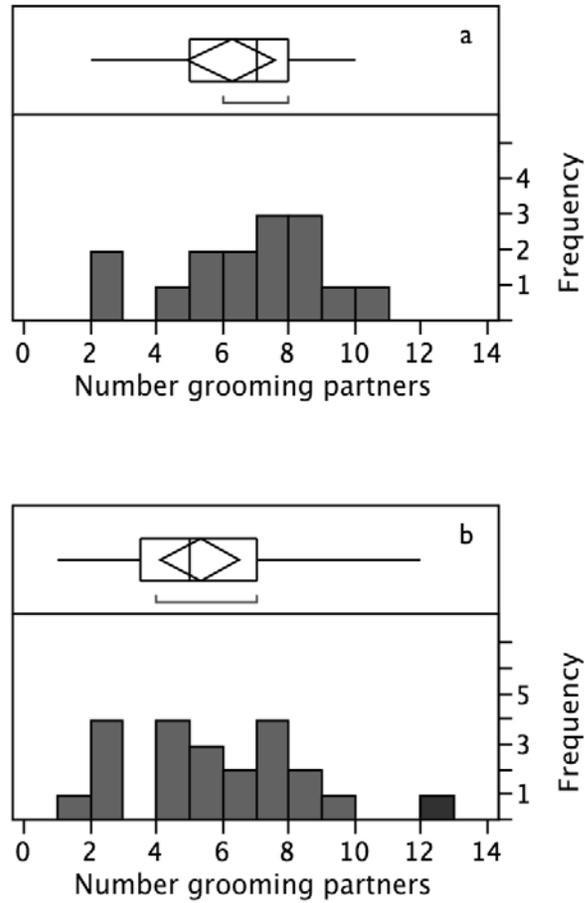


Figure 4.6. The distribution of grooming clique size for RBM (a) and RST (b), together with box-and-whisker plots. These indicate both the range (whiskers) and interquartile range (box), together with the median value (line inside box), the mean and 95% CI (means diamond).

4.13.5 *Grooming Clique Size and Rank*: There was no correlation between NDS, as a measure of rank, and the number of grooming partners at Samara ($r_{\text{RBM}}=0.18$, $N=15$, $p=0.51$; $r_{\text{RST}}=-0.002$, $N=23$, $p=0.99$. Figure 4.7).

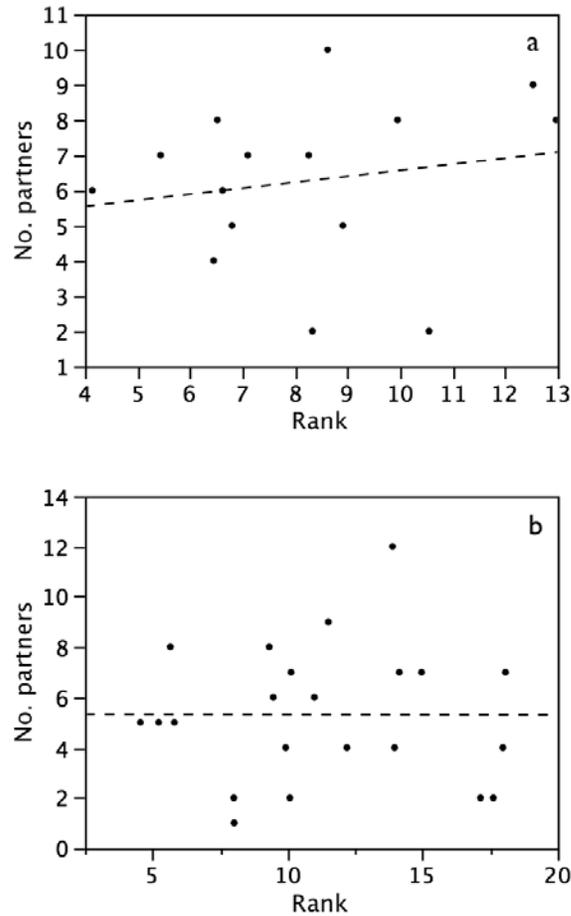


Figure 4.7. The relationship between dominance rank (NDS) and clique size in RBM (a) and RST (b). The dotted line indicates the regression.

4.13.6 *Grooming Clique Size, Cohort Size and Social Time*: The relationship between grooming clique size and cohort size in the three populations for which there are data, suggests that clique size matches cohort size until cohort size reaches about eight,

after which clique size declines. In line with this, a second-order polynomial provides the best fit to the data ($r=0.63$, $N=7$, $p<0.01$. Figure 4.8a). This relationship may well be complicated by site-specific time budgets (Dunbar, 1992, Henzi *et al.*, 1997), which circumscribe the time that can be allocated to different females. One way to control for this is to consider the average grooming time available for allocation to other clique members or to other cohort members (Figure 4.8b). The best-fit curve for the allocation of grooming time to other clique members is described by the equation:

$$y=1.72+1.365*x+1.64/x^2 (R^2=0.99),$$

while that for the allocation to other cohort members is:

$$y=1/(9.22+7.44*\ln(x)) (R^2=0.99),$$

where y =Percentage grooming time and x =Cohort size.

What Figure 4.8b indicates is that whereas available time for cohort members continues to decline, time available to other clique members stabilizes or, possibly, increases as a consequence of smaller clique sizes in larger cohorts. The question that arises is whether this reduction in clique size is a strategic response designed to arrest the decline in time available to groom other partners or whether it is a by-product of size-related changes in spatial association that make social coordination more difficult (Henzi *et al.*, 1997). One way into this question is to consider spatial associations themselves and to compare these to patterns of social interaction.

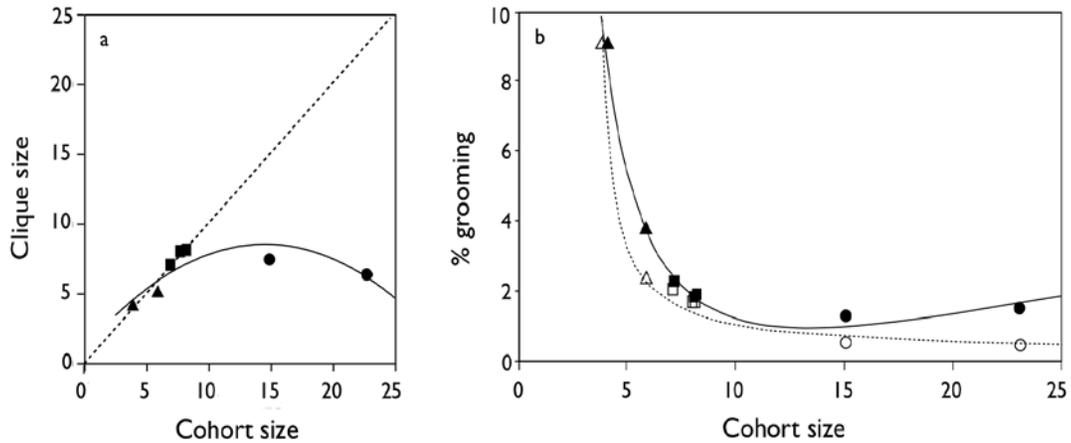


Figure 4.8. (a). The relationship between the size of the female cohort and female grooming clique size. The solid line indicated the polynomial fit and the dashed line indicates where cliques and cohorts are of equal size. (b). The relationship between cohort size and the percentage of social time available to each female if she is to allocate time to all other clique (solid line) and cohort members (dashed line) equally. Loskop: triangles; Amboseli: squares; Samara: circles.

4.14 Spatial Association

I used scan data to identify each female's nearest female neighbour when she was foraging in order to assess the null model that grooming cliques mirror general spatial association – i.e. when females are free to groom, they engage with those females who are nearby.

4.14.1 Number of Nearest Neighbours: In contrast to the restricted number of grooming partners, females in both troops encountered many more females as nearest

neighbours ($\text{Mean}_{\text{RBM}}=11.46$, 2.74 *SD*; $\text{Mean}_{\text{RST}}=18.26$, 3.75 *SD*). Neither distribution (Figure 4.9) differed from the Poisson model (Kolmogorov Test: $D_{\text{RBM}}=0.19$, $N=15$, $p=0.43$; $D_{\text{RST}}=0.19$, $N=23$, $p=0.18$) although the central tendencies were significantly different (Wilcoxon test: $Z=-4.14$, $p<0.001$).

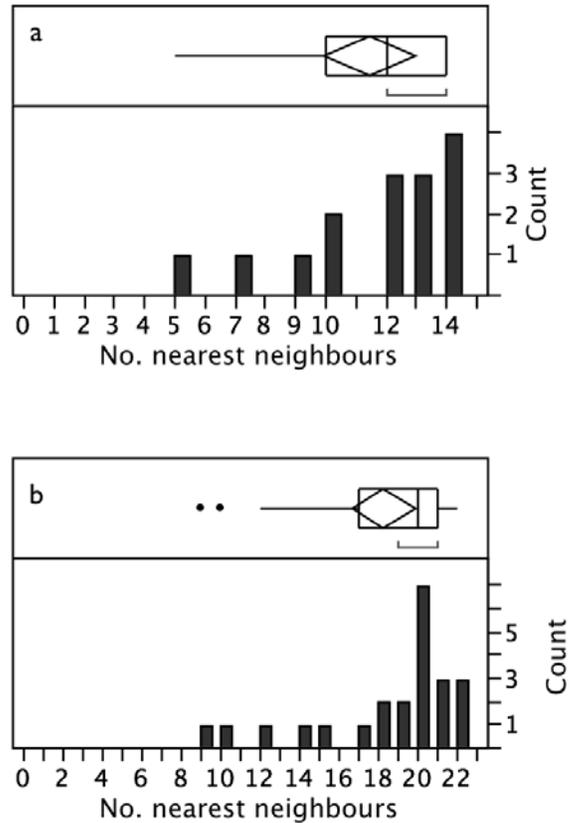


Figure 4.9. The distribution of the number of nearest female neighbours for RBM (a) and RST (b) females, together with box-and-whisker plots. These indicate both the range (whiskers) and interquartile range (box), together with the median value (line inside box), the mean and 95% CI (means diamond).

4.14.2 *Number of Nearest Neighbours and Rank*: To assess the possibility that there was a relationship between rank and the number of nearest neighbours, I ran an ordinal logistic regression with number of nearest neighbours as the DV and NDS and Troop as main effects in a full factorial model. While the main effect of troop was significant ($R=19.47$, $p<0.001$) neither that of NDS ($R=0.01$, $p=0.9$) nor their interaction ($R=1.45$, $p=0.22$) were (Figure 4.10).

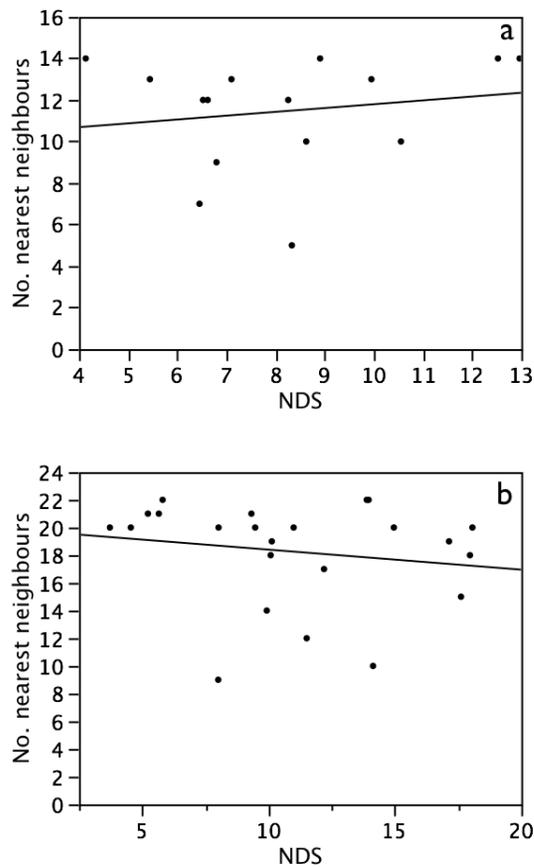


Figure 4.10. The relationship between dominance rank (NDS) and the number of nearest neighbours in RBM (a) and RST (b). The dotted line indicates the regression.

4.14.3 Nearest Neighbours and Rank Distance: I determined the proportion of each female's scans allocated to each of her nearest neighbours as well as the absolute difference in NDS between them (RD). To assess the relationship between rank distance and the frequency with which females are nearest neighbours, I ran a mixed model with proportion of scans as the DV, Target female identity (within Troop) as a random effect and RD and Troop as fixed effects in a full factorial model. The analysis indicates a significant negative correlation between RD and the likelihood of two females being nearest neighbours (Table 4.7), although the slope was not steep. While there was a significant main effect for Troop, Troop*RD was not significant (Table 4.7).

Table 4.7. Comparison of proportion of foraging time that females at Samara were nearest neighbours, in relation to their rank difference.

Parameter Estimates					
Term	Estimate	Std Error	DFDen	t Ratio	Prob>t
Intercept	0.083	0.0045	78.44	18.44	P<0.001
Troop (RBM)	0.015	0.0033	26.74	4.54	P<0.001
RD	-0.002	0.0009	540.8	-2.13	P<0.05
(RD-4.66171)*TROOP	0.001	0.0009	540.8	1.30	P=0.19
Fixed Effect Tests					
Source	Nparm	DF	DFDen	F Ratio	Prob>F
Troop	1	1	26.74	20.6184	P<0.001
RD	1	1	540.8	4.5158	P<0.05
RD*Troop	1	1	540.8	1.6923	P=0.19

4.14.4 The Relationship Between Relative Grooming Allocation and Degree of Spatial Association: In order to determine whether the relative representation of grooming partners for each female was a consequence of their general pattern of

association, I entered the proportion of grooming given to each partner as the DV, with female ID (within Troop) as a random effect. I entered Troop and Ordinal spatial rank as the two fixed, main effects. Ordinal spatial rank allowed me to compare the two troops as it dealt with the problem of different cohort sizes. I derived ordinal spatial rank simply by allocating rank 1 to the female who, of all her grooming partners, was most frequently the target female's nearest neighbour. So, whereas the four grooming partners of a target female might have the actual spatial ranks of 6, 12, 14 and 18, their ordinal spatial ranks would be 1, 2, 3 and 4. I did not specify an interaction term because doing so led to lost DFs and a failure of the model to converge. I found no main effect for either Troop ($F_{1,7.2}=0.017, p=0.9$) or ordinal spatial rank ($F_{10,121}=1.17, p=0.31$). The absence of an effect of ordinal spatial rank held for the two troops analysed separately (RBM: $F_{9,59.4}=0.77, p=0.63$); RST: $F_{10,84.61}=0.85, p=0.58$). Not surprisingly, therefore, there is no significant relationship between proportion of grooming and actual spatial rank (results not presented). To indicate the lack of close correspondence between grooming and spatial ranks in another way, I calculated the mean spatial association rank of each female's top-ranked grooming partner. For RBM, this was 6.0 (+/-2.45 *SD*), while for RST it was 9.8 (+/-6.9 *SD*). There was no relationship between female dominance rank (NDS) and the spatial association rank of her most frequent nearest neighbour ($r_{\text{RBM}}=0.145, N=15, p=0.6$; $r_{\text{RST}}=0.13, N=21, p=0.59$). Note that two females in RST had top-ranked grooming partners that were never recorded as their nearest neighbours.

4.15 Trade

4.15.1 Possible Role of Trade in Structuring Grooming Associations: The data indicate that the capping of clique size is not a consequence of restricted access to other females during the day. The question then arises as to whether realized grooming associations, in the absence of rank-effects, are a consequence of tactical partner choice by females, or whether they reflect mechanical constraints such as greater spatial dispersion and time budget asynchrony (Henzi *et al.*, 1997b). In the absence of evidence for an increased need to sustain advantageous alliance partnerships, the seasonal shift in foraging-related aggression suggests the possibility that the overall association patterns may reflect seasonal shifts in partner choice, with grooming being traded for tolerance when food is scarce (Barrett *et al.*, 2002; Henzi *et al.*, 2003). I test this hypothesis here, using immediately reciprocated grooming data from each of the two periods (Low aggression: January-April; High aggression: July-October. See Figure 4.2). More specifically, I test the predictions that (i) there will be an increase in rank difference among grooming partners when aggression is high and (ii) that increased absolute rank difference will be positively correlated with the absolute discrepancy in grooming time provided by each of the two groomers. As my sample size is small ($N=42$), this can only be a preliminary assessment (I do not analyse the two troops separately) and I begin by presenting the seasonal correlations between rank distance and grooming time discrepancy (Figure 4.11). The data indicate no correlation when aggression is low ($r=-0.06$, $N=21$, $p=0.77$) and some suggestion of a negative correlation when it is high ($r=-0.33$, $N=21$, $p=0.14$), which goes against the prediction. To account for the variable, repeated contribution of individual females, I entered grooming time discrepancy as a DV

in a full factorial model with AGG (Aggression level) and ABS RD (rank difference) as fixed, main effects and groomer ID as a random effect. While there are no significant main effects, the results provide some suggestion of an interaction between levels of aggression and rank differences in relation to differences in the amounts of immediately reciprocated grooming (Table 4.8). However, as Figure 4.11 indicates, this is likely to go against the biological market prediction.

Table 4.8. The relationship between grooming time discrepancy (DV), rank difference (ABS RD) and aggression level (AGG).

Parameter Estimates					
Term	Estimate	Std Error	DFDen	t Ratio	Prob>t
Intercept	204.32	38.81	38	5.26	P<0.001
ABS RD	-8.000	9.682	38	-0.83	P=0.41
AGG*ABS RD	12.635	6.76	38	1.87	P=0.07
AGG	35.639	23.1	38	1.54	P=0.13
Fixed Effect Tests					
Source	Nparm	DF	DFDen	F Ratio	Prob>F
ABS RD	1	1	38	0.68	P=0.41
AGG*ABS RD	1	1	38	3.49	P=0.07
AGG	1	1	38	2.38	P=0.13

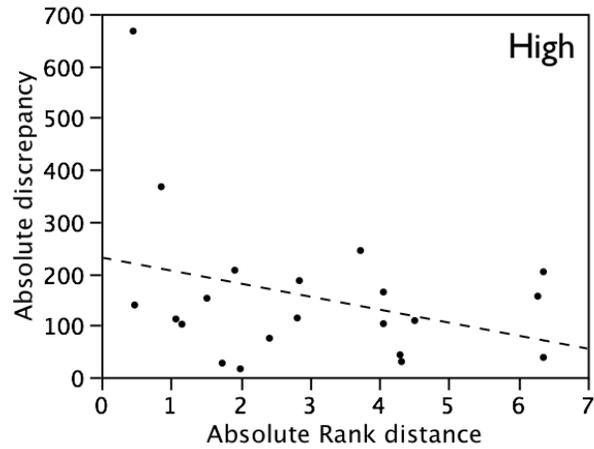
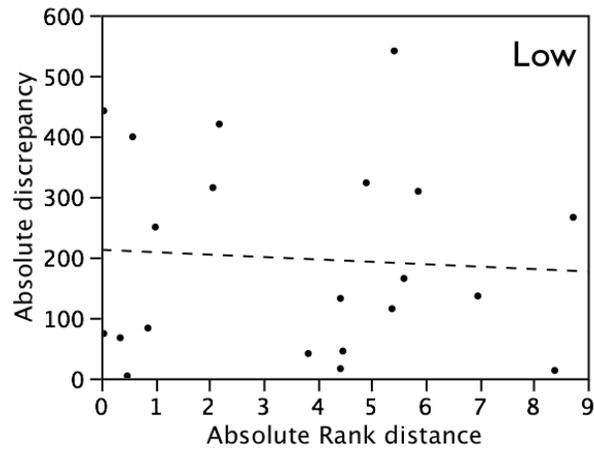


Figure 4.11. The relationship between the rank distances and discrepancies in grooming time of female participants in individual, reciprocated grooming bouts when levels of aggression are low ($N=21$) and when they are high ($N=21$).

Table 4.1. Normalized David's scores (NDS) and ordinal rank order for all focal females.

RST ID	NDS	Ordinal Rank	RBM ID	NDS	Ordinal Rank
PJ	18.07	1	AM	12.97	1
IZ	17.97	2	SA	12.53	2
QT	17.62	3	FA	10.55	3
ME	17.14	4	MI	9.95	4
DO	14.96	5	LO	8.91	5
AL	14.14	6	PE	8.62	6
HE	13.96	7	SC	8.33	7
WI	13.89	8	TS	8.26	8
CL	12.20	9	GI	7.10	9
EL	11.51	10	VA	6.80	10
NI	11.00	11	DS	6.62	11
TE	10.13	12	RO	6.52	12
RU	10.09	13	KA	6.45	13
XA	9.93	14	OC	5.44	14
SF	9.47	15	HO	4.14	15
UM	9.32	16			
GL	8.02	17			
VV	8.01	18			
ZI	5.81	19			
LI	5.66	20			
FE	5.23	21			
JE	4.55	22			
KI	3.72	23			

DISCUSSION

4.16 Summary of Findings

Social relationships are structured by numerous social factors, including dominance. In the current study, all five troops (RBM, RST, AMB-A, AMB-B, AMB-C) had linear dominance hierarchies, with the smaller Amboseli troops having steeper hierarchies than the larger Samara troops. Where dominance relations are linear, females are likely to have differential, rank-related access to resources (Melnick & Pearl, 87). According to Seyfarth (1977), female vervets exhibit rank related attraction towards female grooming partners and compete over high-ranking females because their rank related ability to procure resources makes them valuable coalition partners. In the current study, however, females rarely competed over access to female grooming partners. Instead, the majority of competition, in each of the study troops, was food related (RBM: 52%, RST: 54.04%).

According to Seyfarth's (1977) grooming for support hypothesis, where competition exists (e.g. over food) females are expected to compete over access to grooming partners in order to procure coalitionary support and thereby increase the chances of defending or obtaining resources. That females are suggested to benefit from engaging in coalitions and the majority of competition at Samara was food related eludes to the possibility that coalitionary support could have been advantageous during competitive food related interactions. However, in contrast to Seyfarth's assumption, female-female coalitions against female targets were rarely observed in the two study

groups at Samara. Similarly, Seyfarth (1980) later revealed that males, not females, were the targets of most (70%) female-female coalitions.

It should be noted, however, that although Seyfarth's Amboseli vervets exhibited rates of aggression that were three times higher than the Samara vervets, the methodology used to calculate rates at Amboseli is likely to have resulted in an overestimation of aggression. Also, although the frequency of aggression involving coalitions are not provided for the Amboseli groups, the frequency of coalitions at Samara (1.05%) was found to be very similar to those reported in a more recent study on baboons (0.9%, Wittig *et al.*, 2007). The extremely low occurrence of female coalitions towards female targets supports previous research on Old World primates and alludes to the possibility that coalitions are unlikely to be a central organising component of female social relationships (Fairbanks, 1980, Henzi *et al.*, 1997b, Ron *et al.*, 1996, Silk *et al.*, 2004).

Seyfarth (1977) also suggested that female competition for access to high-ranking grooming partners promotes competitive exclusion, thereby restricting grooming to adjacently ranked females. Although at Samara female rank distance was not negatively correlated with the proportion of grooming allocated to female grooming partners, which is what we would expect if females were not competing for access to high-ranking grooming partners, a significant effect was found in a reanalysis of Seyfarth's Amboseli data using David's scores, indicating as female rank distance increases, the proportion of grooming decreases. The current findings from Samara corroborate with previous studies on a variety of Old World primates indicating females are not restricted to grooming adjacently ranked females and do not compete for access to high ranking partners (Chapais, 1983, Silk, 1982, de Waal & Luttrell, 1986).

4.17 Seyfarth's Grooming for Support Model

There are several possible reasons why female grooming patterns generally do not corroborate Seyfarth's (1977) model. First, that females are suggested to groom one another in exchange for future support implies these individuals are planning for the future and thereby have the cognitive ability to think ahead and plan accordingly.

Although monkeys are capable of solving problems, whether they are cognitively capable of off-line thought and thus have the ability to plan ahead is, however, questionable (Barrett & Henzi, 2002, Roberts, 2002). Also, that females have previously been found to groom one another in the absence of coalitions, coupled with the general rarity of coalitionary aid, suggests coalitions are unlikely to be a central organising feature of sociality in female bonded primate species (Barrett & Henzi, 2002, Henzi *et al.*, 1997b, Henzi *et al.*, 2003). Furthermore, that the females in the current study mostly competed over food resources, did not groom closely ranked partners and aggression fluctuated across the year, suggests variation in resource availability may structure female social relationships and that reconsideration of the function of grooming is timely and necessary.

Social relationships, as defined by grooming and association patterns, have previously been shown to fluctuate in accordance with variation in local socio-ecological circumstances, suggesting females respond to current, local conditions and do not, as proposed by the grooming for support model, plan for the future (Barrett & Henzi, 2002, Seyfarth, 1977). According to the biological market model and empirical findings, grooming can be exchanged for access to other resources or interchanged for further grooming (Barrett *et al.*, 1999, Fruteau *et al.*, 2009). Like the biological market model,

the grooming for support model acknowledges the importance of exchange, partner choice and competition (Seyfarth, 1977). These factors, coupled with consideration of changes in local circumstances and fluctuations in partner value, are key components of the biological market paradigm. However, unlike Seyfarth's (1977) model, the biological market paradigm does not assume that the primary function of grooming is to secure coalitionary support. Instead, grooming is considered a valuable service that, through immediate exchange or interchange, provides access to commodities, including, but not limited to, coalitionary support, access to infants and tolerance (Barrett & Henzi, 2002, Barrett *et al.*, 1999, Chancellor & Isbell, 2008, Fruteau *et al.*, 2009).

4.18 Aggression

Rates of aggression were also assessed in the two study troops at Samara. The largest troop (RST) was found to consistently experience higher monthly rates of aggression across the year. Variations in rates of aggression have been associated with group size effects and the level of competition within groups. Specifically, animals in larger groups experience greater resource competition than animals in smaller groups and females, being the ecological sex, are particularly responsive to fluctuations in local resource competition (Gaulin & Sailer, 1985, van Schaik & van Noordwijk, 1988). Group size effects may therefore have contributed to the difference in rates of female aggression between the two study troops.

4.19 Clique Size

In the current study, there was no effect of rank on clique size but there was an effect of group size on clique size. An inter-population assessment of the relationship between grooming clique size and female cohort size in relation to available social time revealed all females groomed one another in the three Amboseli troops, as did all females in the Picnic troop at Loskop. Samara females, however, have bigger cohorts but are represented by a small mean clique size of 5-6 females. Previous research indicates that the diversity of grooming is affected by group size with individuals in larger groups grooming a small number of partners such that as group size increases, grooming diversity decreases (Dunbar, 1991, Nakamichi & Shizawa, 2003, Silk *et al.*, 1999). According to Dunbar (1992) the greater foraging effort required in larger troops constrains social time such that females are unable to maintain reciprocal grooming relationships or service relationships with potential coalitionary partners. Females are subsequently forced to reduce their clique size and focus their grooming efforts on a smaller number of partners. Although the females in the current study rarely engaged in coalitions, it is possible that time constraints associated with foraging demands could have limited the amount of time a female was able to allocate to grooming. Females at Samara spent more than half of their time foraging and only 8.5% of their time engaged in social interactions, which is much smaller than the amount of social time reported in other vervet troops (e.g. Baldellou & Adan, 1997). It is therefore not surprising that females with limited social time were found to have small clique sizes.

Small clique sizes in large cohorts have also been attributed to a female's inability to access grooming partners. It is quite possible, in large groups, that individual

dispersal physically restricts access to partners and thereby limits clique size. Henzi *et al.*, (1997a), for example, indicate a linear relationship exists between group size and group spread such that as group size increases so does group spread. Thus, in large troops, such as those at Samara, females may have difficulties locating grooming partners. In the current study, however, association patterns revealed that female accessibility, as reflected by the number of nearest neighbours, was not constrained. Instead, females encountered many more females as nearest neighbours than grooming partners. Thus, that females are not physically constrained by partner accessibility, yet have small clique sizes and unusually large troops, suggests activity budget constraints may be restricting female grooming diversity (Dunbar, 1992).

4.20 Spatial Association and Trade

Association patterns also revealed that grooming partners were not a consequence of general patterns of association or rank. Specifically, there was no relationship between the proportion of grooming and the spatial rank of associates and no relationship between female dominance rank and the spatial association rank of a females' most frequent nearest neighbour. It is possible that realized grooming associations, in the absence of rank-effects and restricted access to partners, are a consequence of tactical partner choice by females. Specifically, the overall association patterns may reflect seasonal shifts in partner choice, with grooming being traded for tolerance when food is scarce (Barrett *et al.*, 2002; Henzi *et al.*, 2003). The results, however, do not support biological market predictions. There was no relationship between rank distance and grooming time discrepancy when aggression was high or low and the interaction between levels of

aggression and rank differences in relation to differences in the amounts of immediately reciprocated grooming also went against the biological market prediction. Collectively the results suggest females were not trading grooming for tolerance.

That the current findings do not support the biological market model is surprising. Previous research on primates indicates that grooming is exchanged for a variety of resources, including access to infants, food and tolerance (Barrett *et al.*, 1999, Barrett *et al.*, 2002). The results in this study are, however, preliminary and are derived from a small sample size, which limits exploration of the biological market paradigm. Also, it is interesting to note that although the females in each of the study troops had access to social partners, as indicated by the presence of nearest neighbours, both troops experienced difficulty maintaining coordination. Specifically, the RBM troop had split on numerous occasions whilst *en route* to a new water source, resulting in individuals sleeping at two separate and distant sleep sites at opposite ends of their territory. Individuals in the smaller sub-group exhibited vigilant behaviour, including scanning from tree tops, and did not leave their sleep site until the larger sub-group had returned to their main territory and rejoined with the smaller sub-group the following day. It is possible, with their unusually large troop size, that coordination of activities is becoming increasingly difficult.

RST is the larger of the two study troops, consisting of a total of 69 individuals. During the study, RST formed sub-troops. A reduction in troop size, resulting from individuals splitting off into sub-troops, may occur when group size and the associated time constraints of living in a large group no longer allow females to groom other individuals sufficiently in order to service and maintain their social relationships. Social

relationships weaken and group cohesion subsequently declines (Dunbar, 1991, Henzi *et al.*, 1997a). Depending on the size of the groups after sub-trooping, individuals may be more vulnerable to the risk of predation (Stacey, 1986). It is, however, possible that splitting off into sub-troops may mitigate some of the costs associated with large troop size. Specifically, for the vervet population at Samara, a reduction in troop size may decrease the amount of time females allocate to travelling and foraging and therefore free up time for other activities such as resting and social engagement. Also, with the troops at Samara being unusually large, a reduction in troop size would probably result in troop sizes that are similar to an average sized vervet troop.

A permanent reduction in troop size could occur via fissioning. Whether the troops can fission is, however, debatable. That there is already a high population density of vervet troops in the study area suggests there may be no space for troops to fission, therefore impeding a troops ability to disperse. If it is the case that there is no space for troops to fission, this may explain why there are unusually large troop sizes at Samara and why when RST was beginning to show signs of fissioning they did not enter into new territory, rather the sub-troop separated themselves from the majority of the troop at the sleep site, sleeping in an area that was on the periphery of their territory. Also, the sub-troop delayed leaving their sleep site, waiting for the main troop to move off from their sleep site before coming down from their sleep trees to forage.

Despite the lack of supporting evidence in the current study, biological markets provide a useful framework for understanding cooperation and female social relationships. Specifically, in contrast to previous cooperative frameworks, the biological market model recognises the importance of partner choice and explores variance rather

than disregarding it as noise (Axelrod & Hamilton, 1981, Barrett & Henzi, 2006, Chancellor & Isbell, 2008, Noë & Hammerstein, 1995). Biological markets also takes an individual approach and this may explain why with the limited sample size I was unable to glean any insight into the possible role of biological markets in vervet female sociality. It is likely that larger sample sizes are necessary to explore female social relationships under this framework. Furthermore, that one of the troops exhibited signs of compromised cohesion may explain why females did not exchange grooming for feeding tolerance. That is, depending on how the troops dispersed it is possible that exchange partners were not readily available and females were subsequently confronted with the challenge of locating dispersed grooming partners and was therefore unable to engage in commodity exchange.

Also, although previous research has demonstrated biological market effects using rates of aggression, this may not be the most appropriate approach to understanding commodity exchange in a market place (Barrett *et al.*, 1999, 2002). According to Chancellor and Isbell (2009), inferring the strength of competition from rates of aggression may not capture the dynamic nature of individual responses to competition. Specifically, agonistic behaviour is typically used as an indicator of contest competition and other responses to competition, such as changes in ranging behaviour, are not taken into consideration. Gray-cheeked mangabeys (*M. albigena*), for example, have been found to respond to feeding competition by increasing inter-individual distance rather than engaging in agonistic behaviours (Chancellor & Isbell, 2009). That the troops in the current study fragmented, slept at separate sleep sites, split into sub-troops during

foraging and exhibited high feeding competition suggests these animals may also be responding to competition by avoiding aggression and dispersing.

4.21 Conclusions

The results in the current study indicate that coalitions are rare and in contrast to the biological market paradigm females do not exchange grooming for access to other resources. Female sociality is therefore unlikely to be contingent upon the need to service coalitionary relationships and coupled with the absence of biological market effects raises the issue of what factors could be structuring female grooming patterns.

That smaller clique sizes were found in larger troops suggests cohort size and the possible time constraints associated with living in larger groups may play an important role in structuring female sociality. Also, that the study troops showed signs of fragmentation and spent the majority of their time feeding and traveling suggests ecological constraints and, or spatial constraints, may be affecting female social interactions (Dunbar, 1991, 1992). Specifically, restricted access to partners may have constrained the exchange of commodities between females. It is therefore suggested that further exploration of the biological market paradigm, applied to a larger sample size with greater spatial data and diverse competition data, will provide a step in the right direction towards improving our understanding of the dynamic and flexible nature of female social engagement.

CHAPTER 5

GENERAL DISCUSSION

5.1 Summary of Key Findings

The current study examined the ecological structuring of social opportunity and the patterning of sociality in two large troops of free-ranging vervet monkeys (*C. aethiops*) in an attempt to better understand the effects of social and ecological factors on female sociality. In Chapter Three the time budgets and association patterns of free-ranging adult vervet monkeys (*C. aethiops*) were explored to determine the extent to which temporal factors, such as time of day and social factors, such as dominance rank, structure the time available for social interaction among females and, as a comparison, males. The data revealed that season and sex were significant predictors of grooming time across the year with females grooming more than males and the least amount of grooming occurring during the mating season. Variation in nearest neighbour distance was significantly effected by sex, season and activity with significant interaction effects occurring between sex and season and activity and rank. Grooming was not traded off against other activities, instead the strongest trade-off occurred between feeding and resting and feeding and moving. Diurnal assessment of grooming indicates time block, rank and sex had significant effects on grooming and that rank significantly interacted with time block. The findings from this chapter suggest that female rank manifests little of the predicted effects on the structuring of activity and, particularly, on the availability of time for grooming and the closeness of other females. Rather, ecological factors, such

as season, and sex appear to be playing a fundamental role in structuring social activity and inter-individual proximity. Data also suggest that the vervets in the current study traded feeding time off against moving and resting, thereby leaving grooming time buffered against daily time constraints.

In Chapter Four, patterns of aggression were explored to determine the context and distribution of agonistic interactions across the year. Grooming patterns were assessed to determine whether rank and cohort size play a role in structuring female social interaction. The relationship between grooming, rank and aggression was also explored to determine how competition and dominance effects structure female social relationships. Finally, the effect of rank on the distribution and distance of female neighbours was explored to determine the extent to which dominance structures female association patterns. The data revealed that competition was not evenly distributed across the year, that females predominantly competed over access to food resources and the larger of the two study troops exhibited the highest rates of aggression. Although mean grooming clique size was similar across all three vervet populations (Amboseli, Loskop, Samara), the Samara population, comprising of the largest vervet troops, did not groom all females in their troop. Thus, whereas available time for cohort members continued to decline at Samara, time available to other clique members stabilized or, possibly, increased as a consequence of smaller clique sizes in these larger cohorts.

Furthermore, although females were restricted in the number of grooming partners, females in both RST and RBM encountered many more females as nearest neighbours. There was no rank effect on the number of nearest neighbours. There was also no relationship between rank and grooming clique size at Samara nor was the

capping of clique size a consequence of restricted access to other females during the day. The relationship between grooming clique size and cohort size in the Amboseli, Loskop and Samara population indicates clique size matches cohort size until cohort size reaches about eight individuals, after which clique size declines. A significant negative relationship was found between rank distance and the likelihood of two females being nearest neighbours. Finally, there was no significant relationship between the relative representation of grooming partners for each female as a consequence of their general pattern of association.

That the females in the current study mostly competed over food resources, did not groom closely ranked partners and aggression fluctuated across the year, suggests variation in the availability of ecological resources may structure female social relationships. It is unlikely, however, that coalitions were advantageous in helping females to procure resources. Also, that the females were not physically constrained by partner accessibility, yet had small grooming clique sizes in unusually large troops, suggests activity budget constraints may have restricted female grooming diversity. It is also possible that realized grooming associations, in the absence of rank-effects and restricted access to partners, were a consequence of tactical partner choice by females.

Finally, given that female vervets are philopatric and therefore related to other female members of their troop, the effect of the presence of kin on female social interactions also requires consideration. It is possible, for example, that grooming interactions may be kin related with females grooming their sisters, mother or grandmother (Schino, 2001). However, although kinship and rank are usually strongly correlated among Old World monkeys, there was no rank related grooming observed in

the current study. The absence of rank-related grooming therefore has implications for kin-related grooming. That is, if close kin are also closely ranked, the results in the current study suggest they are not grooming each other as one would predict with respect to rank, or it is possible that there may not be rank-kinship relationships in the study troops and that alternative factors are potentially driving patterns of grooming. For example, that group size has been reported to interact with kin and rank preferences is of particular interest given that the vervet troops in this study were above average size and showed signs of compromised cohesion. Specifically, the effects of attraction towards high ranking individuals and kin are not accumulative and furthermore, cohesion appears to be greatest in small groups consisting of low-ranking matriline (Schno, 2001).

5.2 Limitations and Problems

The unusually large troop sizes in the current study constrained the amount of data collected on each female within the given study period. Compared to previous vervet research by Baldellou and Adan (1997) in which troops sizes were approximately two thirds the size of the Samara troops and the period of data collection was of comparable length, a similar amount of data was collected in RST and approximately half the amount of data was collected in RBM. That there was less data collected in total on the larger troops in the current study indicates it is necessary to ensure that the duration of any given study is appropriate for the size of the study troop and the number of study animals. Studies on larger troops therefore require longer study periods compared to smaller sized troops, which will in turn improve the validity of the research.

It is, however, possible that a greater amount of data could have been collected if the animals in the current study were observed after a longer period of habituation. Although the animals in this study had previously been exposed to humans in game drive vehicles, they had never been followed and observed by people on foot. Thus, although the study commenced after three months of habituation and the majority of animals could be observed with ease, some of the focal animals were not easily followed and exhibited signs of avoidance. Given that humans influence the behaviour of wild animals and the presence of an observer has previously been shown to affect the behaviour of the animals in the current study, a longer period of habituation may have mitigated avoidance responses and thus increased the ease with which the animals could be followed, thereby improving data collection (McDougall, 2011).

The accuracy of the social data may have been compromised by collecting data on a troop in which most, but not all animals were habituated. For example, if the social partners of a given female included some of the least habituated animals, it is possible that those animals did not interact with that female while she was being observed. Again, extending the habituation period prior to data collection could help alleviate this problem.

5.3 Future Directions of Research

That resource competition is an inherent component of group life led Seyfarth (1977) to suggest that grooming is inextricably linked to coalitionary aid such that females groom one another as a means of servicing relationships and thereby securing future social support during competitive interactions. However, the rarity of coalitions, coupled with continued grooming in the absence of coalitions, strongly alludes to the

possibility that factors other than coalitional aid structure female social relationships (this study, Henzi & Barrett, 1999). Furthermore, that grooming persists in the absence of coalitions suggests females engage in grooming for reasons other than servicing relationships in anticipation of coalitional support (Henzi *et al.*, 1997).

The lack of evidence supporting the notion that grooming functions to secure coalitional aid paves way for future research to explore alternative explanations of the social function of grooming. That an animal cannot adequately groom its whole body means individuals are required to cooperate so that they can groom one another and rid themselves of parasites (Barton, 1985). Grooming is therefore considered a service that individuals can exchange with one another. This notion of grooming as a commodity lends itself to the biological market paradigm in which individuals exchange or interchange resources (Henzi & Barrett, 1999).

Unlike previous socio-ecological models, the biological market approach does not inextricably link grooming to coalition formation. Rather, individuals may circumvent some of the rank related costs of within group competition by exchanging grooming for tolerance or, where grooming cannot be exchanged for other commodities, individuals may simply groom one another for its intrinsic benefits (Barrett, Gaynor & Henzi, 2002, Henzi & Barrett, 2002). Also, in contrast to previous models of cooperation, such as the prisoner's dilemma, the biological market approach does not place constraints upon individual partner choice and therefore provides a more valid approach to assessing female sociality. Furthermore, fluctuations in local conditions are an integral component of the framework, allowing for the assessment of behaviours that are contingent upon changes in local circumstances. Contingency is key to understanding female social

interactions since the value of a partner may fluctuate over time in relation to changes in local circumstances and therefore in the competitive regime. Thus, unlike Seyfarth's (1977) model, which did not consider changes in the competitive regime, biological markets is based upon such complexities, requiring a dynamic landscape upon which the intricacies of female sociality can be explored.

Thus, although the preliminary findings in the current study did not concur with the biological market paradigm, which is likely due to the limited sample size and possible lack of cohesion in these unusually large troops, this paradigm extends beyond Seyfarth's (1977) model, which has played a pertinent role in the study of female sociality, and provides direction for further exploration of the social function of grooming in female relationships. Specifically, that valid tests of biological markets hinge upon fluctuations in the marketplace means primate species living in seasonal habitats, such as vervet monkeys, provide excellent subjects for assessing how fluctuations in local market forces shape female social relationships.

That the females in the current study mostly competed over food resources, the larger of the two study troops exhibited the highest rates of aggression, females did not groom closely ranked partners and aggression fluctuated across the year, suggests variation in resource availability is likely to play a key role in shaping female social relationships. Future research should therefore aim to assess the ecological structuring of female relationships in further detail. Specifically, given that some food resources are more desirable than others (e.g. mushrooms, termites), assessments of competition should explore the type of food that females compete over and how this structures trade.

Furthermore, that vervet monkeys have linear dominance hierarchies means the effect of power differentials, which allow dominant individuals to procure more grooming from lower ranking individuals, can also be explored to determine how partner control affects vervet markets. Thus, given that studies assessing the biological market paradigm have demonstrated that grooming is a key commodity within primate markets, the way in which females supply grooming to their partners is also of interest and requires exploration. Previous research illustrates that female baboons exchange grooming incrementally such that a single grooming bout is comprised of several grooming episodes (Barrett *et al.*, 2000). According to Connor (1995) parceling grooming in this manner reduces the risk of being cheated. Thus, to determine whether females are capitalizing on a strategy that provides good partner value and minimizes cheating, future biological market studies could increase our understanding of grooming supply by exploring the parceling effect.

5.4 Summary

In the current study the social and ecological structuring of female vervet relationships was explored. That vervets live in a seasonal habitat, were observed to compete over food resources and exhibited fluctuations in aggression across the year alludes to the possibility that female social relationships are structured by local ecology. Also, given the rarity of coalitions and the observation that grooming occurred in the absence of coalitions means Seyfarth's (1977) grooming for support hypothesis, in which coalitions are the central organising feature of female social relationships, can be dismissed. More detailed research is now required to explore the extent to which

females are shaped by their local socio-ecological environment. Specifically, detailed assessments of seasonality, including fluctuations in food and water availability, and detailed assessments of dominance effects are requisite to improving our understanding of the role of ecology and rank in shaping female affiliative and agonistic social interactions. Furthermore, that females did not trade grooming time to engage in other activities highlights the importance of affiliative social interactions. Understanding the context in which grooming occurs and the extent to which grooming interactions are structured by rank and are contingent upon local ecology (e.g. biological markets) will provide a step in the right direction towards refining our understanding of female sociality.

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APPENDIX

5.5 Activity states for focal animal sampling

Table 2.4. Details of individual and social activity states for focal animal sampling.

Activity	Options	Sub Options
<i>Individual States</i>		
Autogrooming	n/a	n/a
Feeding	1) Location	i) Ground
		ii) Open Ground
		iii) Shrub
		iv) Tree
	2) Food Item	i) Acacia
		ii) Digging mixed
		iii) Grass
		iv) Gum
		v) Insects
vi) Karee tree		
vii) Mushrooms		
viii) Pepper Tree		
ix) Shrubs Succulents		

		xj) Succulents
		xii) Shoots
		xiii) Other
		xiv) Other tree
		xv) Unknown
	3) Food Part	i) Bark
		ii) Flowers
		iii) Fruits
		iv) Leaves
		v) Pepper corns
		vi) Pods
		vii) Unknown
Drinking	1) Location	i) Tree holes
		ii) Ground
		iii) Rocks
		iv) Other
Moving	1) Location	i) Ground
		ii) Open Ground
		iii) Shrub
		iv) Tree

Resting	1) Location	i) Ground ii) Open Ground iii) Shrub iv) Tree
Sniff	1) What was sniffed 2) By whom? 3) Individual sniffed	
Out of view	n/a	n/a
Other	n/a	n/a

Social Interactions

Allogrooming	1) Partner ID	
	2) Focal animals role	i) Groomer ii) Groomee
	3) Initiator	i) Focal animal ii) Partner iii) Unknown
	4) Requested?	i) Yes ii) No iii) Unknown
	5) Terminator ID	n/a

-
- Aggression
- 1) Focal animals role
 - i) Initiator
 - ii) Victim
 - iii) Joins Aggression - ID of who is joined
 - 2) Aggression partners ID
 - 3) Location at the start
 - i) Ground
 - ii) Open Ground
 - iii) Shrub
 - iv) Tree
 - 4) Context
 - i) Feeding – Contested food item
 - ii) Resting
 - iii) Travelling
 - iv) Infants
 - v) Other
 - vi) Unknown
 - 5) Aggression Type
 - i) Bite
 - ii) Chase
 - iii) Displace
 - iv) Eye lid threat
 - v) Supplants
 - vi) Swipe
-

vii) Vocal threat

6) Victims Response

i) Physical counter aggression

ii) Non physical counter aggression

iii) Exits feeding tree

iv) Runs away <2m, >2m

v) Walks away <2m, >2m

vi) Ignores individual

vii) Vocalises

viii) Not visible

7) Individuals $\leq 5m$

n/a

8) Is aggression polyadic? i) No

ii) Yes – Individuals joining focal animal

Individuals focal animal joins

Copulation 1) Partner ID

2) Initiator

i) Focal animal

ii) Partner

iii) Unknown

3) Copulation successful i) Yes

ii) No – Female refused

Male did not complete

		iii) Interrupted – ID of interrupter
Play	1) Partner ID	n/a
Approach	n/a	n/a
Leave	n/a	n/a

5.6 Grooming distribution

Table 4.2. Distribution of grooming (min: sec) in RBM focal females, organized according to Norm DS.

		Recipients													
		AM	SA	FA	MI	LO	PE	SC	TS	GI	VA	DS	RO	KA	OC
Groomers	AM		0:20	2:57	3:24	3:38	1:20	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
	SA	2:14		0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	4:14	0:00	0:00	1:42
	FA	2:42	0:00		0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
	MI	7:22	7:31	0:00		0:00	0:41	0:00	0:00	3:56	0:00	0:00	2:44	0:00	5:34
	LO	15:18	0:00	0:00	2:14		0:31	0:00	0:00	0:00	0:00	2:58	0:00	0:00	0:00
	PE	0:29	0:11	0:00	0:46	0:00		0:00	0:00	0:10	0:00	1:53	0:00	0:00	0:35
	SC	0:00	0:00	0:00	0:00	0:00	3:15		0:00	0:00	0:00	0:00	0:00	0:00	0:00
	TS	0:16	4:17	0:21	0:00	0:00	0:00	0:00		4:11	4:52	0:00	2:20	0:00	1:56
	GI	0:00	0:00	0:00	0:50	0:00	2:42	0:00	2:13		5:25	8:29	8:46	1:15	2:17
	VA	0:00	0:00	0:00	0:00	0:00	0:00	0:00	6:06	0:00		0:00	0:00	0:00	0:00
	DS	2:59	8:14	0:00	0:47	0:16	2:09	0:00	0:00	5:36	0:00		0:00	0:00	0:00
	RO	0:00	0:28	0:00	0:32	0:48	2:44	0:00	0:14	2:15	1:01	0:00		0:00	0:00
	KA	0:00	0:12	0:00	0:00	0:00	0:00	0:00	0:00	2:28	0:43	0:00	0:00		0:00
	OC	1:11	0:44	0:00	3:45	0:00	0:00	0:00	0:14	0:00	0:38	0:00	0:00	2:59	
HO	0:00	3:14	0:00	0:00	0:00	0:00	1:29	0:00	7:01	0:33	0:00	0:00	0:00	0:00	

Table 4.3. Distribution (Groomers down the left) of grooming (min: sec) in RST focal females, organized according to Norm DS.

		Recipients																					
	PJ	IZ	QT	ME	DO	AL	HE	WI	CL	EL	NI	TE	RU	XA	SF	UM	GL	VV	ZI	LI	FE	JE	KI
PJ		0:00	14:07	7:58	0:16	0:00	0:00	2:29	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
IZ	0:32		0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:06	2:22	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
QT	14:19	0:00		0:00	0:00	0:00	0:00	3:10	1:58	0:00	0:00	0:37	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
ME	7:57	0:00	0:00		8:40	0:00	0:00	4:23	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
DO	1:27	0:00	0:00	1:40		0:00	4:11	4:11	0:32	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	2:11	0:00	0:00	0:00
AL	0:00	0:00	0:23	0:00	0:00		0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00
HE	3:56	0:00	0:00	0:00	8:21	3:15		2:26	0:00	0:00	2:11	0:00	0:00	0:00	0:00	0:00	0:22	0:00	0:00	0:00	1:25	0:00	0:00
WI	8:58	0:00	4:39	1:43	6:24	0:00	0:00		0:17	2:21	0:00	0:00	0:12	0:00	0:00	0:00	14:38	0:00	0:00	0:00	0:00	0:00	0:00
CL	0:00	3:03	10:59	0:00	0:00	0:00	4:17	0:00		0:00	0:00	0:49	2:19	0:00	0:06	2:11	0:00	0:00	0:00	0:00	4:17	0:00	0:00
EL	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00		0:00	0:00	0:00	0:00	0:00	0:00	2:00	0:00	0:00	0:00	10:45	0:00	0:00
NI	0:00	0:00	0:00	0:00	0:00	0:00	5:49	0:00	1:40	0:00		1:41	0:00	0:00	2:08	7:01	1:02	0:00	0:10	0:00	0:00	0:13	1:50
TE	1:34	0:32	0:12	0:00	0:00	0:00	0:35	0:00	6:04	0:00	0:18		17:31	0:00	0:42	0:00	0:00	0:00	0:53	7:39	3:14	4:20	3:10
RU	0:00	2:51	0:00	0:00	0:00	0:00	0:00	0:15	6:27	0:00	0:32	13:46		4:15	0:00	0:11	1:41	0:00	0:00	16:51	0:10	0:00	7:52
XA	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00		4:00	0:00	0:00	3:47	0:00	2:57	0:00	0:42	0:00
SF	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	13:02	0:00	0:00	15:07		2:31	0:00	0:00	0:00	0:00	0:00	0:00	0:00
UM	0:00	0:00	0:00	0:00	0:00	7:40	0:00	0:00	1:41	2:33	0:00	0:00	0:00	1:17	0:00		0:00	0:00	0:00	0:00	0:08	2:39	0:38
GL	0:00	0:00	0:00	0:00	0:00	0:00	0:00	14:26	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00		0:00	0:00	0:00	0:48	1:43	3:14
VV	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	3:58	0:00	0:00	0:00		0:00	0:00	0:00	0:00	0:00
ZI	0:00	0:00	0:00	0:00	0:00	0:00	0:00	5:00	0:00	0:00	0:00	1:23	0:00	0:00	0:00	0:00	0:00	0:00		0:00	0:00	0:00	0:00
LI	0:00	0:00	0:00	0:00	0:54	0:00	0:58	0:00	0:00	0:00	0:00	1:56	16:21	6:20	0:00	0:00	0:00	0:00	0:00		0:00	0:00	0:00
FE	3:24	0:00	0:00	0:00	0:21	0:00	11:17	0:00	0:32	12:48	0:00	7:34	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00		0:00	5:54
JE	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	3:33	0:00	4:31	2:04	0:00	0:00	1:02	0:00		0:00
KI	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	0:00	4:52	0:00	0:00	3:51	1:20	0:00	0:00	0:00	0:00	0:00	