

NEGOTIATING SOCIAL SPACE IN VERVET MONKEYS

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ABSTRACT

This study explores the effect of changing ecological conditions on female social organization among free-ranging vervet monkeys (*Chlorocebus aethiops pygerythrus*) in the Klein Karoo, South Africa. Comparison was made between a previous study conducted during a period of drought in 2009, and my own study conducted when conditions were much wetter and hence, less ecologically stressful. In addition, animals in the present study also experienced conditions of low demographic stress. Compared to 2009, females displayed lower rates of competition and aggression, did not compete for access to grooming partners, and did not preferentially groom those of high rank, nor did they do so more frequently. Females did, however, preferentially associate spatially with those they groomed most; a finding in contrast to the previous study. Females did not groom those of adjacent ranks more frequently, nor was there any relationship between rank difference and spatial association. In addition, there were rank differences in vigilance were found between females, and vigilance costs overall were affected by total group size. Overall, these findings support some aspects of the socioecological model used to predict group structure in primates, but other aspects of social organization remain puzzling, and may reflect larger overall group sizes in the Samara population, which changes patterns of engagement between females in ways not fully captured by current models.

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CHAPTER ONE: GENERAL INTRODUCTION

Understanding the organising principles that underlie female social behaviour is a topic of central interest in primate behavioural ecology (Dunbar 1988, 1992; Sterck, Watts & van Schaik 1997, van Schaik, 1989). Female social behaviour is most useful when examining aspects of group life and sociality among the Old World cercopithecines, like vervet monkeys, as females tend to be the philopatric sex (i.e., to live in their natal groups for life), forming the stable core of the group. Vervet monkeys also tend to have strictly linear dominance hierarchies. In addition, vervets are widely distributed across Africa, and live in a variety of habitats (Tappen, 1960) which makes them a useful species to explore questions relating to behavioural flexibility and how this related to their social strategies.

Early studies by Seyfarth (1977) and Wrangham (1980) examined how female social relationships were structured in relation to ecology. Wrangham, (1980) outlined a general argument in which primate groups were categorized as female-bonded or not female-bonded. Female-bonded primates show female philopatry, and females engage in a variety of important social behaviours such as grooming, huddling, resource defence and dominance interactions that were argued to make up the internal structure of the group in predictable ways.

Seyfarth, (1977) had a more narrow focus on female grooming relationships alone and proposed a model that predicted how dominance and grooming behaviour

interacted to produce the behaviour patterns he observed among vervet monkeys in Amboseli, Kenya. Seyfarth (1977) argued that grooming behaviour primarily constituted the affiliative bonds between members of a troop, and that females used grooming to form alliances with other females to mitigate the negative effects of within group competition, via coalition formation. His model has some problematic assumptions, however, in that it implicitly relies on the monkey's ability to internally represent other individuals and track their relationships over long time periods, but he provided no support that monkeys were able to achieve such a feat. Seyfarth (1977) also assumed that high-ranking females are the most attractive and valuable grooming partners, as they can offer the best coalitionary support in a future conflict. His results indicated that females who groomed one another most often also supported one another in aggressive interactions (Seyfarth, 1980).

His model, though useful in some respects, does not have much empirical evidence to support it (Henzi & Barrett, 1999), and yet its influence has been pervasive in studies of primate behaviour. For example, in Seyfarth's (1980) study, he found a strong correlation between grooming partners and coalition alliance formation, but 70% of those coalitions were formed by females against a male third party, rather than against other females. As Seyfarth's (1977) model was based on the assumption that coalitions are formed against other females, the conclusion that these empirical studies support the model are not fully warranted, and so are not fully convincing. Despite this, the impact of his model has been so great that all future studies of female sociality were influenced heavily, sometimes to the point where researchers attempted to apply their

models, even when conditions did not merit the application (Di Bitetti, 1997; O'Brien, 1993).

Stepping away from Seyfarth (1977, 1980), who argued that grooming primarily facilitated social bonding, there are others who have argued that grooming in itself is a valuable behaviour. Grooming is argued to be important as a hygienic component to primate life (Hutchins & Barash, 1976; Parr, Matheson, Bernstein, & De Waal, 1997) and examinations of why monkeys groom must not discount the inherent value grooming has to these animals.

More recently, an integrated approach incorporating aspects of Seyfarth's model and the intrinsic value of grooming has emerged suggesting that grooming may be traded as a commodity (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Noë & Hammerstein, 1994). Instead of trading grooming for alliance formation, as Seyfarth suggests, grooming is traded in the biological market as either a direct exchange, of grooming for grooming, or in exchange for another valued commodity, such as tolerance from a high-ranking female.

Dunbar (1992) also brings an important factor to the discussion with his analysis of time constraints in a monkey's daily life. Dunbar (1992) argues that individuals in a group act to meet their daily nutritional requirements, and balance the costs involved with achieving their nutritional goals. Ecological conditions, including an aspect of group size, will exert an influence here, by determining how much time and effort is required to meet nutritional goals and what kind of adjustments need to be made. Under certain

ecological condition, group cohesion is put at risk because there is insufficient time available to engage in grooming of all available social partners, and maintain affiliative bonds. As a result, groups may become fragmented and may fission into two smaller groups. One way to avoid this is to restrict other aspects of their daily time budgets to ensure an adequate level of grooming is maintained, such as time spent resting. Dunbar (1992) argues that if, after such compensations are made to maintain grooming, females still cannot groom sufficient other females, then bonds holding the group together will deteriorate, and fission will then occur.

Fission itself can be problematic because it must occur at a group size whereby the two daughter groups are sufficiently large enough to maintain protection against predators, which is the primary evolutionary driver of group living among the primates (Kappeler & Schaik, 2002; Rubenstein, 1978; van Schaik, 1983). When moving throughout the day, a troop of monkeys must have a certain level of vigilance, in the form of scanning behaviour to reduce the risk of predation. Cowlishaw (1997) demonstrated that predation considerations were the most influential factor in choosing foraging locations for chacma baboons (*Papio cynocephalus ursinus*). His study showed that baboons chose the safest habitats preferentially, despite lower food abundance in such areas, thus deviating from an ideal free distribution.

Living in groups to avoid predation thus poses the challenge of competition. In groups, where competition is high and there is a strong dominance hierarchy, animals must also attend to internal threats to their safety in the form of aggression from

higher-ranking individuals. Both group size and the forms of dominance hierarchies have been shown to influence scanning behaviour in primates (Caine & Marra, 1988; Cowlshaw, 1998; Treves, 1999). As female vervet monkeys have strict, linear dominance hierarchies, there exists an internal level of competition that influences how females are positioned spatially in a group. Vigilance within a group may therefore be driven by both the need for predator detection and social vigilance designed to reduce competition and aggression from others.

According to Hamilton (1971), safety in a group setting is determined solely by how many neighbours you have around you. With fewer animals in proximity and larger inter-individual distance, the risk of predation increases. Thus, the safest spatial position in a group is at the center, where there are many neighbours around you. However, being in the center of the group presents another problem involving competition from other individuals. If a female is high-ranking, she can challenge other females for the safest group positions. On the other hand, if a female is low-ranking, she must balance her spatial position to best avoid the two risks presented to her. How these females achieve this balance is rooted in social vigilance behaviour, and must be traded off against predator vigilance (assuming that it is not possible to perform both forms of vigilance simultaneously).

A consistently observed pattern that emerges in primate studies is the concentration of dominant individuals at the center of a group, with the subordinate individuals making up the periphery (Hemelrijk, 1998, 2000). This result has been

proposed to reflect the dominance hierarchy, with this pattern emerging primarily as a result of competition and displacement during foraging (Rasmussen & Farrington, 1994). It could be argued, however, that the same pattern can emerge without feeding competition, as seeking safety from predators is also a factor and it could be competition for safety that drives these effects. In either case, the pattern still emerges from within group competition, and occurs as a result of females monitoring their surroundings, and adjusting their position on local immediate cues. For example, a low ranking female is motivated to stay within a certain distance of another female to reduce her risk of predation, but she is also actively avoiding potentially aggressive high-ranking individuals.

Evers, de Vries, Spruijt, & Sterck, (2012) present a model that attempts to demonstrate how scanning and social vigilance behaviour operate on a simple set of rules that, when put into action, results in the dominant-center, subordinate-periphery pattern. Evers et al. (2012) argue that females are not necessarily competing for safe spatial positions within a group. Instead, they are moving based on their nutritional requirements and due to the avoidance of dominant individuals by subordinates, the pattern happens to emerge. In other words, predator vigilance is completely ignored by their model. Despite this, the model provides a very useful starting point for examining patterns of vigilance. By observing real life scanning and vigilance behaviour we can attempt to separate the factors involved in the emergence of the dominant-center, subordinate-periphery pattern.

Accordingly, the aims of my study are to investigate how ecological conditions influence patterns of social behaviour, and then perform a test of Evers et al.'s (2012) model of social vigilance. Specifically, I first conduct an analysis comparing aspects of female social behaviour observed under highly ecologically stressful conditions (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013) with the same behaviours observed under very different, low ecologically stressful conditions. By examining the effect of changing ecological conditions on various aspects of social behaviour, we can begin to determine exactly what value grooming holds for females in my study population, and provide support for or against the various models currently used to explain this behaviour.

Second, I examine whether the simple scanning and social vigilance rules posited by Evers et al. (2012) can predict behaviour of the vervets in my study population. I also examine the effect of habitat type on social vigilance and whether this affects the model's assumptions. Lastly, I test whether the vervets in my study actually demonstrate this pattern of a dominant-center and subordinate-periphery by analysing measures of nearest neighbours and inter-individual distance.

CHAPTER TWO: GENERAL METHODOLOGY

2.1 Study Animals

2.1.1 Taxonomic affiliation and distribution

Vervet monkeys (*Chlorocebus aethiops pygerythrus*) are a small-bodied sub-Saharan species of primate, through Ethiopia and East Africa to the southernmost tip of South Africa (Figure 1)(Tappen, 1960). Vervet monkeys were originally classified as *Cercopithecus aethiops*, which is within the genus of guenons. This classification is incorrect as guenons are typically forest dwellers, whereas vervets live a semi-arboreal, semi-terrestrial life (Fedigan & Fedigan 1988). Although vervets are now classified as the genus *Chlorocebus*, the literature has many interpretations and often misidentifies the six species of vervet and eight other sub-species as a combined taxon of *Chlorocebus aethiops*. The taxonomic status is still under debate and classification may continue to change in the future.

Vervets are described as opportunists as they can forage on a variety of food sources and live in very diverse habitats. Vervets are able to overcome certain demands of environmental change due to this level of flexibility and can capitalize on less desirable habitats (Fedigan & Fedigan, 1988). Despite this ability to exploit less desirable habitats, vervets are still constrained by local conditions of seasonal variation in food and water availability, with a high risk of mortality when water is absent for prolonged periods of time (Fedigan & Fedigan, 1988; Struhsaker, 1967a; Wrangham & Waterman, 1981).



Figure 2.1 Distribution of Vervet Monkeys. IUCN 2013 (International Union for Conservation of Nature). IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>.

Downloaded on 10 September 2013.

2.1.2 Ecology

Vervet monkeys are abundant in areas of riparian vegetation, but can utilize less productive habitats, such as riverine forest, karoo semi-desert and they may even infiltrate urban areas (Henzi, 1979, Struhsaker, 1967a). The varied habitat use is constrained by a factor other than water: availability of sleeping trees (Wrangham, 1980). Predation is a serious risk to such a small bodied primate and suitable sleeping trees provide safety from various predators at night (Chapman & Fedigan, 1984; Fedigan

& Fedigan, 1988). Vervets are omnivores, and have many sources of food such as fruits, flowers, fungi, grasses, gum, shoots, and leaves. Other food sources such as bird eggs and chicks can supplement their diet when the opportunity arises (Struhsaker, 1967a). The average troop size is 20 monkeys (Fedigan & Fedigan, 1988), although mean troop sizes can fluctuate greatly, as has been reported throughout the literature (Cheney & Seyfarth, 1983; Willems & Hill, 2009).

2.1.3 Physical description and reproduction

Vervets are a small to medium bodied monkey. They have a silvery grey coat and purely black face with a white band of fur across the brow and surrounding the face. Their hands and feet are also black and the skin on their abdomen is blue covered by white fur. Males have colourful genitalia (blue scrotum and red penis) and are larger bodied than the females weighing on average, 5.5kg compared to 4.1kg for females (Cawthon Lang, 2006).

Males and females have slightly differing rates of sexual maturation. For females, reproductive age is reached at around 36 months of age, whereas males reach sexual maturity around 48 months (Turner, Anapol, & Jolly, 1997). Vervets are seasonal breeders and the mating season typically lasts from April to June in South Africa. Gestation lasts approximately 163 days, on average (Melnick, 1987), and the birthing season is normally September to December, with a female producing a single offspring and a range of inter-birth intervals from 11 months to 24 months (Cheney, 1988,

Melnick, 1987). Infanticide is not a phenomenon observed in vervets presumably because males are unable to reproductively coerce females (Seyfarth, 1980).

2.1.4 Social Organization

Vervet monkeys live in multi-male, multi-female groups that are considered to be female-bonded (Wrangham, 1980). That is, females maintain affiliative bonds with other females in the group; this could be via grooming, huddling, resource defense, and dominance interactions. They also, most often, remain in their natal group for their entire lives. Natal males emigrate upon reaching sexual maturity, meaning that adult males in a troop are immigrants from neighbouring troops (Henzi & Lucas, 1980). Males typically move between troops during the mating season (Henzi, 1982), and during transfer they are vulnerable to predators and aggression from males in other troops. These risks may be mitigated by males transferring with another male. Male transfer ensures that males do not inter-breed with their mothers, or their sexually mature female offspring.

Dominance relationships in vervet monkeys are linear, although ranks are acquired differently between males and females. Females acquire a position in the dominance hierarchy that is similar to their mother's rank; often directly beneath her. Since females are philopatric, (Wrangham, 1980) dominance rank remains relatively stable over time, with changes occurring when females with an established rank die (Fairbanks & McGuire, 1985). In contrast, maternal rank has little effect on a male's adult dominance because of male emigration and thus males attain rank through

outcomes of agonistic interactions with other adult males. Male ranks are much less stable than females and are often predicted primarily on size and fighting ability (Cheney & Seyfarth, 1989).

2.2 Study Site

This study was conducted on Samara Private Game Reserve, Eastern Cape, South Africa (32° 22'S, 24°52'E). Samara is located on the Plains of Camdeboo, south-east of the town of Graaff-Reinet, and is an area of semi-arid karoo, with a riverine forest of Acacia karoo trees (Figure 2.2). The vervet populations in this study are centered on the acacia woodland that borders the Milk River. In past years, the river demonstrated a clearly seasonal variability, where it was often dry during the austral winter and could then flood during the austral summer. During my time in the field, from January to December 2012, the river fluctuated in level but was never dry.

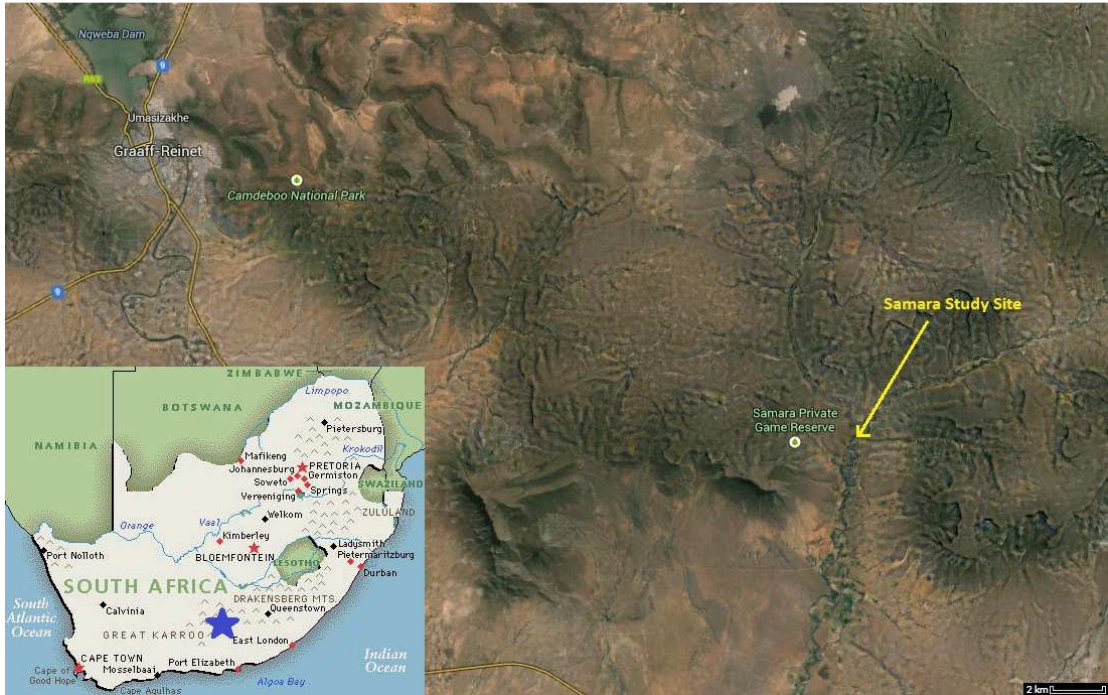


Figure 2.2 Inset map of South Africa retrieved from <www.greenwichmeantime.com> and satellite map from Google Earth, Downloaded on the 8 November 2013. The location of the study site; represented by the blue star. Samara site in relation to the town of Graaff-Reinet.

2.2.1 Climate and Seasonality

In the Karoo, the summer season typically ranges from October to April and the winter season ranges from May to September (Dean & Milton, 1999). This study period occurred from January 2012 to December 2012 and during this time the mean monthly precipitation was approximately 24.89mm, with most of the rain falling during the month of December (Figure 2.3). Average monthly temperature was 16.2 °C (Courtesy of South African Weather Service) with monthly average maximums and minimums displayed in Figure 2.4. Daylight hours peaked in December at 14.1 hours and were reduced to 9.6 hours in June.

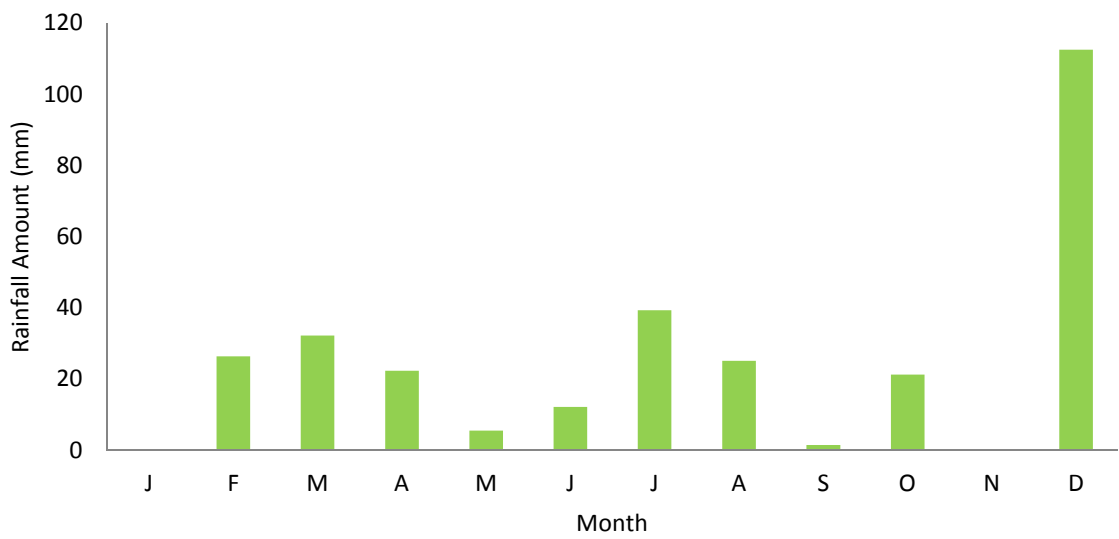


Figure 2.3 Total rainfall (mm) per month, for the town of Graaff Reinet, 33km from the study site, during the study period.

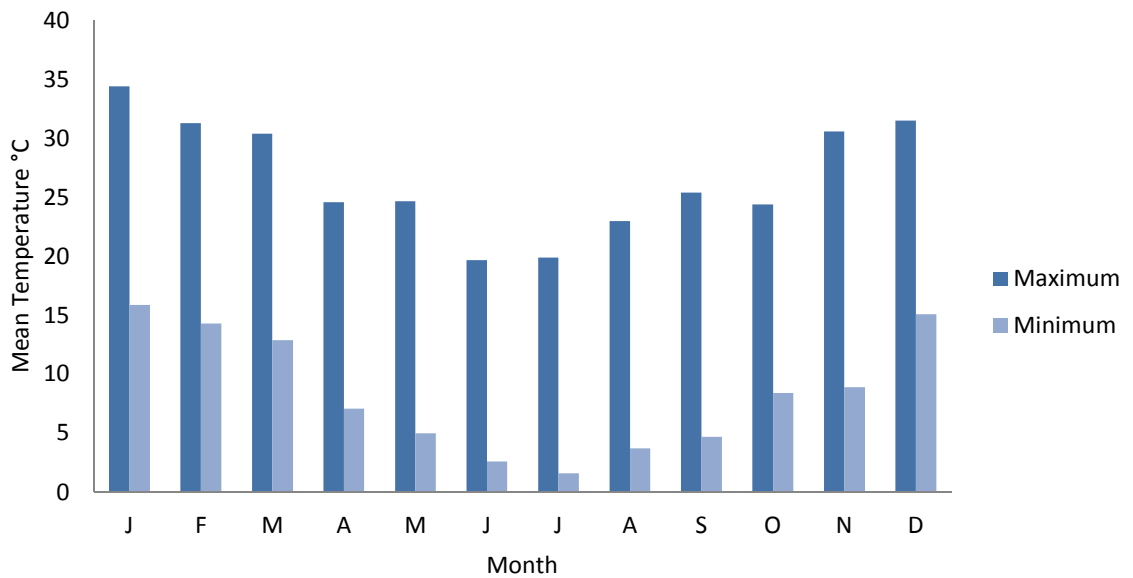


Figure 2.4 Mean temperature values (°C), for the town of Graaff Reinet, 33 km from the study site, during the study period.

2.2.2 Flora and Fauna

Samara is host to a wide variety of mammal species; some of these being very large. Large species include giraffe (*Giraffa camelopardalis*), Cape buffalo (*Bubalus bubalis*), white rhino (*Ceratotherium simum*), eland (*Aurotragus oryx*), kudu (*Ragelaphus strepsiceros*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus caama*), black wildebeest (*Connochaetes gnou*), Burchell's zebra (*Equus quagga burchellii*) and Cape Mountain Zebra (*Equus zebra zebra*). Smaller mammals are represented by the blue duiker (*Philantomba monticola*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), springbok (*Antidorcas marsupialis*), aardvark (*Orycteropus afer*), African porcupine (*Hystrix cristata*) and bushpig (*Potamochoerus larvatus*). Carnivores include cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*). The only other primate on the reserve was the chacma baboon (*Papio ursinus*). Samara's flora was highly varied but consisted mostly of Acacia trees (*Acacia karoo*), karee (*Rhus lancea*), and Peruvian pepper trees (*Schinus molle*). Other species of bush, such as fire-thorn karee (*Rhus pyroides*), Common Spike-thorn (*Gymnosporia heterophylla*) and bluebush (*Diospyros lycioides*) were common food sources for the vervets (Figure 2.5).



Figure 2.5 Clockwise from top left; Cheetah (*Acinonyx jubatus*), Cape Mountain Zebra (*Equus zebra zebra*), Vervets foraging on Firethorn (*Rhus pyroides*), and on Acacia (*Acacia karoo*).

2.3 Study Troops

Data presented in this thesis were collected from two troops of vervet monkeys (River Side Troop, RST, and River Bend Mob, RBM) over an 11 month period from January to December 2012. The troops were located in adjacent territories of approximately 25ha along the Milk River. These troops have been studied since September 2008, and were both fully habituated to human observation prior to data collection taking place. During the course of this study, RBM used two sleep sites located at different points along the river (Figure 2.6), while RST used upwards of seven different sleep sites during the study period and would often split into sub-groups with separate sleep sites. Toward the end of the study, RST began using one of RBM's sleep sites, but would not often share the site.

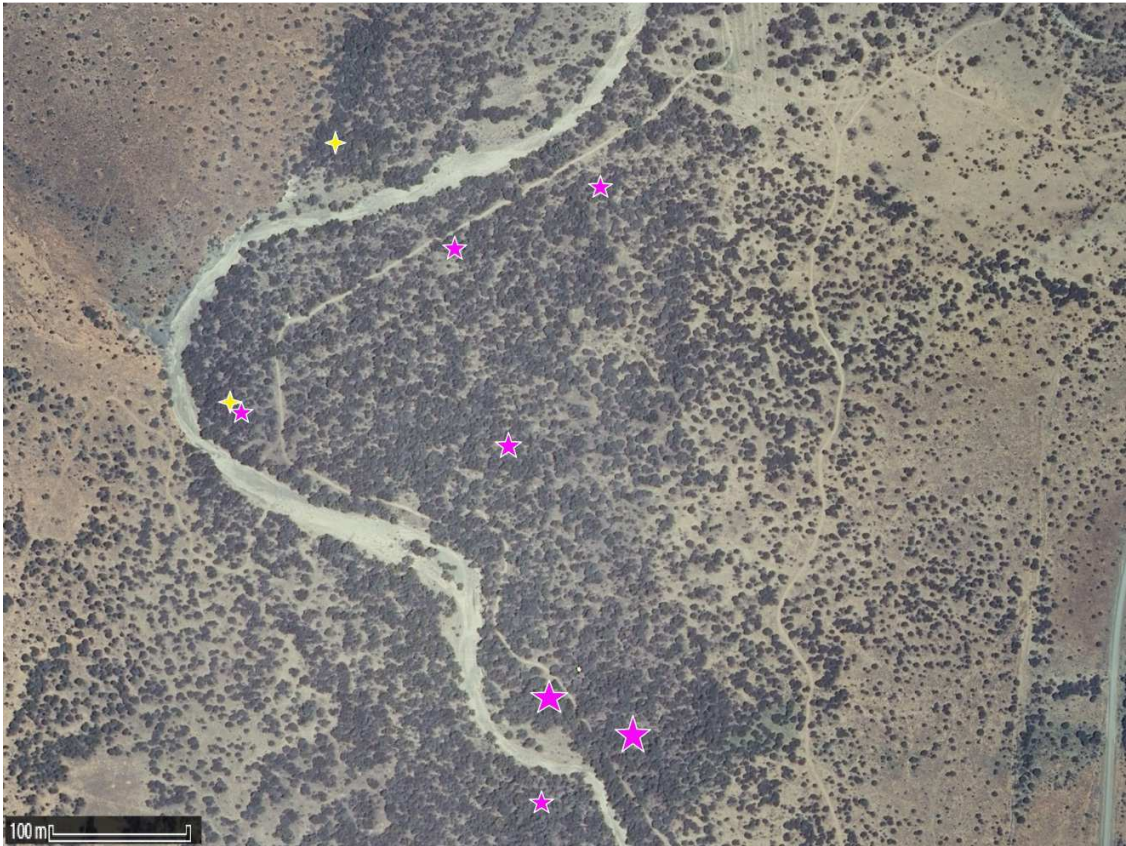


Figure 2.6 A map of Samara field site. Four-pointed yellow stars represent RBM sleep sites, and five-pointed pink stars represent the location of RST sleep sites during 2012. The large stars represent RST's main sleeping locations.

2.3.1 Demographic Structure of Study Troops

The two troops had unusually large group sizes when this study began in January 2012, with RST having approximately 60 members and RBM having approximately 49 members; numbers that are much higher than the expected average of about 20 -25 individuals (Fedigan & Fedigan, 1988). By December 2012, however, these numbers had dropped substantially for both troops. Group size, and composition of the group in January 2012 and December 2012 are represented in Table 2.1. In contrast to other

observed compositions of vervet troops (Henzi & Lucas, 1980), including those of earlier years at this site, the troops in 2012 had sex ratios that differed slightly, with RBM having a higher proportion of males to females (2.14:1) and a very slight ratio for RST at (1.5:1) males to females.

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

	RBM		RST	
	Jan 2012	Dec 2012	Jan 2012	Dec 2012
Adult Males	15	5	12	14
Sub-Adult Males	6	1	6	6
Adult Females	7	10	18	15
Sub-Adult Females	6	0	5	1
Juveniles/Infants	15	11	19	11
Troop Size	49	27	60	47

The table above demonstrates clearly that both troops suffered large drops in population over the study period due to deaths, and migrations. Birth rates in 2011 were very low, with only five infants born across the two troops (RST: 4, RBM: 1) and of those five only one, in RST, survived to December 2012. These births also happened unusually late in the season, with the first being born early December 2011, and the last was born mid-February 2012, which may have been a contributing factor in their mortality. This birth pattern is quite atypical for these vervets: in past years these troops

have seen the majority of their births occurring during October (RST: 40%, RBM: 80%) and November (RST: 55%, RBM: 20%).

Migrations into and out of the troop were recorded for the entirety of 2012, with RST gaining 9 male immigrants and RBM gaining 4. Of the RST immigrants, all were observed to copulate with females in their new troop during the mating season, whereas of the 4 males that immigrated to RBM, only one of them was observed to copulate with females, and the same single male was also the only one to remain with the troop to Dec 2012. Over the course of the year, there were significant losses to the troops due to predation. In many cases, death was confirmed by the discovery of fur and/or bones on site. In the case of some female disappearances, death by predation was concluded as the most likely cause as they were observed to be healthy and active prior to disappearance. The majority of the migrations occurred during the mating season, and the majority of confirmed deaths occurred during the mid-winter months of July and August.

2.4 Data Collection

Data collection for this study began in January 2012 and continued to early December 2012. Animals in both troops were followed at a distance of 3 to 5 meters, depending on the animal's comfort level. If the individual began demonstrating signs of extra attentiveness to the observer, distance was increased to a point at which the individual would resume regular behaviour. All adults and sub-adults were identifiable by individual characteristics, including facial features, (such as brow shape, and any

unique colour patterns under the eyes or chin) body size, tail length and any distinguishing wounds or scars present on the body (Figure 2.7).



Figure 2.7 The female in the top left has distinctive white marks on her eyes and chin, and a shortened tail, the female in the top right has a plain face and a smoothly curved brow, and the male on the bottom has a sizeable piece missing from his left ear.

From January to May, and September to December, the animals were followed on foot for 12 hours a day, four days of the week, alternating early and late starts when daylight hours exceeded 12 hours per day, to ensure an even distribution of data collection across all daylight hours. During the winter months, the daylight hours dropped to 9.5 hours and the animals were followed from dawn to dusk, 5 days a week. Focal animal sampling was divided into four, approximately 3 hour, diurnal time-blocks, and the females were sampled randomly, with weekly checks to ensure all females maintained an even distribution across time-blocks. Data were collected using a Trimble Nomad handheld data logger, using Pendragon Forms Manager 5.1. Three sampling techniques were used: Instantaneous Scan Samples, Focal Animal Samples, and Ad libitum Samples (Altmann, 1974).

2.4.1 Instantaneous Scan Sampling

This method was used to capture details about an individual's activity state, as well as the identity and distance in meters of their nearest male and female neighbours. These scans provided the main body of data for analysis of female-female spatial and activity related interactions. These samples were taken at thirty minute intervals and were conducted on all adults that could be found during the ten minute scan period. Aggression, grooming, auto-grooming, resting, foraging, moving, playing and an 'other' category were the various activity states recorded. Table 2.2 outlines the exact definitions of each of these behaviours. Location was recorded as being on the ground, open ground (e.g. on the ground in the middle of a clearing, with no overhead cover),

shrub and tree. Nearest neighbour distances ranged from contact to 20+ meters from the scan subject and in cases where no neighbours were visible around the subject a zero was entered as the ID and an estimate of the distance in which there were no neighbours was recorded in the distance category. A total of 29,111 scan samples were collected, with 16,206 of those on females.

Table 2.2 Definitions of observed behaviours

Behaviour	Definition
<i>General:</i>	
Autogrooming	When an animal combs through its own fur with hands and/or mouth.
Resting	Animal is not moving, usually sitting or lying down.
Moving	Animal is in a state of locomotion, in the ground or in the trees.
Foraging	Animal is in the process of eating or finding food.
<i>Social:</i>	
Grooming	If an animal is grooming another individual with their hands and/or mouth they are classified as the allogroomer in the interaction whereas the individual being groomed is the receiver.
Agonistic	Includes physical and non-physical interactions:

Physical interactions include, bite, swipe, grab and chase and non-physical interactions include:

supplanting - when an aggressor takes the spatial location and engages in the activity of another animal.

displacement - when an approaching aggressor causes another individual to move from its current spatial location.

eye-lid threat - the white area of the eye-lid is exposed.

bob threat - either bipedal or quadrupedal, involves a quick dip of the head while staring at the individual being threatened.

vocal threat - aggressor directs a vocalization towards the recipient.

Coalitions Occurs when a third party joins one of the two animals involved in an aggressive social interaction.

Copulation Females or males may initiate copulation. Females initiate copulation by presenting their hindquarters to a male. The male solicits copulation by placing his hands on the female's hindquarters. Copulations were measured as successfully completed, or interrupted, either by a third party male or resisted by the female.

2.4.2 Focal Animal Sampling

Focal animal sampling was used to continuously sample a focal female for a 20 minute period. Prior to each focal sample, the female's ID, date and time-block were recorded and at every 5 minute interval information on the female's current activity and nearest neighbours within 15 meters were recorded. When an animal went out of sight of the observer, the time was noted, and was noted again when the subject was within sight again. If the total observing time of the focal was less than 15 minutes the focal was discarded. Also, if the focal subject was in the middle of a grooming bout when the focal ended, the focal was extended until the grooming exchange was complete. This was done to get an accurate account of time spent grooming and receiving in a grooming session.

The focal sampling technique was used to assess whether two aspects of social vigilance followed predictions about spatial organization and avoidance amongst female vervets. The first aspect was defined as a group scan, and was recorded when a female would observe the group, turning her head in a wide arc to take in her surroundings. A scan was defined as a smooth turn of the head, greater than 90 degrees, in either direction. An animal that scanned turning her head one direction, then back the other was recorded to have scanned twice (one direction, as long as it is greater than 90 degrees, counted as one scan). The other aspect was defined as social vigilance, and was recorded when a female attended to the approach of another female. A female who was observed to attend another female was defined as a sharp turn of the head to

direct her gaze at the approaching female. Three attributes were measured when a social vigilance occurred: at what distance did the focal female attend to the other female, whether the focal subject moved as a result of her approach, and if she did move, how far away did the focal female move from her original position. Table 2.3 shows the females in my focal sample, and their David's scores.

Table 2.3 Focal sample females.

RBM	David's score	RST	David's score
Be	-29.65	Do	1.81
Dq*	-9.42	El	-2.31
Fa	19.59	Fe*	-4.19
Gi	-20.65	He*	1.76
Ho	-16.89	Iz*	6.94
Lo*	6.39	Jo*	-3.63
Oc	-22.98	Ki	-16.54
Sa	47.5	Me	22.95
Sc	28.06	Ni	-8.75
Wb	-8.23	Pr +	35.52
		Ru +	-21.26
		Sh +	-8.77
		Um*	-1.39

Note: * = females dead mid-2012; + = females added to sample mid-2012.

2.4.3 Ad Libitum Data Collection

A variety of behaviours were observed and recorded in an ad libitum fashion and included copulations, wounds, aggression and other dominance interactions (e.g., supplanting, eye-lid threatening) (Altmann, 1974). Aggression and dominance data were primarily used to construct dominance hierarchies for both the males and the females of the two troops. Later on in the study period, any social vigilance that was observed between two females was recorded, under the same protocols defined for focal sampling, to try to increase the sample size for this observed behaviour. These observations, though perhaps biased to particularly conspicuous behaviour, were crucial to the establishment of reliable dominance matrices and added a large proportion of data to the overall sample.

2.4.4 Statistical Analysis

Analysis was conducted using IBM SPSS Statistics 21 software program. The level of statistical significance (alpha level) was set at $p = 0.05$ where appropriate. More detailed descriptions of statistics used are outlined in the methods section of each data chapter.

CHAPTER THREE: VERVET SOCIAL ORGANIZATION

3.1 Group life

Vervet monkeys (*Chlorocebus aethiops pygerythrus*) are small-bodied sub-Saharan species of primates, widely distributed across Africa (Tappen, 1960). They live in multi-male multi-female groups that are considered to be female-bonded (Wrangham, 1980). That is, females that maintain affiliative bonds with other females in the group; these bonds consist of engaging in behaviours such as grooming, huddling, resource defense, and dominance interactions.

As group-living primates, vervets encounter certain challenges that more solitary animals do not face. Suggested benefits of group life include, but are not limited to, predator detection and avoidance, and resource defense against neighbouring troops (Krebs & Davies, 1993, Terborgh & Janson, 2013; van Schaik, 1983; Wrangham, 1980). Living in groups poses costs, however, the primary cost being an increase in feeding competition, which has two components; a direct or contest competition, and an indirect or scramble competition (Isbell, 1991; van Schaik, van Noordwijk, Boer, & Tonkelaar, 1983). Contest competition is related to dominance interactions amongst females. Dominant females potentially can monopolise high quality food patches by displacing more subordinate females, and denying them access. Scramble competition is an effect of group size: animals in larger groups experience higher levels of scramble competition because access to food sources is influenced by the rate at which group

members deplete available resources, and so limit the intake of other group members (Sterck et al., 1997; van Schaik & van Noordwijk, 1988).

There are several theories regarding the evolutionary benefits of group living. One theory developed by Wrangham, (1980) suggests that living in groups helps reduce inter-group competition for food resources. An alternative theory is one developed by van Schaik, van Noordwijk, Isbell and others that suggests living in groups is a response to predation risk and, in some cases, the risk posed by infanticidal males (Hamilton, 1971; van Schaik et al., 1983; van Schaik, 1983). Wrangham's explanation of group life requires a certain level of between group feeding competition, which arises when high-quality food is distributed in defensible patches. However, there is little evidence that between-group competition is the main driving factor for primates living in groups. Instead, levels of within-group competition more clearly influence the degree to which groups are considered female-bonded. This suggests that group living and female philopatry is not solely determined by feeding competition (Barton, Byrne, & Whiten, 1996; Koenig, 2002). Van Schaik (1989) and later Sterck et al. (1997) argued that more factors were involved. In particular, within-group competition determines female dominance patterns. As well as the distribution of feeding patches and whether they are dispersed evenly, or clumped, drives within and between group feeding competition, and the vigilance costs involved with predator detection (Snaith & Chapman, 2007; van Schaik et al., 1983; van Schaik & van Noordwijk, 1988; van Schaik, 1983).

The current “ecological model” of female-female social relationships states that predation risk forces females to live together in groups, increasing competition among females (Sterck et al., 1997; van Schaik et al., 1983). The strength of the contest competition between females then drives the dominance interactions and social relationships between females, resulting in groups with different categories of dominance, i.e.: Dispersal-Egalitarian, Resident-Nepotistic, Resident-Nepotistic-Tolerant or Resident Egalitarian (Sterck et al., 1997). In the case of vervets, there are formal dominance relationships that are stable and linear, meaning decided agonistic interactions in which the dominant individual consistently wins, and the subordinate individual consistently loses. In such societies, females are usually philopatric, and remain in their natal group for their entire lives. According to this model, our vervets can be classified as Resident-Nepotistic-Tolerant. These females exist in a relatively stable social hierarchy, providing us with a defined basis for questions regarding the social strategies by which females maintain a balance between social and environmental pressures.

3.2 Time Budgets

During the daily life of a vervet monkey, certain activity requirements need to be met to ensure survival, and, as argued by Dunbar (1992), to maintain group cohesion. Time budgeting, then, is an important consideration if monkeys are to maximize the benefits of group life while compensating for the intra-group costs. There are a number of factors that influence a troop’s time budgeting strategies. These include variations in

group size, resource availability, climatic factors (e.g., temperature and rainfall) and variation in day length seen in a seasonal environment. An animal's time budget is constrained in various ways by these factors, and an optimal balance between foraging, resting, moving and grooming is sought to ensure an individual's fitness is not compromised (Dunbar, 1988).

Dunbar (1992) presented a model to explain how animals adjust their time budgets in the face of these various constraints. Dunbar (1992) suggested that basic time budgets include four key activities: foraging, resting, moving, and social time. The importance of the first three may be obvious but the last, social time, is seen as an equally important activity and pervasive throughout group living primates. According to Dunbar, social time is the "glue" which maintains group cohesion. He argues that social interactions are essential for group cohesion as grooming encourages affiliative bonds between females in the troop. Without the maintenance of these social relationships, the group will fragment and eventually fission completely (Dunbar, 1984).

This conclusion is attributing much more to grooming relationships than may be wise, as it makes an assumption about vervet cognition and the animal's ability to mentally represent the relationships amongst females across long periods of time (Dunbar, 1992; Seyfarth, 1977, 1980). Dunbar (1991) argues that because grooming frequency is correlated with group size and not with body size, this is sufficient evidence to discount grooming as having a purely hygienic function. This result, combined with Wrangham (1980) and Seyfarth's research (1977, 1980) has been taken as the basis of

evidence that grooming has a primarily social function. On the other hand, there is another view that group formation and social cohesion in primates arises from the need to detect predators, capitalize on feeding benefits such as patch return time, and for hygienic grooming (Isbell & Young, 1993; Kappeler & Schaik, 2002; Sterck et al., 1997; van Schaik et al., 1983; van Schaik, 1983).

When dividing up activities throughout the day, Dunbar points out that time is the key factor that ultimately influences foraging, resting, moving and social time. Each activity has time requirements involved. Animals must maintain a level of foraging that meets their daily nutritional requirements while balancing energy out-put costs such as digestion, travel and thermoregulation and still have time set aside for important social activities. What happens when an individual is forced to adjust its time budget based on any of these factors? Certainly there is flexibility amongst vervet monkeys as they live in a very wide variety of habitats, with differing levels of food quality and abundance, but vervets also tend to have a constrained range of group size. Generally they are found in groups of 20-25 individuals or fewer (Fedigan & Fedigan, 1988; Struhsaker, 1967a), even in areas of high resource availability. This restriction on group size seems to be the simplest adaptation to various time budgeting needs, and Dunbar described a formula upon which a measure of maximum ecologically tolerable group size (METGS) can be calculated and applied to various habitats and species. The METGS of a troop calculates the maximum size a group may reach before it is predicted to undergo fission and produce two smaller groups. The METGS can be used, therefore, as a measure of the

'demographic stress' experienced in a given population by comparing observed group sizes to the calculated METGS value.

The argument here is that, with increased group membership and poorer ecological conditions, there is less time to maintain social relationships, which leads to the potential fragmentation of the group, and hence to fission. It is this tension between maintenance needs and social needs that gives rise to demographic stress. Henzi, Lycett, & Piper, (1997) tested this idea using data from chacma baboons living in a poor quality environment, the Drakensberg Mountains, but found little support for it. Instead they documented a wide variety of group sizes, each spending a similar amount of time on essential behaviours. The females compensated for a lack of social time by capping their grooming cliques (i.e., by reducing the number of females in the group that they spend time grooming, engaging with only a sub-set of those available) and they spent most of their time outside the grooming relationship in proximity to females in their grooming cliques. The group that was observed to fission in this population, divided along these clique lines. Henzi et al., (1997) concluded that though fission was likely driven by a lack of social time in larger groups, it also appeared that group size had little effect on the female's time budgets. Instead it was the tendency of these females to associate spatially with each other, rather than a factor of demographic stress, that caused them to fission.

The vervet population at Samara therefore provides an interesting test case to examine the idea of demographic stress. Some sectors of the vervet population live in

unusually large troops (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013). These troops should therefore experience high levels of demographic stress, because they exceed the METGS for this region. Henzi et al., (2013) reported that no group fission was observed, however, suggesting that demographic stress may not operate as Dunbar (1992) originally hypothesized. Other factors, such as predator density and water availability, may have influenced troop size at Samara: a large group may be necessary to detect and deter predators, and the need to defend water sources against other troops on their forays into each other's territory to get water may also mean that these advantages outweigh the social stress created by large group size (Pasternak et al., 2013). If these aspects of the model do not hold true, then other factors argued to maintain social cohesion, such as grooming time, also need to be examined thoroughly.

3.3 Grooming

The value of grooming to primates is a topic that was first examined by Seyfarth in his model of social grooming (Seyfarth, 1977) where he proposes grooming is not just useful for the removal of parasites, but is a behaviour used to facilitate affiliative bonds with other females. He says when a female grooms another female, a bond is formed with her, and in the future the same grooming female can solicit assistance from the receiver in an agonistic interaction with a third party. This grooming for support hypothesis takes into account the dominance and rank structure of the species involved. Highest ranking females are argued to be the most valuable coalition partners with whom a female can pair, as her dominant position allows her priority of access to the

best resources. This attraction to higher ranking females causes females to compete for access to those of the highest ranks. If all females in a troop are directing their grooming towards higher ranking individuals in an attempt to gain valuable coalition partners, there exists a passive competition among the ranks. This passive competition involves lower ranking females being blocked from grooming very high-ranking females by other high-ranking females who are also competing for access to her. This creates a pattern of grooming relationships where the majority of grooming dyads are females of adjacent rank, where grooming amounts are close to reciprocal, and with increasing rank distance there will be an increase in effort on the part of the lower-ranking female in terms of amount of grooming given. More specifically, Seyfarth's model predicts that: 1) females of higher rank will receive more grooming than they give in a grooming bout, 2) females will tend to groom those adjacently ranked to them the most, and 3) when coalitions are formed, the coalition partners involved should receive a higher proportion of grooming within the relationship.

The evidence presented by Seyfarth primarily relates to grooming frequency and correlated coalition formation and proximity measures, i.e., females who groom one another the most should also most frequently form coalitions together and should be seen in most frequent proximity to one another outside a grooming bout. Data showing strong correlations between grooming dyads and coalition dyads (Seyfarth, 1980) are taken as evidence for this model. However, in 70% of the cases where females formed a coalition, the third party opponent was a male, negating the claim that these coalitions somehow serve to boost the dominance of the lower-ranking female in the coalition

(Seyfarth, 1977, 1980). There are other models, developed more recently, that do a better job explaining the grooming behaviour of females. The key factor of Seyfarth's model is that females develop and track long-term affiliative bonds to improve their overall fitness. This assumption alone presumes that monkeys have the cognitive capacities to track the value of other females to them and make decisions based on this internal representation of another.

There is not much evidence for Seyfarth's model, outside his Amboseli studies (Cheney & Seyfarth, 1984; Seyfarth, 1980). His theory holds a lot of sway in primatology, however (Di Bitetti, 1997; L. A. Fairbanks, 1980; O'Brien, 1993; Silk, 1982), even when the evidence against the model is strong (Parr et al., 1997). Silk (1982) studied bonnet macaques and found that females rarely preferentially supported females who groomed them the most. Similarly, Fairbanks (1980) failed to show a pattern of reciprocation of grooming and coalitionary support in vervets. Parr et al. (1997) had a captive population of brown capuchins that directed grooming down the dominance hierarchy. In a key example, baboon populations with no propensity for coalition formation and therefore no need to groom for support, still had formal grooming interactions and females adjusted their time budgets to allow for grooming (Henzi et al., 1997). Therefore any model to explain the nature of grooming in female relationships cannot be solely based on coalition formation and agonistic interactions. There do exist other models of social grooming, foremost amongst these is the biological markets model (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Noë & Hammerstein, 1994). This model suggests that grooming is, in and of itself, a valuable commodity and grooming is exchanged between

females in a variety of possible exchanges, including for coalitionary support (Barrett et al., 1999; Barrett & Henzi, 2006; Henzi & Barrett, 1999; Henzi et al., 2003). The biological markets model, most importantly, doesn't rely on the assumption that females maintain long-term grooming relationships. Instead, the observed patterns of grooming in the long-term arise from simple patterns in individual decision making, which are influenced by ecological factors.

The model proposes that instead of grooming to promote long-term relationships among females, grooming is a commodity that is exchanged (Barrett et al., 1999). Seyfarth's model of grooming for coalitionary support can also be explained by the biological market model. When grooming is traded for grooming, immediate reciprocation is the norm to prevent cheating, and the exchange will have a more equal contribution from both individuals. When grooming is traded for tolerance, the exchange is expected to be less equal; specifically, the lower-ranking female will groom the higher-ranking female more. This exchange for tolerance is still in the short term, for example, a lower ranked female wants to forage in a choice location, but she understands she could be attacked and prevented from foraging beside the more dominant female, so instead she approaches the female and grooms her. When finished grooming, the dominant female is in a more relaxed state and is more likely to not attack the female, who was just grooming her, and is now foraging nearby.

There is a group size and dominance effect that determines whether or not a troop will have reciprocal grooming or tolerance-based grooming (Barrett et al., 1999;

Henzi & Barrett, 1999). An individual's position in the dominance hierarchy will determine what kind of commodity she can contribute to the market; high-ranking females can exchange grooming directly or for tolerance whereas low-ranking females will only be able to exchange grooming. When resource competition is high and dominance gradients are steep, reflecting the intensity of competition among individuals (Vehrencamp, 1983), relationships between distantly ranked individuals will be based on grooming in exchange for tolerance and between closely ranked individuals, it will be based on reciprocal grooming.

A female's ability to offer tolerance is dependent on a sufficient amount of competition in the market. Therefore, in smaller female cohorts it is less likely that there will be much grooming in exchange for tolerance, because the rank differential across the whole female cohort will be too small. An exchange of grooming for tolerance is only seen when dominance hierarchies are sufficiently steep and the power differential is high. Therefore, when there is little demographic stress in an environment, the dominance hierarchy will be shallower and the majority of grooming interactions should be reciprocal. This version is similar to Seyfarth's model; however the key difference is that high ranking females have conditional "attractiveness" to lower-ranked females based on their ability to offer more in return for grooming.

3.4 Dominance

Dominance is an interesting factor to analyze, because, despite great variation in group size and composition in vervet monkeys, there often exists a strong linear

dominance relationship among females of vervet monkey troops (Struhsaker, 1967a, 1967b; Wrangham, 1980). Dominance is primarily thought to influence contest competition between females in a troop (Isbell, 1991; van Schaik & van Noordwijk, 1988) as well as increased competition for risk-reducing spatial positions (Barton & Whiten, 1993). Dominance is known to exist but there is debate over the effect that dominance has on the female-female relationships in a troop. Whitten (1983) described a particular relationship between an animal's diet and their dominance rank. She found that when a preferred food is distributed in clumps that are therefore monopolizable, a clear differentiation in rank-related differences in food intake emerges. This priority of access to the best foods then leads to better nutrition and enhances an individual's fitness.

Rank acquisition in vervets has two components. The first being that a mother intervenes on behalf of her young in dominance disputes, and that juveniles passively accept their position in the hierarchy based solely on how their mothers interact with others, before ever engaging in dominance interactions on their own (Horrocks, Hunter, Hill, & James, 1983). Usually then, the offspring of females tend to acquire a rank very near hers in the hierarchy. In captive vervets, Fairbanks and McGuire (1986) showed that females didn't diminish participation in dominance interactions with age, and that young females with their mothers still present in the dominance interactions of the troop would improve their overall reproductive success. Female social relationships with one another are important in their own right, as a measure of differential success in reproduction and foraging, and as a factor contributing to other aspects of their social

interactions and use of space. With these effects on the fitness of an animal, it would be in a female's best interest then to achieve the highest rank possible to reap the benefits high rank allows.

3.5 Predictions

In this thesis I have a unique opportunity to examine how changing demographic stress will affect female-female relationships by comparing the results from Henzi et al., (2013) to the results from the same troops three years later. During this time, ecological conditions at Samara changed quite dramatically. Of most importance, environmental conditions were milder during my study (e.g. the river on Samara was constantly flowing throughout 2012, which was not the case in 2009) and female cohort size, and overall group sizes of the two troops, were significantly smaller. Table 1 provides a comparison of group size and climatic conditions between the two study periods.

Table 3.1 Demographic data for Samara troops.

	2009	2012
Troop Size (RST, RBM)	72, 48	54, 38
Total Rainfall (mm)	216.42	298.66
Mean Temp (°C)	17.28	16.16

Note. Troop size data from Henzi et al.,(2013), rainfall and temperature data from

Tutiempo Network SL. (2012). Climate in Graaff-Reinet. Retrieved from

<http://www.tutiempo.net/en/Climate/GRAAFF-REINET/01-2012/687370.htm>

With these two data sets we can ask, do ecological conditions matter? Are there significant changes in social relationships between the two periods to suggest that Dunbar and Seyfarth's theories are correct? The animals in the earlier study were under high levels of demographic stress (Henzi et al., 2013; Pasternak et al., 2013). There were large female cohorts and the data presented suggests that they were also under conditions of high feeding competition, with over half of the agonistic interactions occurring over food. Despite this, the females in these troops showed very few of the effects predicted by Dunbar and Seyfarth.

Dunbar predicts that with high intra-group feeding competition and reduced time to dedicate to social activities, females will adapt by capping their grooming clique size to optimize grooming time (Dunbar, Korstjens, & Lehmann, 2009; Dunbar, 1992; Lehmann, Korstjens, & Dunbar, 2007). They may also begin to lose group cohesion and should be seen to subgroup more often and even fission into two separate troops. The females at Samara did show a capping of clique size (RBM = 6.26, RST = 5.32) but there was little evidence for subgrouping nor did they fission (Henzi et al., 2013). One possible explanation for these results was that predation pressure was sufficiently high at Samara that group fission was the less favourable option. Another possibility is that the capping of clique size is a sufficient adaptation to ensure enough grooming between females and therefore to maintain group cohesion. Finally, perhaps Dunbar is partially correct in that females do seek to maintain grooming time, through the capping of

clique size, but incorrect in assuming that social grooming is the “glue” holding these groups together. Perhaps the external predation pressure, and increased need to feed most efficiently as suggested by van Schaik, (1983), is sufficient for maintaining group cohesion in this population.

Grooming and rank effects were absent in the Samara population as well. Seyfarth’s model predicts with high feeding competition, females should experience more aggression and therefore will compete for access to high-ranking grooming partners. The females at Samara in 2009 had relatively low rates of aggression despite having high feeding competition, (RBM = 1.00 instances/hour, RST = 1.02 instances/hour, Seyfarth’s vervets (Seyfarth, 1980) showed rates from 2.6 instances/hour to 3.5 instances/hour, they rarely formed coalitions, (RBM = 1.33%, RST = 0.78%, of all aggressive interactions) and had very few instances of aggression over access to grooming partners. There was no relationship between rank and grooming in RST and the relationship was the opposite direction to that predicted for RBM (i.e., females more frequently groomed more distantly ranked females) and no evidence that females were directing their grooming efforts up the hierarchy in either troop. Also, there was no evidence that females associated with their grooming partners more often when engaged in other activities (Henzi et al., 2013).

One possible explanation is the confounding effect of kinship, as this is unknown for the Samara troops. Nevertheless, these results are particularly unusual for vervets, as the consensus view is that adult kin will be adjacently ranked. The findings of Henzi et

al. (2013) suggest that females living in larger groups do not sustain matrilineal kin relationships or perhaps that the mechanism behind rank acquisition is different. Both troops had large female cohorts and presumably, high power differentials among these females. Therefore, we should observe grooming for tolerance exchanges, and in RBM this could be the explanation for why more distantly ranked females engaged in more frequent grooming. Why then did RST not show the same effect? Given that this was a larger troop, one would expect them to show this, perhaps with an even stronger effect. One possibility is that the large troop size of RST ($N = 72$), allowed them to cover a larger area while still maintaining the safety of the group. That is, a female could theoretically avoid all females that she would have to groom in return for tolerance, while still remaining within the group bounds and avoid increased predation pressure. The smaller troop, in contrast, showed evidence of grooming for tolerance, possibly caused by high feeding competition, but it may also have been because the troop was not sufficiently large for females to avoid those most likely to require appeasement and still remain within the safety of the group.

To test whether changing demographic stress levels affected female social relationships, I developed the following set of predictions:

1. As the slope of a dominance hierarchy is indicative of the strength of dominance interactions in a troop, and group size influences dominance through increased competition, I predict the larger troop to have a stronger, linear dominance slope.

2. As the animals in my study were under less demographic stress, I predicted that we should see an overall decrease in feeding competition and, given that most aggression in 2009 was over access to food (Henzi et al., 2013), I predict an overall decrease in aggression rates.
3. As demographic stress didn't appear to affect coalitions (Henzi et al., 2013), coalition formation in 2012 was not expected to change.
4. A reduction in demographic stress should lead to larger grooming cliques due to more time available to maintain grooming relationships with all other females.
5. With lower levels of demographic stress, there should be a drop in feeding competition. Though competition for safe positions in the group may still be contested, an overall drop in grooming for tolerance will follow the drop in feeding competition. The majority of grooming exchanges are predicted to be equitable.
6. High demographic stress resulted in trading grooming for tolerance only in the smaller troop (Henzi et al., 2013), suggesting that group size and area of utilization influences type of grooming exchanged. With smaller troops and thus smaller safety regions and more widely dispersed food, I predict grooming for tolerance to be low, but higher overall in the smaller troop (RBM).
7. If the disassociation between grooming cliques and spatial association in the previous study were caused by high levels of demographic stress (Henzi et al., 2013), then I

predict a decrease in demographic stress will result in a stronger relationship between grooming and spatial association.

3.6 METHOD

The data presented here were collected from two troops of vervet monkeys (RBM, RST) in the Samara Private Game Reserve, Eastern Cape, South Africa ($N_{\text{RBM}}= 38$, $N_{\text{RST}}= 54$), between January and December 2012. Instantaneous scan sampling, performed at 30 minute intervals, was used to record the activity of all observable animals, along with the identity and distance of their nearest neighbours (NN). All frequency data were converted to proportions either of the individual female's total number of scans or of the total number of scans for the group, depending on the prediction being tested (e.g., If looking at a target female's nearest neighbours, the proportion would reflect the target female's total number of scans. When investigating which female had the most NN overall, the proportion reflected the total female cohort). The total number of scans collected on females was 16,206. Table 3.2 outlines the activities and their definitions relevant to the tests in this chapter. A more complete table of behaviours and their definitions can be found in the Methods section of this thesis.

Table 3.2 Activities and their definitions

Behaviour	Definition
Autogrooming	When an animal combs through its own fur with hands and/or mouth.

Resting	Animal is not moving, usually sitting or lying down.
Moving	Animal is in a state of locomotion, in the ground or in the trees.
Foraging	Animal is in the process of eating or finding food.
Grooming	If an animal is grooming another individual with their hands and/or mouth they are classified as the allogroomer in the interaction whereas the individual being groomed is the alloreceiver.
Agonistic	Includes physical and non-physical interactions: Physical interactions include, bite, swipe, grab and chase and non-physical interactions include: <i>supplanting</i> - when an aggressor takes the spatial location and engages in the activity of another animal <i>displacement</i> - when an approaching aggressor causes another individual to move from its current spatial location <i>eye-lid threat</i> - the white area of the eye-lid is exposed <i>bob threat</i> - either bipedal or quadrupedal, involves a quick dip of the head while staring at the individual being threatened vocal threat - aggressor directs a vocalization towards the recipient
Coalitions	Occurs when a third party joins one of the two animals involved in an aggressive social interaction.

3.6.1 Time budgets and demographic stress

The formula for calculating the METGS of a group was produced based on Dunbar's calculations involving moving time, day journey length along with the minimum requirements of social, resting and feeding time and a species specific calculation based on body weight (Dunbar, 1992). The METGS is the maximum number of individuals that can live together in a group and still meet the minimum time budget requirements.

Time budgets were calculated using the half hour instantaneous scan data. An estimate of the amount of time the troop spent foraging, resting, moving, and grooming, was calculated by converting frequencies of observed behaviours to proportions of total observed activities and expressed as a percentage. Time spent autogrooming was considered as resting time and added to the resting frequency total. To calculate time budget based METGS, the following formula was used: $\text{METGS} = (\text{Coefficient of environmental factors} - \text{coefficient of seasonality} * \text{Foraging percentage})/0.52$. Environmental factors that were shown to affect the METGS formula were measures of rainfall amount and rainfall diversity.

3.6.2 Dominance

Dominance hierarchies were constructed for the females in each troop based on decided agonistic interactions. Agonistic interactions were collected ad libitum. David's Scores are a way of measuring the actual difference in dominance between two

females, rather than simply computing ordinal ranks, and it is the most suitable measure of the steepness of the hierarchy (de Vries, Stevens, & Vervaecke, 2006). In order to have a steepness measure on a scale of 0 to 1 the David's scores must be normalized. Normalized David's scores (NDS) (de Vries et al., 2006) were calculated by taking the David's Score and dividing by the total number (N) of individuals in the troop, to give a score that ranges between 0 and N-1. From this range, all females were assigned an ordinal rank (highest NDS was assigned rank 1) as well as a standardized rank to use when doing cross-troop comparisons. Standardized ranks were calculated as follows: $StdRank_{ij} = NDS_{ij} / \max(NDS_j)$; the standard rank of individual i in troop j is the ratio of the NDS of i and the NDS of the highest ranking female in the troop (Highest ranking female $StdRank = 1$).

To measure variation in the strength of dominance relationships, the Normalized David's scores were plotted against the ordinal ranks assigned to each female. The slope of that line is then used to determine the actual difference between the ranks of females in a troop. A shallow line demonstrates a small difference in dominance between two adjacently ranked females whereas a steep slope demonstrates high dominance differentiation between two females.

3.6.3 Grooming and rank effects

Clique size: Grooming relationships among females can be spread across the entire female cohort or restricted to a portion of the cohort, referred to as a clique.

Grooming cliques were calculated simply by tallying the total number of unique females a given individual was observed to groom.

Grooming index: To measure if grooming was distributed evenly amongst females in a clique or directed towards higher ranking individuals, a grooming index (GI) was calculated following Trusina, Maslov, Minnhagen, & Sneppen (2004). In the case presented here, the index is defined as an estimate of the ratio of the average amount of time a female grooms another higher-ranking female (females with higher NDS) to the average amount of time she grooms any other female. If females do not prefer to groom their higher ranking partners, then GI = 1 and if they do prefer to direct their grooming up the hierarchy then the GI > 1.

$$GI = \frac{\sum_{k=1}^m a_{ik} / m}{\sum_{k=1}^n a_{ij} / n}$$

$NDS_k > NDS_i$, $a_{ik} \neq 0$, and $a_{ij} \neq 0$.

For a target female, i , m is the number of females whose NDS is greater than i , and n is the number of the female cohort – 1. a_{ik} is the amount of time female i spends grooming female k and a_{ij} is the amount of time i spends grooming female k .

Grooming equity: Rank and rank distance effects were calculated using an estimate of the proportion of grooming that female i gave to j (when $G_{ij} \neq G_{ji}$) given the total amount of grooming i gave (G_{ij}/G_{total}) compared with the related females individual ranks or the rank distance that existed between them. Pearson correlations were calculated using IBM SPSS Statistics 21.0, to examine these comparisons

statistically. According to Seyfarth, (1977), we should see the highest allocation of grooming towards those females who are adjacent in rank to the target female. We calculated the proportion of grooming accounted for by females of adjacent rank two ways. First, we look at the number of dyads with females of adjacent rank over the total number of dyads. Secondly, we examined the total amount of grooming accounted for by adjacent ranked individuals over the total amount of grooming observed.

$$\text{Proportion} = \frac{N_{\text{dyads adjacent}}}{N_{\text{total dyads}}}$$

$$\text{Proportion} = \frac{\text{Grooming}_{\text{adjacent}}}{\text{Grooming}_{\text{Total}}}$$

3.6.4 Spatial Association

Evaluating whether females show similar preferences for grooming partners and those with whom they associate spatially requires a calculation of ordinal allocation of grooming and an ordinal ranking of spatial associations. The ordinal allocation of grooming was measured as an order of preference among a female's grooming clique. For example, if female *i* has four grooming partners, rank number 1 would be assigned to the partner who was most often *i*'s grooming partner. The spatial association rank (SAR) was measured similarly; a SAR of 1 was assigned to the female who was most often observed to be the target female's nearest neighbour. The proportion of grooming female *i* gave to female *j*, was compared to *j*'s SAR in relation to *i*. If females tend to associate spatially with those they groom most frequently then there should be a strong negative correlation between the proportion of grooming given and spatial association rank of the receiver.

3.7 RESULTS

3.7.1 Maximum ecologically tolerable group size and Demographic stress

Table 3 shows the time budgets for both troops during the study period. RBM has a calculated METGS of 53.1 and RST a METGS of 53.3. RST had an average group size of 54 which is slightly outside the METGS measure, but RST had close to 60 members in January and they were down to 50 members by the beginning of April, so RST is considered to not be under demographic stress. RBM had an average of 38 putting them well within the maximum ecologically tolerable group size for this habitat. It can be concluded that the females were under less demographic stress than in the previous study period (Henzi et al., 2013).

Table 3.3 Percentage of time dedicated to essential behaviours.

Activity	RBM	RST
Foraging	37.90%	37.79%
Grooming	6.14%	6.33%
Moving	28.15%	25.11%
Resting	26.90%	29.85%

3.7.2 Dominance Slope

The dominance slope for RBM = -0.416 and RST = -0.084; Figure 3.1. The graphs clearly show that, despite a smaller group size, RBM has a much steeper dominance slope. This result means the rank differentials between members of RBM are much stronger than those in RST. This result is contrary to predictions about group size and competition.

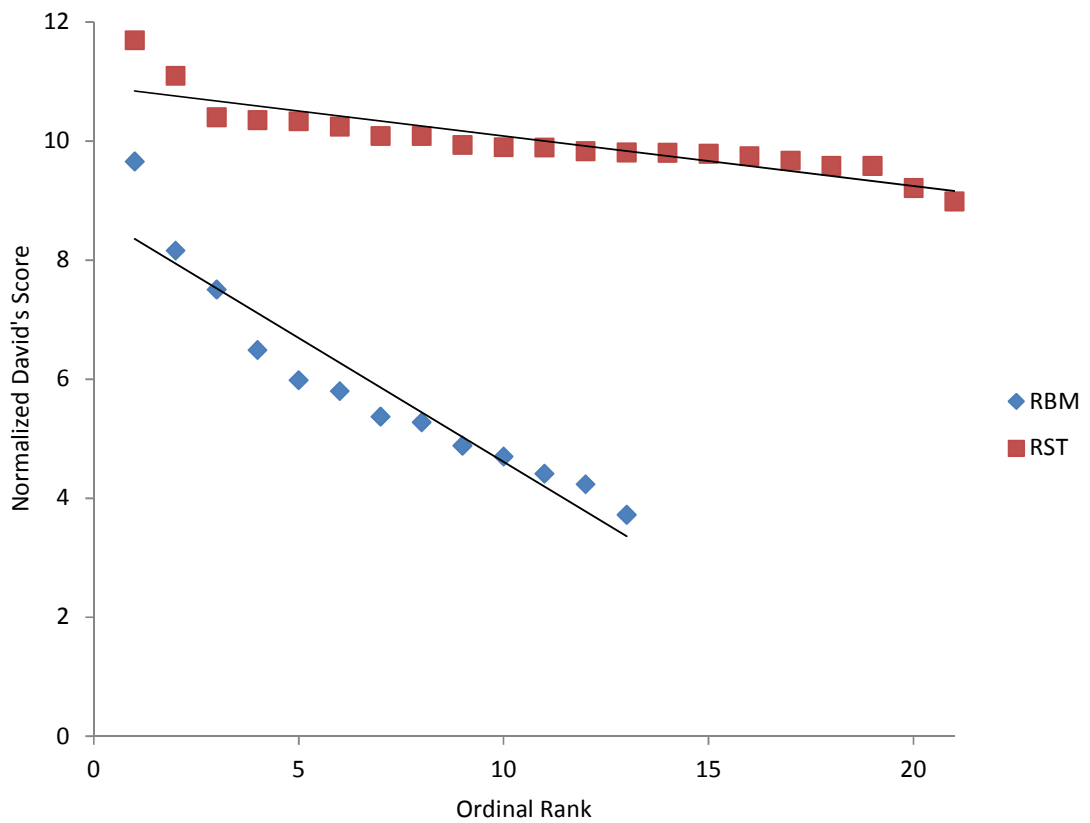


Figure 3.1 Relative strength of the dominance hierarchies for RBM and RST.

3.7.3 Aggressive Interactions

RBM had 280 female-female agonistic events and RST had 147. This gives a rate of 0.017 instances/female/hour (~ 0.23 instances/hour) for RBM and 0.006 instances/female/hour (~ 0.12 instances/hour) for RST. This is a marked drop from the rates in the previous study (RBM = 0.067 instances/female/hour, 1.00 instances/hour: RST = 0.044 instances/female/hour, 1.02 instances/hour: Henzi et al., 2013) and the difference is statistically significant (RBM: $t(14.9) = -2.477$ $p = 0.026$; RST: $t(22.4) = -4.129$, $p < 0.001$). Thus, in line with prediction, there was an overall decrease in aggression and feeding competition.

Incidents of female-female coalitions against female targets accounted for 1.10% of all aggression for RBM and 3.40% for RST. Comparing this result to Henzi et al., (2013) (RBM = 1.33%; RST = 0.78%) it would seem that contrary to prediction, coalition formation did change, with a drop in the smaller troop and an increase in the larger troop.

3.7.4 Grooming and rank effects

Clique size: The mean number of grooming partners was not significantly different between the two troops (RBM = 4.25, range: 2-7, RST = 4.67, range: 1-9, independent samples t-test: $t(31) = .05$, $p = .961$) but females in both troops capped clique sizes, i.e., they did not groom all available females. The females in the 2009 study also show a capping in clique size (RBM = 6.26, range: 2-10, RST = 5.32, range: 1-12: Henzi et al.,

2013). The difference between clique sizes across the two studies is only significant in RBM: $t(26) = -2.507, p = 0.019$. RST: $t(35.8) = -0.774, p = 0.444$. The females in my study have smaller clique sizes on average suggesting a decrease in demographic stress may have had an effect on this behaviour, but the result does not follow prediction.

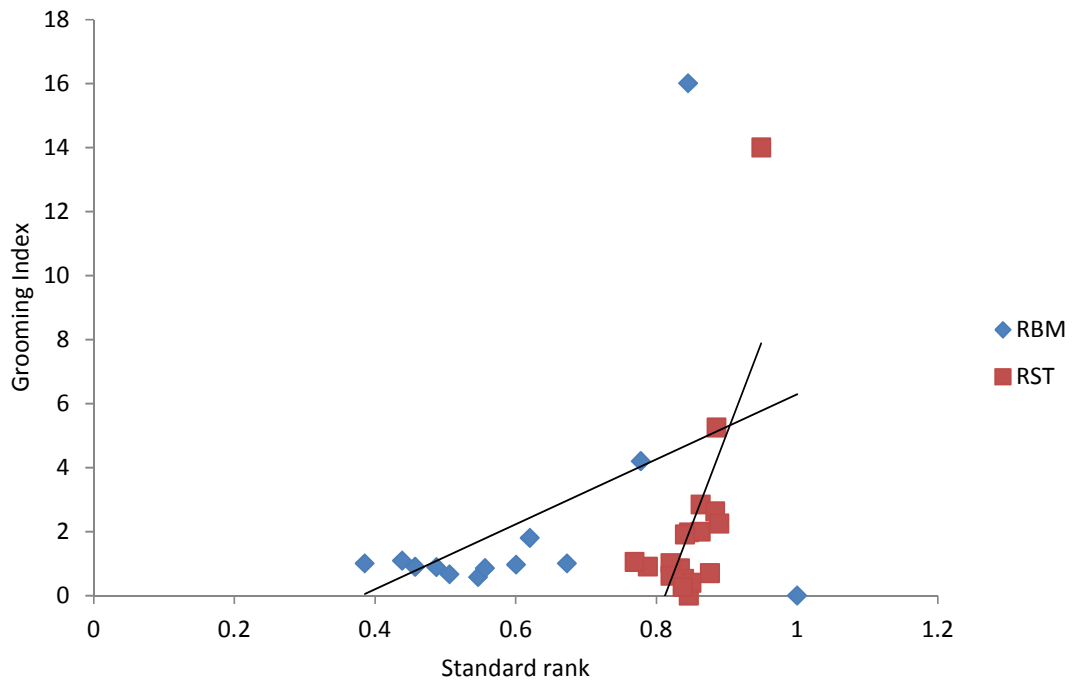


Figure 3.2 Grooming index and standard rank for females in RBM and RST.

Grooming index: To test whether females direct their grooming towards high-ranking individuals, a grooming index was calculated for each individual. For RBM the average GI was 1.16 (SD = 1.04), and for RST it was 2.10 (SD = 3.13). There was no significant difference in the grooming index values for RST and RBM, ($t(30) = -.235, p = .816$).

Figure 3.2 demonstrates the relationship between a female's grooming index and her standardized rank. There was no significant relationship between an individual's GI and standard rank for RBM: $r = 0.530, p = 0.063, N = 13$. There was, however, a significant relationship in RST: $r = 0.728, p < 0.001, N = 19$, indicating that as an individual's rank increases their grooming index also increases. The graph also shows two points that appear to be outliers. Though they are not statistical outliers, I removed them from analysis and ran the correlation again. Both correlations dropped in power but there was no change in statistical significance RBM: $r = 0.190, p = 0.555, N = 12$; RST:

$r = .526, p = 0.025, N = 18.$

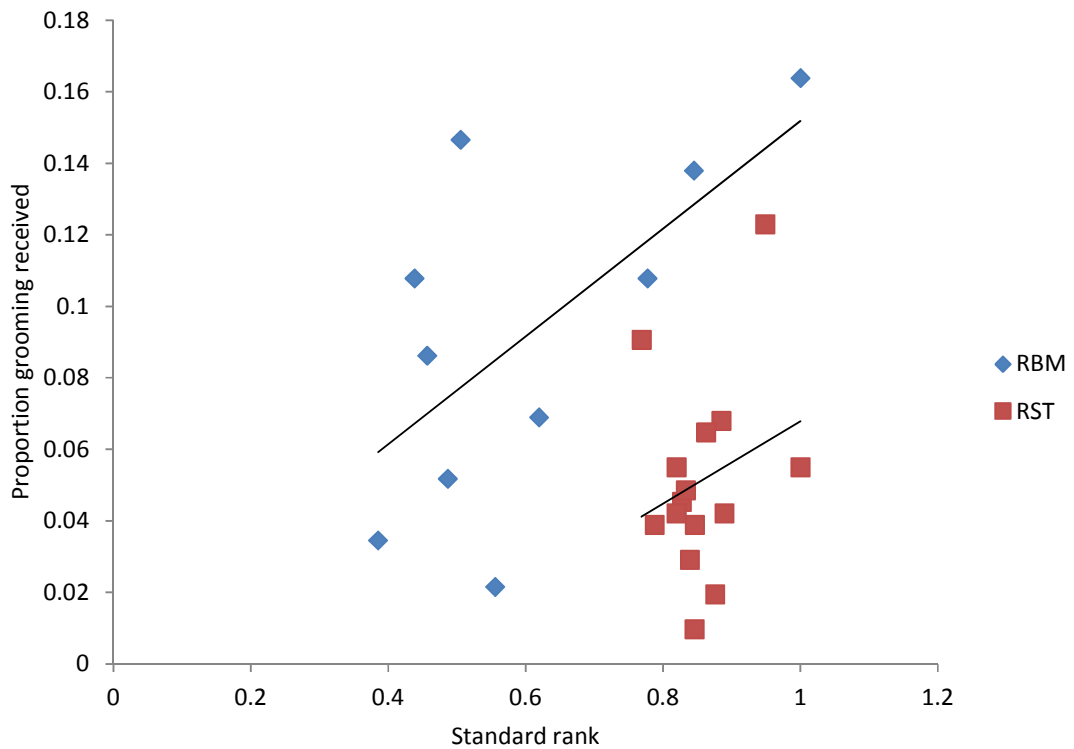


Figure 3.3 Relationship between proportion of grooming received and standard rank.

Grooming equity: In line with prediction 5, both RST and RBM showed no significant relationship between the proportions of grooming received and rank. This relationship is plotted in Figure 3.3 with the correlation for RBM: $r = .628, p = .052, N = 10$, and for RST: $r = .243, p = .384, N = 15$. Though neither correlation is significant, in line with prediction 6, the smaller troop has a stronger relationship between rank and amount of grooming received. To assess the equity of grooming another way, the difference proportion between all grooming received and given for each female was compared with her standardized rank, with no effect in either troop (RBM: $r = 0.209, p =$

0.492, $N = 13$; RST: $r = 0.160$, $p = 0.489$, $N = 21$). Figure 3.4 demonstrates this relationship. The dotted line indicates the expected relationship if high-ranking females were receiving more grooming than they gave and low ranking females groom more than they receive. As the linear regression lines for RBM and RST show, there is no evidence that higher ranking females received more grooming than they gave; instead it appears there is no relationship.

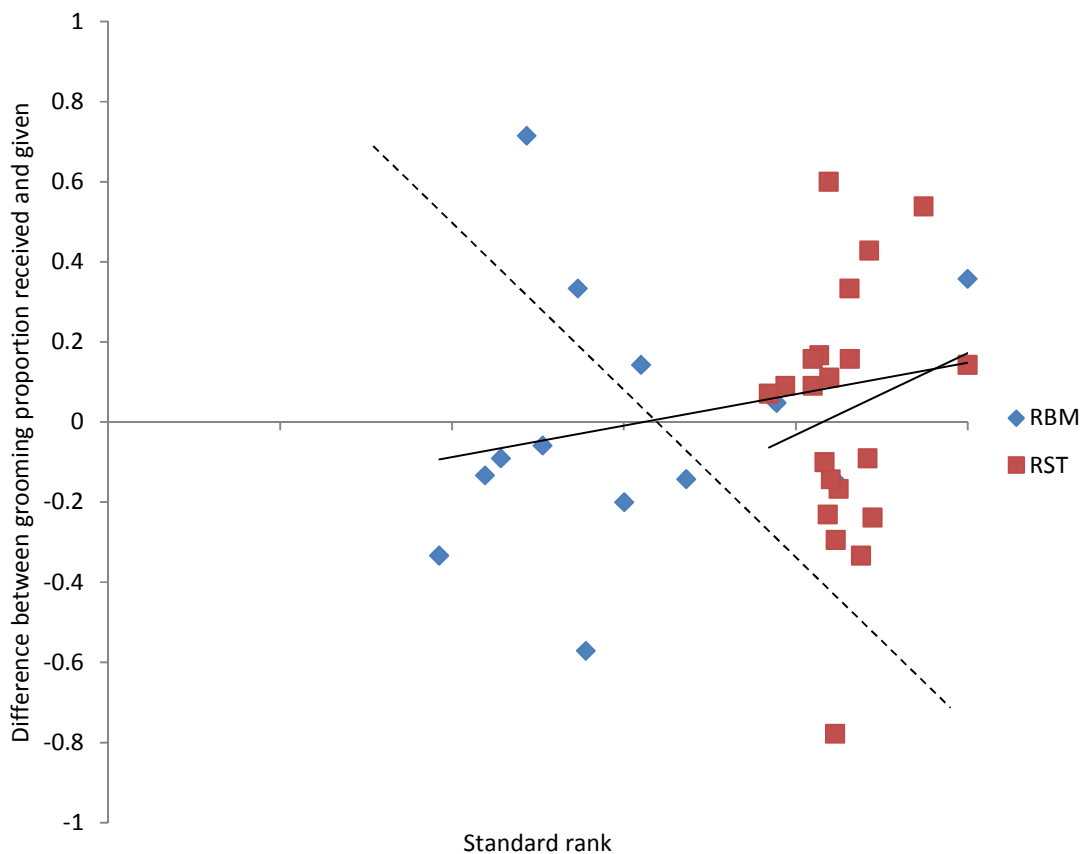


Figure 3.4 Difference between proportion of grooming received and given with standard rank for females in RBM and RST. The dotted line represents the expected relationship.

I examined the female's individual time budgets to gauge whether rank had an affect on how much of each female's active time was committed to grooming. Results are displayed in Figure 3.5 with the percentage of time spent grooming on the y axis and each female's standard rank on the x-axis. Females in neither RBM nor RST showed a correlation between the time spent grooming and rank (RBM: $r = .006$, $p = .985$, $N = 12$; RST: $r = .047$, $p = .839$, $N = 21$).

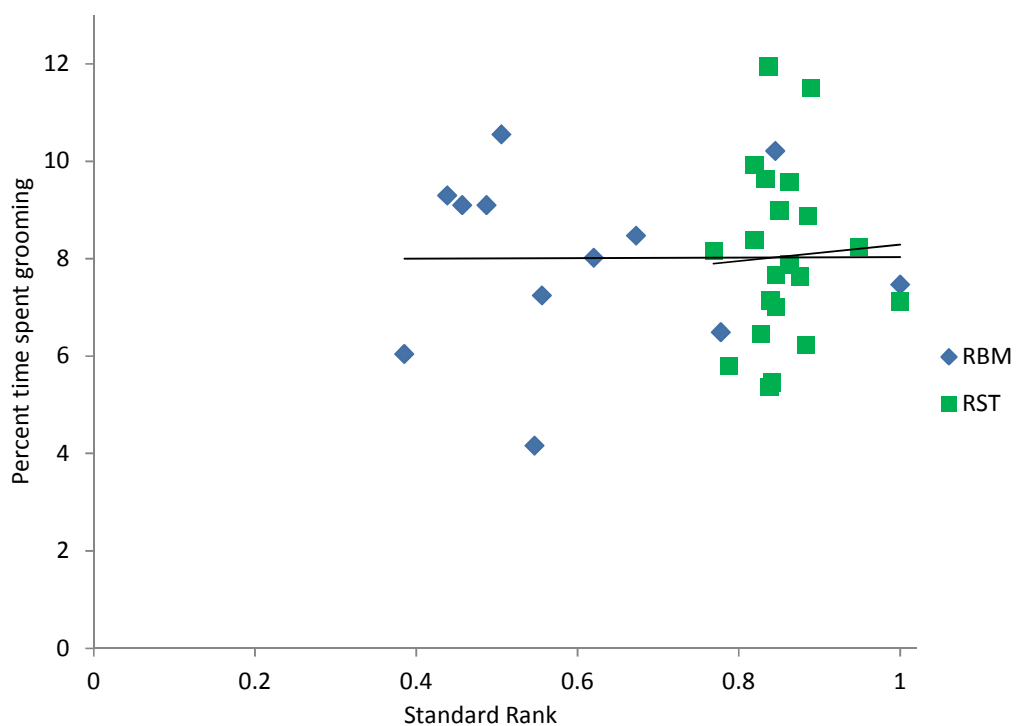


Figure 3.5 Individual time budgets and standard rank for females in RBM and RST.

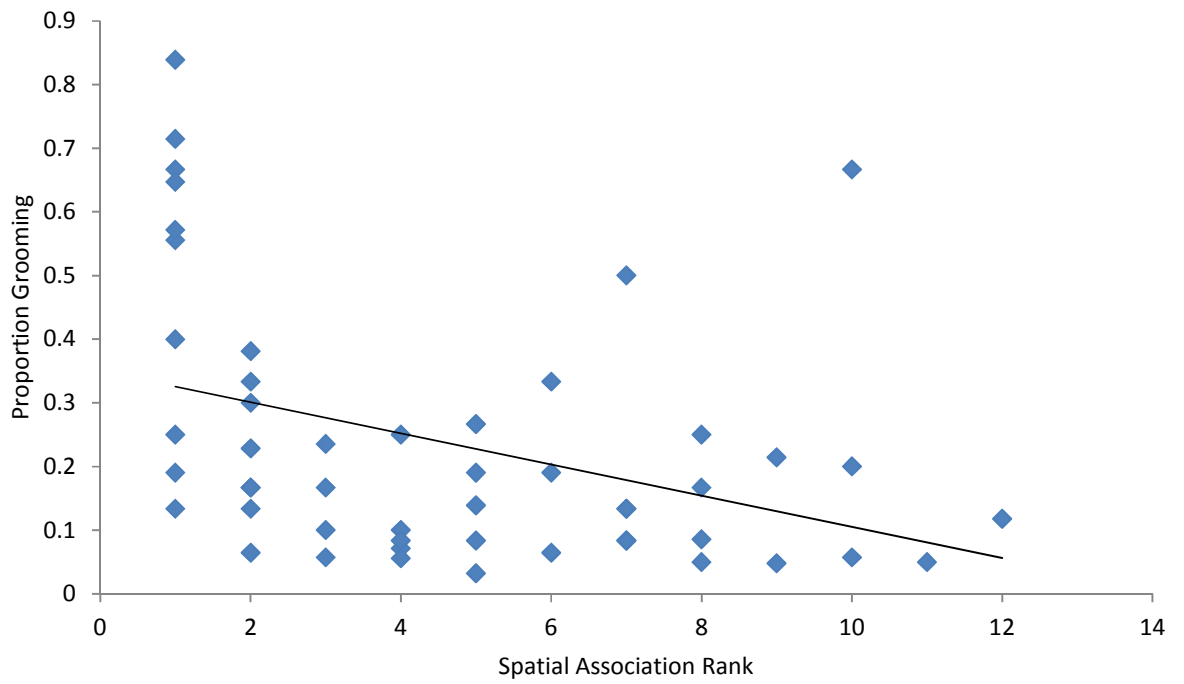
Finally, I tested whether or not females had a preference for grooming those adjacently ranked to them more often. When examining the number of dyads with adjacently ranked individuals as a portion of the total number of dyads observed,

neither RBM or RST show these to be in the majority (RBM = 11/55, or 20%; RST = 11/97, or 11.3%). Then I examined the total proportion of grooming accounted for by adjacently ranked individuals and found for RBM this equalled 28.5% and for RST it was 18.6%. Though RBM did show over a quarter of all grooming accounted for by adjacent ranks, neither number would be considered as evidence for a majority.

3.7.5 Spatial Association

To test whether females were associating with their grooming cliques outside the grooming relationship I calculated the spatial association rank of each female's number one grooming partner. For RBM, the mean was 1.5 and for RST it was 1.7. This is much closer to 1 than Henzi et al (2013) with RBM = 6.8 and RST = 9.5. I tested this relationship in another way with a Pearson's correlation, examining the proportion of grooming given to a partner female, and that female's spatial association rank with respect to the allogroomer. These results are based on numbers of dyads and as such the sample is slightly inflated. The Pearson's correlations were statistically significant with RBM: $r = -.404$, $p = .003$, $N = 51$ and RST: $r = -.514$, $p < .001$, $N = 94$. Plotted in Figure 3.6 is the relationship between the proportion of grooming received and the receiver's spatial association rank, in relation to the groomer. In line with prediction, there is a strong relationship between grooming and spatial association in both troop's females.

RBM



RST

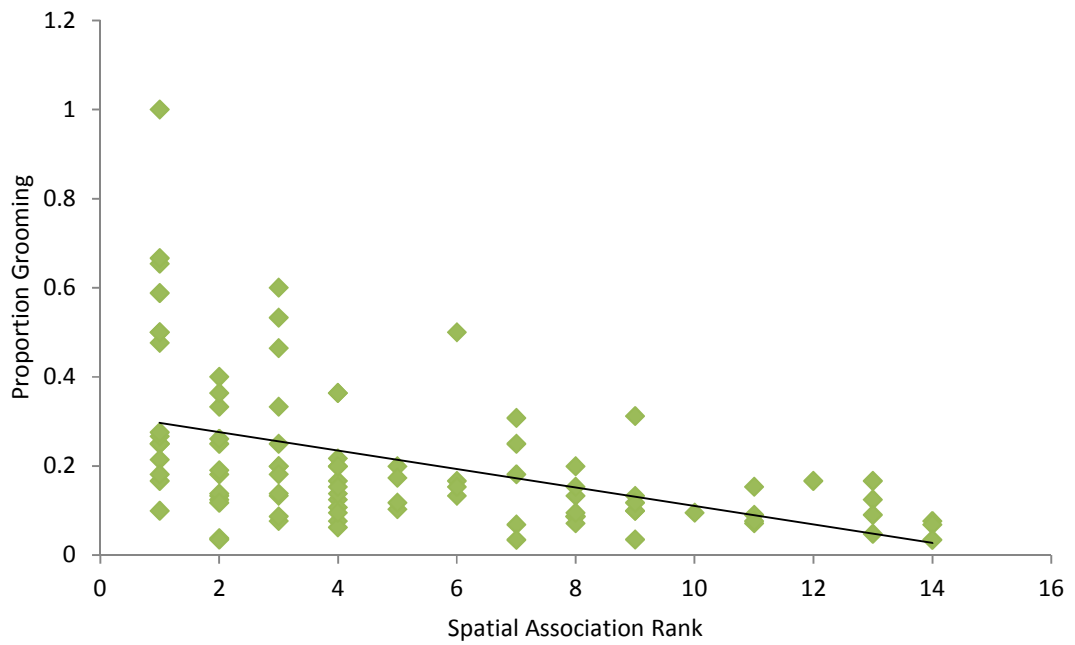


Figure 3.6 Spatial association rank and proportion grooming received for RBM and RST.

3.8 DISCUSSION

My results show that females in this study were not demographically stressed, as they did not exceed the METGS for the habitat. Contrary to prediction the smaller of the two troops has a stronger, more linear dominance hierarchy, but, in line with prediction, aggression and feeding competition dropped with a reduction in demographic stress. Rates of coalition formation changed between the study periods, contrary to prediction, with an overall decrease in the smaller troop and an increase in the larger troop. Despite an increase in available time to groom, females in both troops still capped their grooming cliques. Grooming and rank effects were in line with predictions, with a single exception: higher ranking females in RST showed a slight preference for directing grooming up the hierarchy. Other than this, the distribution of grooming was equitable in both troops. In line with prediction, the smaller troop did show a more disparate grooming distribution. Though this result was not statistically significant, it is worth noting that the correlation was a relatively strong one, at 0.628 and the p value was just outside of significance ($p = 0.052$). Finally, the relationship between spatial association and proportion of grooming was strong for females in both troops, following the prediction.

It is clear that the vervets at Samara experience highly varied ecological conditions. This study has demonstrated that between two study periods, the population went from being under significant demographic stress (Henzi et al., 2013; Pasternak et al., 2013) to conditions that are significantly different, where the improved

climatic conditions and the decreases in troop sizes result in a decrease in demographic stress. With time budgets and troop sizes that did not exceed Dunbar's (1992) maximum ecologically tolerable group size calculations, it can be concluded that the females were not under high demographic stress in my study.

The difference between RBM and RST in terms of relative dominance strength was an overall interesting result, as it is contrary to theories about competition and its effect on strength of dominance relationships. With a large group size, feeding competition is proposed to increase, although the dispersal of the food supply mediates this competition. When food is not clumped and monopolizable, there is little point in contesting a foraging location. The difference observed between these two troops could be as a result of two things. The first is that RST lost many adult females in 2012, and there were also a number of young sub-adult females who reached adulthood and entered the adult hierarchy, creating a period of rank instability. This instability could explain the relatively weak dominance relationships between females in RST. The second explanation for weak dominance in RST, is that females tended to split into sub-groups during my study, which would often not interact the entire day. This may, of course, also be related to the entry of younger females into the dominance hierarchy, and so these explanations are not mutually exclusive. The reason the dominance gradient is so flat seems to be because certain females did not interact with others very often. Of course, these factors could both be contributing to this difference.

This change in demographic stress did seem to have an effect on certain aspects of the females' behaviour; most notably, it led to an overall decrease in aggression and feeding competition, suggesting that Dunbar is at least partially correct in assuming that high levels of demographic stress translate to increased competition and tension among troop members. This drop in competition also had the expected effect on grooming interactions: grooming and rank effects were almost entirely absent for females in both troops. However, it is unclear what role competition actually plays in grooming interactions as grooming and rank effects were absent from the previous study as well (Henzi et al., 2013), when intra-group competition was high.

Coalition formation is a bit more mysterious, and it is difficult to come to a definitive conclusion about the influence of demographic stress. Aggression rates were much lower in my study, yet the larger troop (RST) showed an overall increase in coalition formation. Seyfarth (1977, 1980) proposed that coalition formation occurred as a result of increased competition, but in this study it has already been demonstrated that competition between females was low. Also, the rank effects Seyfarth (1977, 1980) proposed are absent in this population: females in both troops showed no preference for grooming high-ranking females, and the drive to direct grooming up the hierarchy was only true for the high ranks in one of the troops. One possible explanation for such a pattern comes from Silk, Alberts, & Altmann, (2004), who demonstrated that among savannah baboon females, coalition formation occurred most often between kin. When coalitions were formed outside the kin relationship, often the intervening female would be of high-rank, and assist the higher-ranking female involved in the agonistic

interaction. This result suggests that coalition formation occurs more to reinforce the established dominance hierarchy, and is not tied to competition and grooming. This behaviour seems more likely for these vervet females, as the actual difference in rank between females in RST were shown to be very small, and during 2012, RST lost a total of 7 females, with 5 maturing sub-adult females attempted to integrate into the adult dominance hierarchy. The sudden loss and addition of females could have led to instability, and females may have used coalition formation as a means to establish their rank. This is very speculative, however, and more specific research into these patterns is needed to conclusively determine the factors involved with coalition formation in this population.

Following Dunbar (1992), I predicted that, with a decrease in demographic stress, there would be more time available to groom and females should be able to distribute their grooming across a larger grooming clique. In contrast to this prediction, the females still capped their cliques in this study, and average clique size was actually smaller, rather than larger. The difference between the two study periods is significant only for RBM, and although RST was not statistically significant, it was still smaller on average, and this reiterates that these troops are probably not capping clique size for the reasons Dunbar (1992) proposed, given that females at Samara have now been shown to cap clique size under conditions of both high (Henzi et al., 2013) and low demographic stress. Henzi et al. (2013) proposed that the capping of clique size in the population at that time was not simply to reduce effective group size, and re-establish “normal” social organization as seen in other vervet populations (Cheney & Seyfarth,

1984; Seyfarth, 1980). Instead, they suggested that this pattern was perhaps explained by theories originally proposed by Johnson (1982) and White (2003), for human grouping patterns: they argued that, as social groups grow in size, information load increases in a non-linear fashion and, in order to maintain coordination, groups must introduce hierarchical control at a threshold size. White (2003) found that this number was around 6 (+/- 2), which corresponds closely with the clique sizes of Henzi et al. (2013) (RBM = 6.26, RST = 5.32) and this study (RBM = 4.25, RST = 4.67).

Seyfarth's (1977) model of social grooming predicts certain grooming and rank effects to be present; i.e. grooming directed up the hierarchy and high-ranking females receiving more grooming than they give. In the previous study at Samara, the females showed none of the predicted patterns and, at times, displayed strange rank reversal effects (Henzi et al., 2013). A decrease in demographic stress was unlikely to provide evidence for Seyfarth's model as it hinged on specifics relating to coalition formation and competition. However, the biological market model of grooming does not hinge on these points (Barrett et al., 1999; Noë & Hammerstein, 1994), and may thus provide a better base model to test the effect of changing demographic stress. According to the biological markets model, with decreasing competition, there should be less need to trade grooming for tolerance, but this would not change the drive to be safe from predators, and so spatial positions in the group may still have been contested. The absence of grooming for tolerance in the previous study, when demographic conditions were worse, and presumably the competition for spatial position was even higher, suggests that females do not trade grooming for safe spatial positions. Females that

trade grooming for tolerance will already be in proximity to other females and the act of grooming another female is unlikely to cause the target female to give up her safe spatial position. Additionally, the fact that the majority of grooming exchanges were equitable also suggests that grooming in exchange for safe spatial positions is unlikely.

There was one effect of rank and grooming found in the previous study. In the smaller troop, high ranking females were more likely to receive grooming from low-ranking females (Henzi et al., 2013). It was strange to observe this effect in the smaller troop and not the larger one, as the biological markets model proposes that trading grooming for other things, such as tolerance, should occur when power differentials between females is high. The larger troop in the previous study did not show this rank effect, and their grooming was more equitable than the smaller troop. This curious effect could have resulted from the difference in overall troop size. With a very large troop, the area of safety is much larger, as the area of use is necessarily larger to accommodate the foraging needs of all members of the troop. With such a large group, theoretically, a female should be able to avoid a higher-ranking female while still being able to safely forage, rather than appease the high-ranking female with grooming. However, a female in a smaller troop would be unable to do this, as the area of safety of the group as a whole isn't as large, and encountering a potentially aggressive, high-ranking female will happen more often. In my study, high-ranking females received more grooming in the smaller troop and, although this was not statistically significant ($r = .628$, $p = 0.052$), the correlation is strong and the p value is only slightly outside significance. Comparing this result to the larger troop ($r = .243$, $p = .384$), it is obvious

that the relationship is stronger in the smaller troop. This is in line with my prediction and suggests that, once past a threshold size, females trade grooming to avoid aggression from more dominant females, but only when the area of use is too small to easily avoid a particular sub-set of females. The relationship between spatial position and dominance is an interesting factor, and will be covered in more detail in the next chapter.

The females in the previous study were found not to associate with their grooming cliques outside of the grooming relationship (Henzi et al., 2013). Under decreased demographic stress, this pattern changed quite dramatically. Females were more likely to spend time in proximity to those they groomed the most. This is interesting, and suggests that a decrease in demographic stress may be driving this change. The question to be answered now is: why? It is difficult to pin down an answer. The pattern found in this study may be more easily explained by a general drop in tension among group members, as they directed their grooming towards those that were neighbours. However the females in Henzi et al. (2013) seem to have been either using grooming for another purpose or, as the authors suggest, they could have had a harder time coordinating grooming time with preferred partners, due to high competition for food. Thus, females attempted to groom whenever they had the time to do so, and groomed those others with schedules that were synchronized to their own. With the decrease in demographic stress, the females would have more flexibility in their daily activity schedule, and perhaps more opportunity to seek out preferred grooming partners.

It is clear that changing levels of demographic stress has an affect on female-female relationships in this population, but attempting to explain these changes with established models proves to be more challenging. Although the previous study showed that Seyfarth's model did not hold true for the females at Samara, the females at that time had anomalous behaviour patterns according to Dunbar (1992), and the high levels of demographic stress could have lead to this difference. With a change in demographic stress, only two things seemed to change significantly. The first was an overall drop in aggression and feeding competition, which seems an obvious consequence of decreased demographic stress. The second was the propensity for females to spend the most time with those other females they groomed the most. The things that didn't change also tells us something about the behaviour of this population. A decrease in demographic stress did not affect how these females distributed their grooming according to rank. Females in both studies did not seek to groom up the hierarchy, nor did high ranking females receive more grooming than they gave. Despite having more time available to groom other females, cliques were still capped at a threshold size, and changed very little between the two study periods.

Demographic stress, as a changing variable in this environment, did not lead to a major change to grooming patterns among females, though it did seem to affect spatial association. To tease out what is actually going on with the grooming choices these females make will require more indepth examination. At Samara, kinship is currently a factor that is not well understood; however, with more time, kinship can be tracked, and eventually, the same questions can be tested and a proper account of the effect of

kinship can be determined. This could also be useful for determining whether the rank acquisition in the troop is deviating from the norm, which would help explain some of the strange effects seen in Henzi et al. (2013).

The findings presented in this chapter are an important examination of the effects of the environment on female social relationships. It reiterates the point that grooming relationships between females are not directly tied to environmental conditions, and that the patterns observed in these troops over time are persistent. This suggests the true purpose of grooming for these females has more to do with the direct benefits of grooming, or as an immediate response to the proximity of a potentially aggressive high-ranking female. This approach to grooming relationships doesn't require females to maintain a long-term relationship with all other females that. In some sense. Is recognised as such, as Seyfarth's model implies. Instead, it focuses on how females respond in the moment, with the information available to them. The decrease in demographic stress influences how females associate spatially, especially in relation to their preferred grooming partners, suggesting that under high demographic stress, the females had to adapt their grooming habits to fit with their other activity demands, resulting in a disassociation between whom they chose to groom with and those they chose to associate with spatially. Demographic stress is an interesting variable to consider, and because it is constantly changing, more definitive conclusions regarding social relationships, involving kinship and rank acquisition, need further data on how female social behaviour varies over time in relation to demographic changes.

4.1 Forming Groups

Vervet monkeys (*Chlorocebus aethiops pygerythrus*) are group-living primates, and group life has associated costs and benefits. The benefits to animals that live in groups are a reduction in predation costs (Hamilton, 1971; van Schaik, 1983), and an increase in foraging efficiency and resource defence (van Schaik et al., 1983; van Schaik & van Noordwijk, 1985).

The most common cost of group-living is an increase in feeding competition. This also contributes to the other major cost, which is a competition for advantageous spatial position within the group. A position at the center of the group is advantageous as it is the safest from predators (Hamilton, 1971) and there are plenty of neighbours around to decrease the likelihood that you will be the victim of predation.

This combination of feeding competition and spatial competition seems to be driven by dominance, as high-ranking females are able to contest the best food sources, and other females have to compromise their spatial position in relation to such females. On the one hand, being closer to the dominant female is more likely to procure lower-ranking individuals a better food source (in cases where preferred sources are clumped) and provide protection from predators, but it also puts animals at risk of aggression from the dominant female. On the other hand, avoiding the center of the group will decrease lower-ranking female's risk of aggression from the dominant female and other

high ranking females, but this comes at a cost, because females may forage on (potentially) a lower quality food source and will be at a greater risk of predation (Cowlshaw, 1998).

The theory for why the dominance gradient seems to exist in the spatial organization of females, is based on evidence from a variety of studies on primates (Busse, 1984; Caine & Marra, 1988; Chance, 1967; Cowlshaw, 1998; Hall & Fedigan, 1997; McNelis & Boatright-Horowitz, 1998; Rasmussen & Farrington, 1994; Robinson, 1981; Rowell & Olson, 1983; Treves, 1999). If we accept that animals will attempt to maximize their fitness, as the monkeys move and forage throughout the day, their focus will be on attaining the best quality food source, while considering the risks of predation, simultaneously. Due to the social hierarchy that exists between females in this particular species, dominance will have a significant effect on which female gets to monopolize the best food sources, and the best spatial position. For now we will consider her driving motivation to be more foraging than reducing predation risk, thus she will move throughout the day to be in the best position to attain food. Supposing she is the most dominant female in the troop, she will be able to contest the preferred foraging positions of all other females in the troop. If she chooses a particular location and another individual was already feeding there, the more dominant female will be able to contest the feeding patch, and most likely, supplant the subordinate female that previously held that position. The dominant female may continue to do this throughout the day, moving to find new food patches, and potentially supplanting, or potentially acting aggressively towards any other female who happens to be in her way. The other

females of the troop are attempting to maximize their fitness as well and there exists a motivation to be nearer the dominant female, as she has priority of access to the choice foods, and because of this attraction, the female cohort tends to surround the dominant female. This results in her being at the center of the group, through no conscious effort on her part..

It is in an animal's best interest to attempt to maximize the benefits of group life while mitigating the costs, through behavioural strategies such as social scanning, vigilance, and avoidance of potential aggressive females. Predator vigilance is an essential component to primate group life (Caine & Marra, 1988; Robinson, 1981). It ensures early predator detection and thus reduces the risk of being eaten. Social scanning and vigilance, by contrast, is an internally driven behaviour, meaning the stimulus comes from within the group. For example, females also monitor one another to prevent injury from an aggressive interaction (Hall & Fedigan, 1997; Rowell & Olson, 1983). There exists an effect of group size on these behaviours. As discussed in the previous chapter, Dunbar postulates that group cohesion hinges on grooming and maintaining enough time to groom other members of the troop (Dunbar, 1992). Group size affects this group cohesion by limiting the time that each female has to dedicate to every other female; with increasing female cohort size, the same finite amount of time available to groom must be divided among more members. It seems that vervet females employ a strategy of capping grooming clique size in order to maintain a certain level of grooming with each partner. Dunbar (1992) argues that this behaviour has consequences for group cohesion, and if all females cannot groom all other females, the

group is at greater risk of fission. However, Isbell & Young (1993) found that among larger groups of vervets, scanning per capita was lower but predator scanning overall was much higher than smaller groups. This then frees up time for other activities, such as social grooming. This would suggest that a larger group can mitigate the effects of a potential reduction in cohesion by reducing each individual's vigilance costs. There is also evidence from females at Samara that is contrary to Dunbar's hypothesis as the groups greatly exceeded Dunbar's measures of maximum group size, and yet they did not fission (Henzi et al., 2013).

Grooming as a social cohesion mechanism is not particularly well supported in the literature, as many examinations of activity budgets in primate groups reveal a consistent amount of grooming and patterns of fissioning that do not necessarily correspond to shifts in grooming allocation (Henzi, Lycett, & Weingrill, 1997; Isbell & Young, 1993; Sterck et al., 1997). There is also evidence that grooming is a risky behaviour in terms of predator vigilance: females engaged in grooming scan for predators at a much lower rate than when not involved in grooming (Cowlshaw, 1998; Rowell & Olson, 1983). It thus seems unlikely then that grooming acts as social "glue" as Dunbar suggests. Instead, it seems more likely that the cohesion of a group depends on predator detection and group feeding benefits (Sterck et al., 1997; Struhsaker, 1967b).

4.2 Scanning

It has been shown in tamarins, (*Saguinus labiatus*) and squirrel monkeys, (*Saimiri sciureus*) that the presence or absence of a dominance hierarchy affects the animal's

scanning behaviour (Caine & Marra, 1988). Primates living in groups with dominance hierarchies tend to have two types of scanning behaviour: animals will scan the environment around them not only for predators but also for other members of their troop, and so they must divide their vigilance time between watching for predators and watching for aggressive neighbours. A primate living in groups with slight or non-existent dominance hierarchy will not spend as much time monitoring other members of the group, and their scanning behaviour can be almost solely directed towards detecting predators. This has an effect on group size that may seem obvious: those groups that have dominance hierarchies, and therefore must divide their vigilance time, tend to live in larger groups, to compensate for the diminished predator scanning (Caine & Marra, 1988). Again, this suggests that, instead of group size being mitigated by a lack of social time and therefore a lack of group cohesion, it is instead driven by the more pressing need to keep track of predators and other group members, which pose a more immediate threat to females.

There exists a differential preference for spatial positions due to this predation pressure. Hamilton (1971) described the geometry of the selfish herd, and the principles therein apply to most group living animals. The fewer neighbours present around an individual, the more likely that individual will be the victim of predation. With more neighbours the effect of dilution is increased and the likelihood of that individual specifically being the victim of an attack declines. However, dominant females have the ability to contest the best food sources, as well as the best spatial positions in the group, and therefore have priority of access to both of these. Getting too close to higher-

ranking females may result in unwanted aggressive interaction that could cause injury and death. Therefore an individual is faced with a choice; spend its foraging time on the periphery where it is safe from dominant females but less safe from predators or spend time in the center of the group where the risk of aggression is high, but the risk of predation is low. Spending time on the edge decreases social vigilance costs, but increases predation vigilance costs, and vice versa. Depending on the food source availability, animals may also suffer decreased nutritional intake by spending time on the periphery.

4.3 Spatial Arrangement

Seyfarth (1977) argued that dominant females are an attractive force to other females and, as such, females will compete to be near them. He stated that forming a grooming relationship leads to an affiliation between two females that is long term and persistent, where the more dominant female will not only allow lower ranking partners access to better foraging locations, but will also be more likely to form an aggressive coalition with lower-ranking grooming partners in the future. Therefore, lower ranking females wanting to reap these benefits will compete to groom higher ranking females. Through competition among the ranks of females, there arises a pattern where a concentration of high ranking females surrounds the dominant female, and the female rank declines further away from the dominant female. This results in a dominant-concentrated center, with subordinates positioned on the periphery of the group.

There are a few problems with Seyfarth's theory, one of them being the claim that grooming facilitates coalition formation. Evidence for this type of reciprocal interaction is sparse and slightly misleading (Seyfarth, 1980). Seyfarth manages to show a strong correlation between grooming partners and coalition formation; however 70% of the coalitions formed were in response to aggressing males, not females. Aggression against males in a one-on-one interaction will almost always result in a loss for the female, simply as a result of differences in body size. It would make sense that females, as a general rule, would willingly team up against aggressive males and doesn't necessarily say anything at all about the nature of the affiliative relationship between the females. Seyfarth also failed to account for the possible confounding factor of kinship. He compensates for this by explaining that rank acquisition mechanisms lead to a hierarchy in which females hold ranks adjacent to or very close to those of their family members, and since his model predicts an elevated level of interaction between those of adjacent rank, the kinship factor should have little effect on the model. However, the vervets on Samara were found not to spend time with those they groomed the most or with those that were closest in rank to them in the previous study (Henzi et al., 2013), suggesting a variety of confounding factors. A number of factors could be influencing this result. Seyfarth's model may not be quite right and perhaps the way kin attain rank is not typical in this population. Factors involving demographic stress and group size may also be contributing to this result, as was discussed in the previous chapter, where a drop in demographic stress resulted in a reversal of this result, where females do preferentially associate with their grooming partners.

Dominance gradient can, therefore exist via two separate mechanisms; competition over safety and competition for preferred foraging sites. Therefore, the environmental factor of food distribution must be considered to determine which strategy females are employing. When preferred food sources are clumped and monopolizable, then foraging will have an effect on the distribution pattern of females along with predation considerations. However, if food is evenly distributed and feeding contest competition is low, then competition for risk-reducing spatial position can be inferred as a primary driving factor behind the spatial patterning of animals within a troop. In this study, individuals primarily fed on Acacia (*Acacia karoo*), which makes up the majority of vegetation cover at Samara (Pasternak et al., 2013), therefore food sources were not considered to be clumped, suggesting that predation risk should have a significant influence on vigilance and spatial patterning.

A similar argument as outlined above can be applied to the females when her primary driving factor is reducing predation risk rather than monopolizing food sources. If food sources are not clumped, then females will be moving and foraging through the day without much consideration for contesting food patches. In this case, the risk of predation on the periphery of the group is of the biggest concern to the females and positions near the center of the group will be contested. The key difference here, is instead of the dominant female simply ending up in the center of the group due to foraging competition, females would consciously seek out risk-reducing positions, and compete for them within the context of their dominance hierarchy. The same pattern is predicted to emerge, but the motivation is very different.

The pattern emerges from the female's strategies to reduce the two injurious risks involved, risk of injury from dominant females, and the risk of injury and/or death from predators. One solution to avoid injury from these more dominant animals, is to avoid them (Hall & Fedigan, 1997). However, if the pattern holds true, the farther a female distances herself from the most dominant female, the fewer neighbours she has and her risk of predation is steadily greater. This means that a female must make choices as to which behaviours pose the most risk, and when the choice is made she must also adjust her vigilance behaviour to reflect the dangers most pertinent to her. There are a number of studies done on primates that show with a decrease in dominance rank, there is an increase in social vigilance (Caine & Marra, 1988; Chance, 1967; McNelis & Boatright-Horowitz, 1998; Rowell & Olson, 1983). Studies also show that vigilance increases when far from a safe refuge or other members of the troop (Cowlshaw, 1998; Robinson, 1981). If a female chooses avoidance as her main strategy to escape potential aggressors, she must also adjust her vigilance behaviour, by increasing predator vigilance.

Another possible solution is one that involves grooming a higher ranked female in an immediate exchange for tolerance. By doing this the acting female could potentially accomplish two things. First, she has appeased the higher-ranking female, making her relaxed enough to tolerate her presence. Second, there exists a passive deterrence of aggression with other nearby higher-ranking females. When vervets engage in aggression in close proximity to one another, it is often the case that surrounding females get dragged into the conflict through redirected aggression and a

general increase in tension among the troop (Bastock, Morris, & Moynihan, 1953; Kazem & Aureli, 2005). Therefore, maintaining a relatively close proximity to the dominant female will deter aggression from other higher-ranking females also in proximity (Silk, 1982); any aggression initiated would almost surely bring the dominant female into the fight and be detrimental for all involved. There is a flaw in this plan as neither the appeasement of the dominant females, nor the passive deterrence afforded by being in close proximity to her, are a sure way to avoid aggression. Therefore any behaviour of this kind requires a lower-ranking female to increase her social vigilance to monitor the higher-ranking females around her, so she may spot any potential aggression before it happens.

I propose that there are simple mechanisms the females employ on a day to day basis to balance the risk of predation and the risk of aggression in a group. The dominance hierarchy plays a large role in determining the internal spatial organization of the troop. Each female makes a choice based on her position in the dominance hierarchy. She has only a couple options available to her, the most frequent and simplest option being the avoidance of dominant females. The further down the dominance hierarchy a female is, the more females she will have to avoid, resulting in the lower-ranking females making up the periphery of the group. Being on the periphery of the group will increase the amount of vigilance required to spot predators, but decrease the amount of social vigilance needed. That being said, there should still exist a rank differential in vigilance rates, as high-ranking individuals have fewer potential

aggressors and spend their time at the center of the group, they will have a lower vigilance rates overall.

4.4 Model to Test

Evers, de Vries, Spruijt, & Sterck, (2012) applied an agent based model to test whether scanning and social vigilance was sufficient to produce this pattern of a dominant center and subordinate periphery. This model is an interesting starting point to examine whether small individual changes in behaviour will produce this pattern. In their model, an individual will move around in the group randomly but adhere to specific rules that are programmed to reflect differences in dominance and scanning tendency. An individual in the model will be constrained by outer limit maximums, so as to maintain overall group cohesion and, depending on the behaviour being tested, will specify parameters within which the agents can identify potential aggressors, avoid potential aggressors, or engage in an agonistic interaction with another individual. When an encounter has occurred, the outcome is determined by a dominance determined chance to win. That is, when approached, individuals can choose not to engage in a fight by fleeing 2 m away; this would occur when the chance to win was very low for the agent being challenged. If the chance to win is high enough between two individuals a fight will occur, and the winner will be determined stochastically based on each individual's probability of winning any aggressive encounter. The loser of a fight flees 2 meters and the winner chases for 1 m. Avoiding a potential aggressor in this model began at a detection distance of 15 meters. If a potential aggressor is outside a

threshold rank difference, the lower ranked individual will avoid this agent by turning away and moving 2 meters. The maximum distance that an agent is allowed to be from another individual is a function of group size, and is calculated as the preferred distance to the group, (near_Dist = 20m) multiplied by the square root of the total number of individuals. In the case of this model, their group size was 30 and so this max distance was approximately 110m.

The first issue with testing this model using empirical data on real animals is that the model exists in an environmental vacuum. That is, there are no environmental factors calculated into the equation but, in a real life setting, maximum distance values will be constrained by the nature of the terrain and the density of vegetation. This, in turn, will affect the distances over which monkeys will be able to see one another and keep track of the group. This is additionally confounded by differences in scanning from the ground versus scanning from the top of a tree. Due to these extra environmental factors, I did not begin my study by setting these boundaries, instead the first question to be answered with this study is what are the real life parameters within which monkeys make decisions about their social vigilance behaviour. This is tested by assessing the distance at which a female attends to the presence of another female, whether this distance is affected by dominance rank, and the average vegetation density around females when they are scanning. Do individuals tend to scan more on the ground where predation risk is highest or in a tree where the surroundings can be best observed? The final question, which is perhaps easiest to test, is whether it is true that subordinate individuals actually scan more frequently than high ranking individuals.

Another element that the model doesn't account for is predation. The model introduced constraints to maintain group cohesion, which may represent an implicit acknowledgement of the influence of predation, but no effect of predation or predator scanning was part of the agents' decision-making process. Unfortunately, when testing this in my study population, there is always a factor of predation to be considered. Also, in the field it was difficult to differentiate whether an individual was scanning for conspecifics or predators, unless predator alarm calling had taken place. This means that all scanning behaviour collected in this study was only differentiated as predator scanning when the observer was confident the troop were attending to a perceived threat. Despite this, the dominance difference in scanning should still exist, as subordinates should still have more cause to be vigilant than dominants.

The final problem with testing the model was the effect of group size. The model tests a group of 30 individuals, who exist on the same dominance hierarchy and interact based only on a rank difference gradient that is rigid and specific. In the real world, the dominance interactions of individuals within a group are often divided by sex, and the power differentials between individuals are not consistent. This presents an issue with how to test the model this in real life, and to predict a priori the effect that cohort size will have on the observed pattern. It is possible that with a smaller number of females in a cohort, the pattern will not emerge, because their chances of interacting are much lower.

4.5 Predictions

To test the validity of this model and its potential application to real life studies of socio-spatial movement within a group, this study will test the following set of predictions.

1. Terrain as well as risk of predation will have an effect on scanning behaviour. If predation risk is driving scanning behaviour, I predict a high proportion of scanning when the individual is on the ground and when they are in the open, where predation risk is high.
2. In contrast to the previous prediction, if scanning behaviour is driven by the need to keep track of the surroundings, whether for predators or aggressive group members, a position of high visibility distance would be most valuable. Therefore I predict that the highest proportion of scanning will take place when in trees.
3. Assuming that low-ranking individuals have more factors in their environment that they must attend to, be it predators or a high number of potentially aggressive conspecifics, I predict that low-ranking individuals will have a higher rate of scanning than high-ranking individuals.
4. If larger overall group size reduces an individual's vigilance costs, then I predict the larger troop will have a lower rate of scanning per female.
5. When a female actively avoids another female (she chooses to move away from a female that is approaching her), the detection distance will reflect differences in the

dominance hierarchy. The greater the rank distance is between females, the larger the detection distance.

6. Avoidance distance in the model was set to 15 meters. Given that environmental constraints such as vegetation density will affect the distance that females may detect another, I predict that the maximum observed distance a female will attend to another female will be less than 15 m.

7. Along with the previous prediction, an effect of vegetation density could determine this maximum distance as well; I predict that when vigilant to the approach of another, density will affect this distance measure. At high densities, the maximum observed distance at which a female will be vigilant to the approach of another female will be lower than at low vegetation densities.

8. If females in this population are competing for spatial position, then aggression rates will reflect this competition. If the pattern of a dominant heavy center and a subordinate periphery is driven by this competition, I predict that as a female's rank increases the proportion of aggressive interactions in which she is involved will also increase.

9. If the pattern of a dominant center, subordinate periphery holds true for these females, then I would expect that rank will be a factor in determining the identity of a female's nearest neighbours. I predict that as rank distance increases, the likelihood of females being each other's nearest neighbour will decrease.

10. If the dominant center, subordinate periphery is true, I would expect subordinate females to display a greater inter-individual distance between themselves and their nearest female neighbours. I predict that with decreasing rank, the distance between a female and her nearest neighbours will increase.

11. If dominants are attractive and at the center of the group, they should have a higher proportion of nearest neighbours overall. I predict that as rank increases, the proportion of total female nearest neighbours will also increase.

4.2 METHOD

4.2.1 Focal Sampling

Data presented here were collected on two troops of vervet monkeys (RBM, RST) at the Samara Private Game Reserve, Eastern Cape, South Africa. Data was collected between the middle of May 2012 and December 2012. Focal animal sampling was used to continuously sample a focal female for a 20 minute period. Time of day was broken down into 4 separate time blocks in order to ensure focals were evenly distributed throughout the day. These blocks were in 3hr or 2.5hr slots depending on time of year and available daylight hours. Before beginning each focal, the female's ID, date and time-block were recorded and at intervals of 5 minutes, with information on the female's activity and nearest neighbours within 15 meters recorded. Females were sampled only once per day, with some exceptions. For example, when a female had been missed on a previous day she would be sampled twice the next available day to ensure an equal number of focals across the sample. If a female was to be sampled

twice in a day, the focal sample would be at least 3 hours apart, ensuring that the female was never recorded twice in the same time block.

Focal animal sampling was used to collect the majority of the data for this analysis. The original sample of focal females was randomly selected from both troops, by assigning numbers to each female, then using a random number generator to pick 10 females from each troop. Both troops lost females due to predation. In RST, 5 of the original 10 females died or disappeared between late June and early August. In June and July, 3 more females were randomly selected to bring the sample back up to 8 females. In RBM, 2 females were lost in early August and they were not replaced. The sample total was 16 females, and each one was sampled 40 times, with an even distribution of 10 per time block, totalling 13.3 hours per female sampled.

4.2.2 Dominance

There were a number of behaviours also observed and recorded in an ad libitum fashion. This included all aggression and dominance behaviour, wounds, and copulations, and later on in the study, I added female social vigilance. These data were recorded whenever the behaviour was observed, including during a focal sample. The aggression and dominance data was primarily used to construct the female dominance hierarchies, used in this analysis. Though ad libitum data collection is perhaps biased to particularly conspicuous behaviours, they were crucial to establishing the dominance hierarchies and added a significant proportion of data to the overall sample.

Dominance hierarchies were constructed for the females in each troop based on decided agonistic interactions. David's Scores are the most suitable measure of the steepness of the hierarchy, as they were originally developed as a standard ranking method, and hierarchies were constructed from the dyadic agonistic interactions of the females in each troop (de Vries et al., 2006). In order to have a steepness measure on a scale of 0 to 1 the David's scores must be normalized. Normalized David's scores (NDS) (de Vries et al., 2006) were calculated by taking the David's Score and dividing by the total number (N) of individuals in the troop, to give a score that ranges between 0 and N-1. From this range, all females were assigned an ordinal rank (highest NDS was assigned rank 1) as well as a standardized rank to use when doing cross-troop comparisons. Standardized ranks were calculated as follows: $\text{StdRank}_{ij} = \text{NDS}_{ij} / \max(\text{NDS}_j)$; the standard rank of individual i in troop j is the ratio of the NDS of i and the NDS of the highest ranking female in the troop (Highest ranking female StdRank = 1).

4.2.3 Scanning

Definition of scanning: The first aspect of social vigilance was defined as a group scan. This was recorded when a female would observe the group and surrounding area with a wide turn of her head. A scan was defined as an even turn of the head greater than 90 degrees in either direction. If a female scanned one way and then back the other way this was counted as two scans.

Terrain: this was measured by recording the focal subject's relative location as being on the ground (G), on the ground in the open (O), in a shrub (S) or in a tree (T).

Rank Effects: When measuring the difference of rank effects, scanning was calculated as a rate of scans per focal. This was done due to the unequal total number of focal samples of all 23 females.

Group Size: To measure whether or not group size actually reduces an individual's scanning costs, scanning had to be calculated as a rate of vigilance per female. Therefore the total amount of scanning performed was divided by the number of females in the troop.

4.2.4 Vigilance

Density: As well as recording scans, the density of the environment was recorded as being high density, medium density or low density. High density was defined as having a visual range around the focal subject of 10 meters or less, medium density was visibility up to 20 meters from the focal subject, and low density was a visibility range of greater than 20 meters.

Detection distance: The second aspect of social vigilance was a measure of the female's vigilance zone, or their avoidance zone, as Evers et al. (2012) referred to it. When a female was approached by another female, there were three things recorded: the distance at which the focal female attended to the approach of the other female (in meters), whether or not the female moved away in response, and if she did move, how far did she move from her original position (also in meters).

Rank distance: Rank distance was calculated by subtracting one female's standard rank from another, and differs from rank difference in that the sign of the difference is ignored. To determine if detection distance increases as rank distance increases, I took the average distance at which another female of a given rank was detected and compared this to the rank distance between them.

4.2.5 Aggression

Aggressive interactions were recorded ad libitum and were used to assess whether being at the center of the group results in participating in more agonistic interactions. To measure the frequency with which a female was involved in aggression, I calculated the proportion of all aggressive incidences where each female was either the actor or recipient. This was then correlated with standardized rank using a Pearson's correlation.

4.2.6 Nearest Neighbours

Data from instantaneous scan sampling was used to assess the proportions of nearest neighbours (NN). Every 30 minutes, all observable adults were sampled, recording their identity, their activity, and the identity and distance of the closest female and male neighbour. All frequency data were converted to proportions either of the individual female's total number of scans or the total number of scans for the group, depending on the prediction being tested. For example, if looking at a target female's nearest neighbours, the proportion would reflect the target female's total number of

scans. When investigating which female had the most nearest neighbours overall, the proportion reflected the total female cohort. The total number of scans collected on females was 16,206.

When comparing average distance to nearest neighbours, the recorded distances to nearest neighbours in the scan data were averaged, and then females were grouped in three categories of rank: high, medium and low. To measure the strength of the relationship between rank and nearest neighbour distance, Pearson's correlations were used.

4.3 RESULTS

4.3.1 Scanning and Terrain

An independent samples t-test was performed to compare the proportion of scanning locations between RBM and RST. The two troops did not differ significantly in any of the scanning locations. Also there was no clear preference for scanning locations for females of RBM and RST: paired samples t-tests performed on all location data show no statistical difference between any of the locations. The mean proportion of scanning locations is presented in Figure 4.1. This result supports neither the first nor the second prediction. However, the result does provide evidence for predation not being the only driving factor behind scanning behaviour, as females did not prefer to scan when most at risk from potential predators.

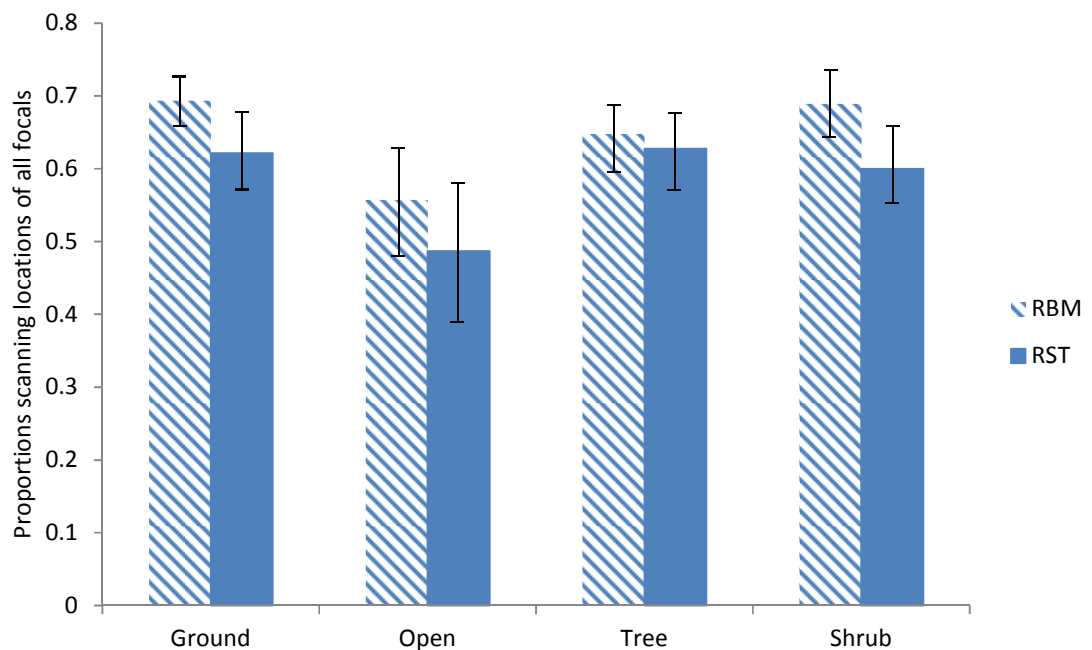


Figure 3.7 The proportion of focal scanning locations for RBM and RST.

Independent samples t-tests were run to compare the density of terrain between RBM and RST. RST has significantly more medium density measures, $t_{(19,2)} = -2.379$, $p = 0.028$, and RBM has significantly more open, low density measures $t_{(21)} = 7.663$, $p < 0.001$ (Figure 4.2). The home ranges that RBM and RST use are very different in terms of terrain. Figure 4.3 shows the home ranges for RBM and RST. It is clear RBM uses a territory that has much more open ground, whereas RST tends to stick to the riverine forest areas.

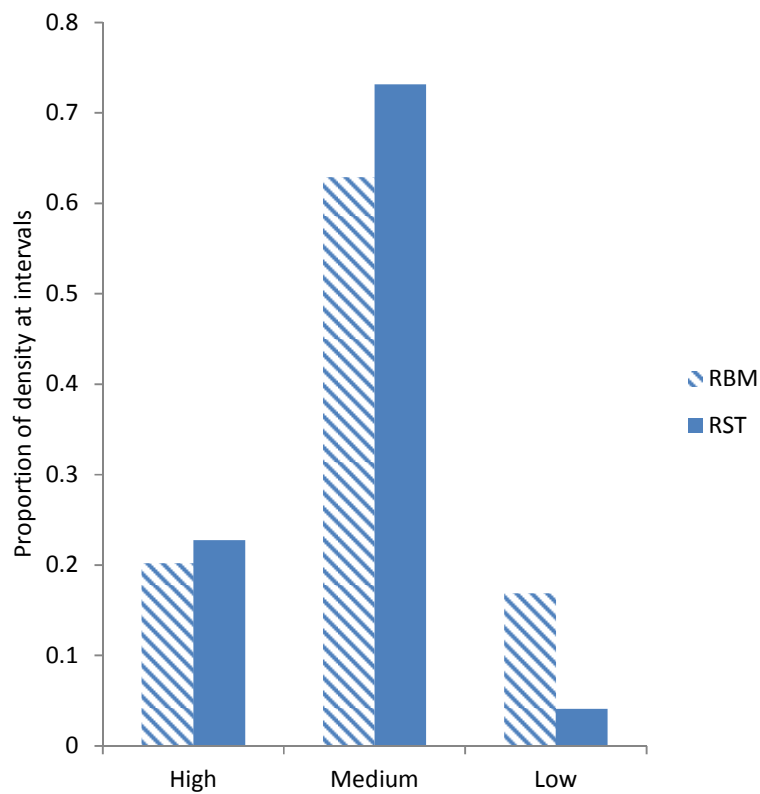


Figure 3.8 Vegetation density measured at focal intervals for RBM and RST.

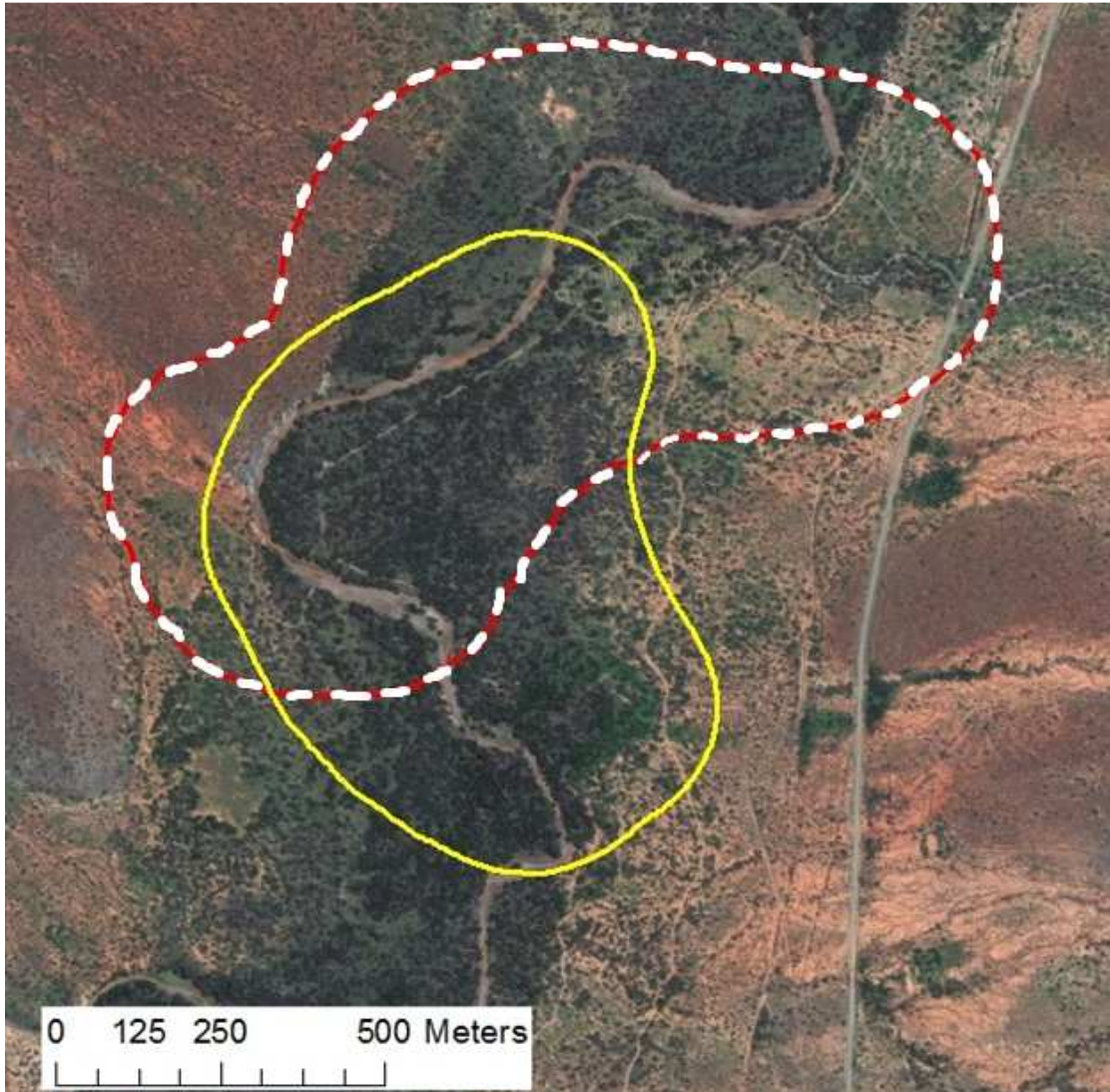


Figure 3.9 RST (solid line) and RBM (dotted line); GPS data collected on individuals in both troops. 90% of each troop's points fell within these boundaries.

Scanning Rank Effects: Pearson correlations were run to measure the strength of the relationship between rank and scanning behaviour. In line with prediction, low ranking females scan significantly more than high ranking females in both troops,

despite the relative dominance strength differences between troops. (RBM $r = -.849$, $p = 0.002$, $N = 10$ and RST $r = -.782$, $p = 0.002$, $N = 13$; Figure 4.4).

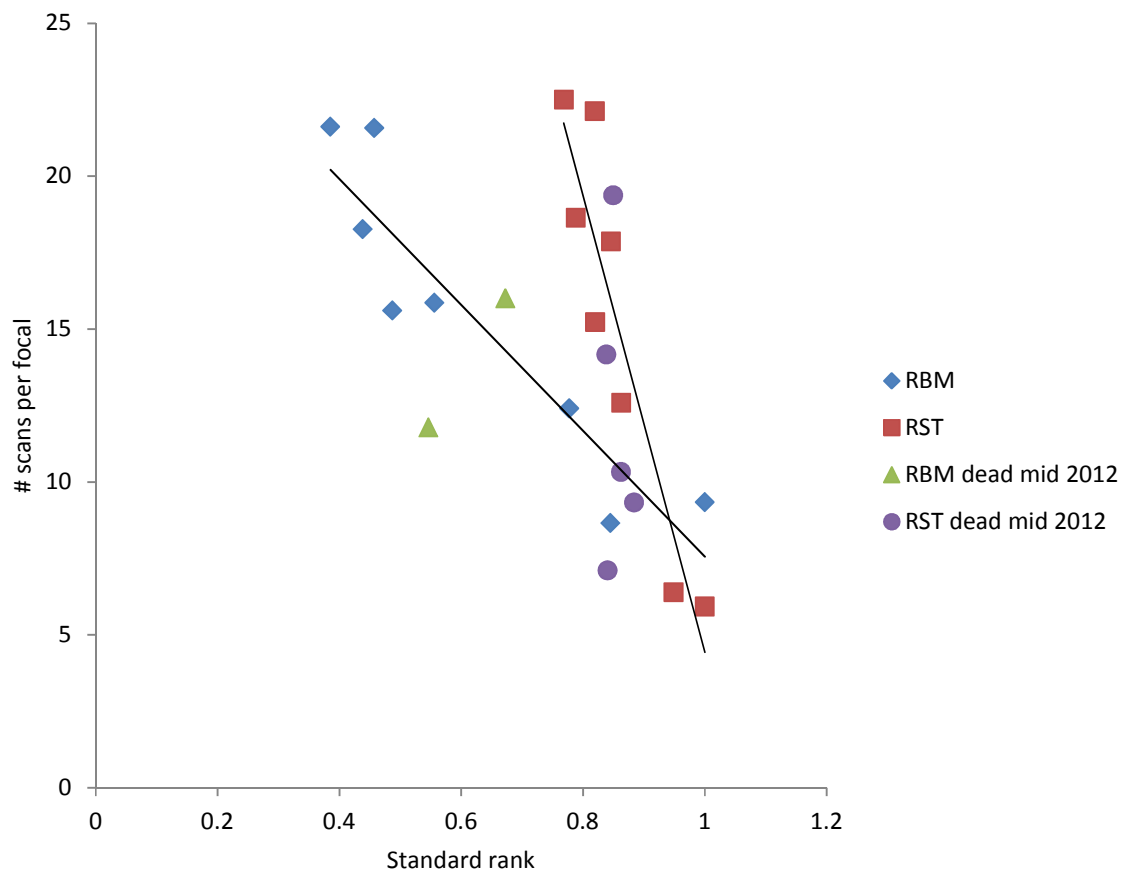


Figure 3.10 Scanning rates and standard rank of females in RBM and RST. Squares represent females who died/disappeared before the end of the study.

Group Size: RBM had a total of 4670 scans across 8 females and 106.67hrs of focal time per female giving a rate of 583.75 scans/female (5.47 scans/female/hour). RST had a total of 4624 scans across 8 females, giving a scanning rate of 578 scans/female (5.42 scans/female/hour). An independent samples t-test reveals that

contrary to prediction, there was no significant difference between individual vigilance rates between females in RBM and RST ($t_{(14)} = 0.051$, $p = 0.960$. Figure 4.5).

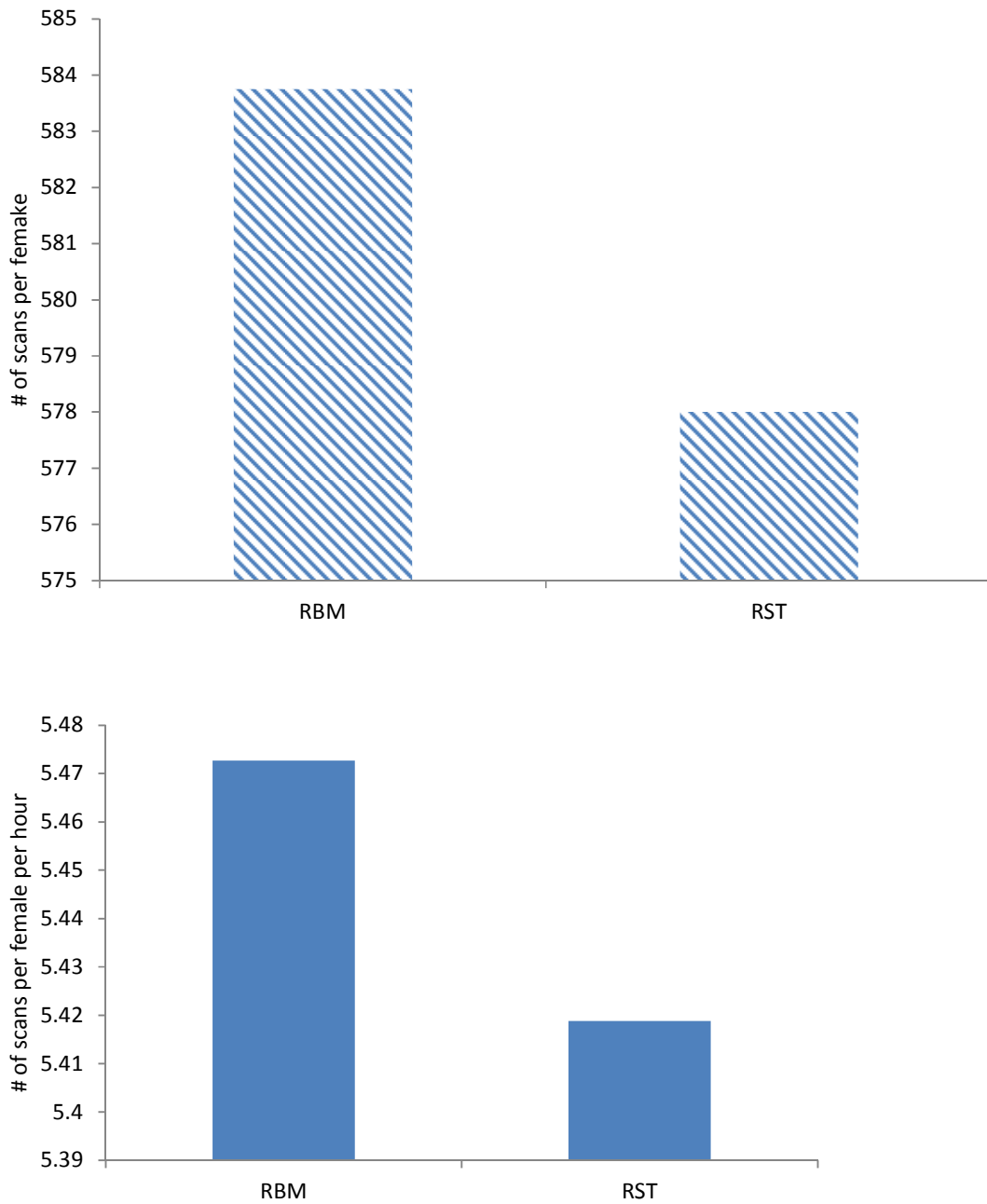


Figure 3.11 Rates of scanning per female (top) and scanning per female per hour (bottom) for RBM and RST.

4.3.2 Vigilance

Detection distance and rank: Detection distance and rank were measured on pairs of females, and as such the sample is inflated slightly. Against prediction there was no relationship between rank distance and detection distance for RBM ($r = .107$, $p = 0.524$ $N = 38$. Figure 4.5). However, in line with prediction, RST did show a significant relationship ($r = .359$, $p = 0.012$ $N = 48$): as the rank distance between two females increased, the distance at which a female is detected also increased.

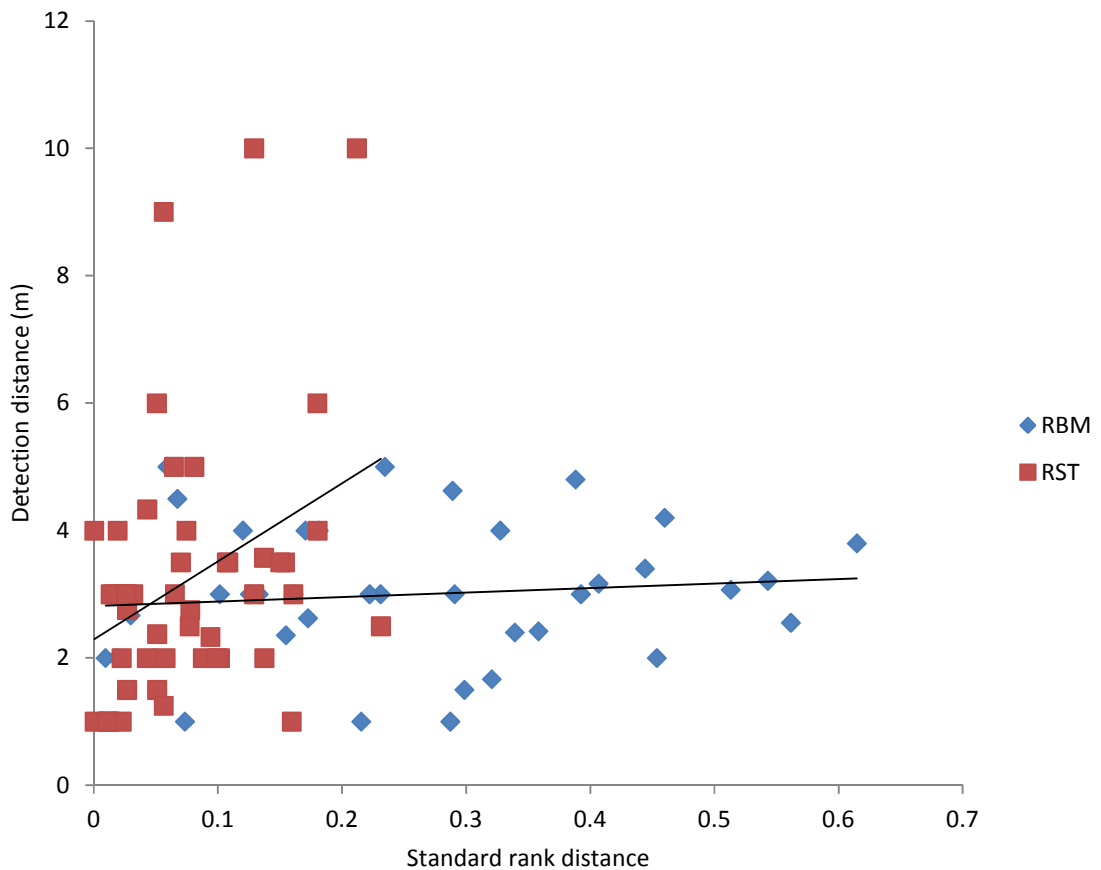


Figure 3.12 The relationship between observed detection distance and rank distance in RBM and RST.

Maximum detection distance: The maximum recorded detection distance of an approaching female for RBM was 10 meters and for RST it was 15 meters. However, both of these were only single instances. Figure 4.7 shows that vigilance detection distance is similar between RBM and RST, with the majority of detections occurring at 3m from the vigilant female.

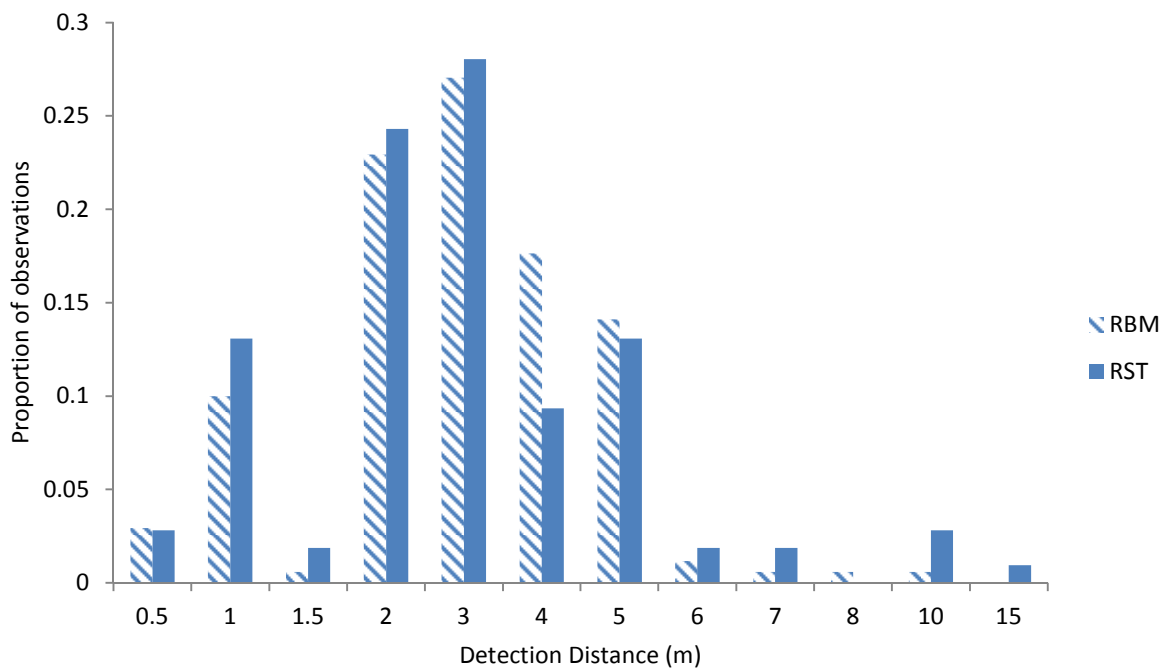


Figure 3.13 Proportions of all vigilance detection distance.

Detection distance and density: Data for vegetation detection and density were recorded ad libitum, as well as in focal samples, and so resulted in a slightly inflated sample. Against prediction, neither troop showed a significant relationship between vegetation density and detection distance (RBM $r_s = -.120$, $p = .178$, $N = 127$; RST $r_s = .062$, $p = 0.587$, $N = 79$.)

4.3.3 Aggression

In line with prediction, both troops showed a significant relationship between proportion of aggressive interactions and rank (RBM: $r = 0.675$, $p = 0.016$, $N = 12$; RST: $r = 0.534$, $p = 0.013$, $N=21$; Figure 4.8). Thus, despite the differences between RBM and RST in terms of relative dominance, and the fact that RST has a weaker dominance hierarchy, both troops show higher ranking females participating in more aggression overall.

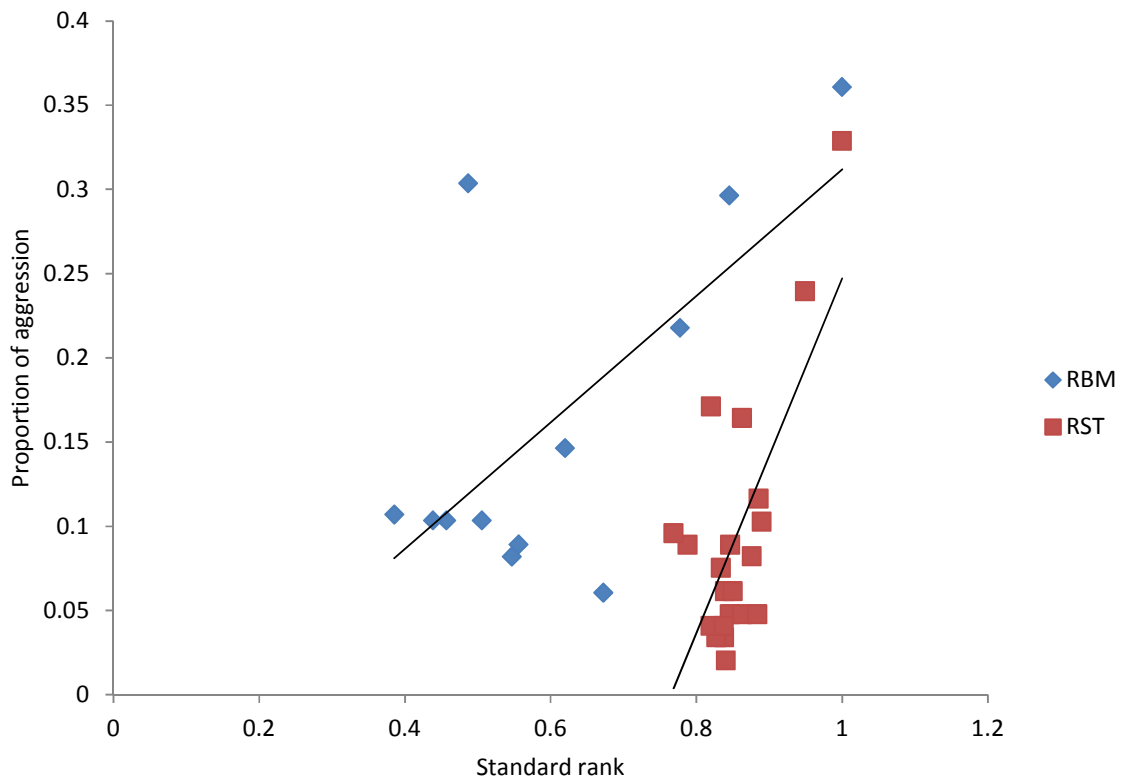
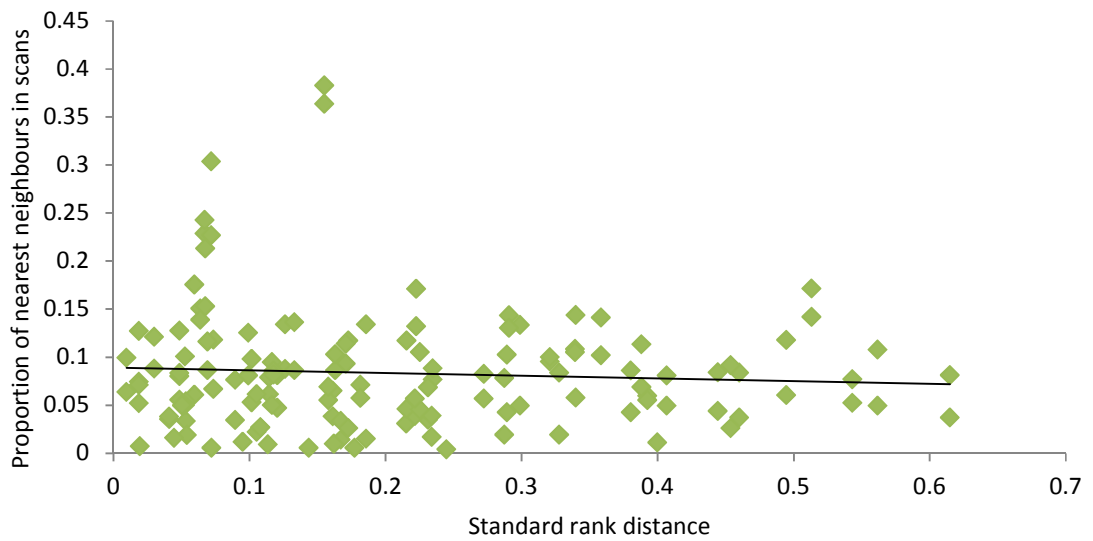


Figure 3.14 Relationship between proportion of participation in aggression and rank for RBM and RST.

4.3.4 Nearest neighbours

Pearson's correlations were used to measure the relationship between how often two females were recorded being nearest neighbours and the rank distance between them; as these reflect dyads, the sample size is slightly inflated. The correlations were not significant for either troop (RBM $r = -.033$, $p = 0.695$, $N = 143$ and RST $r = -.010$, $p = 0.837$, $N = 401$. Figure 4.9). Contrary to prediction, the proportion of scans where females were recorded as nearest neighbours showed no relationship with the rank distance between those two females.

RBM



RST

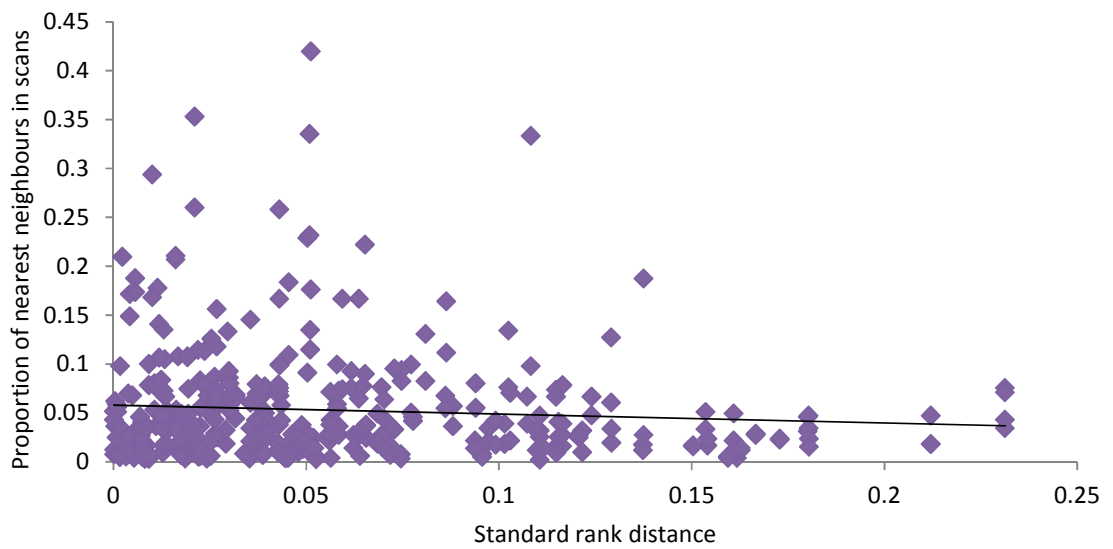


Figure 3.15 Relationship between nearest neighbour proportions and rank distance in RBM and RST.

Rank and inter-individual distance: Against prediction there was no relationship between average inter-individual distance and rank for females in either troop (RBM: $r =$

-0.160, $p = 0.620$, $N = 12$; RST: $r = 0.041$, $p = 0.861$, $N = 21$. Figure 4.10)

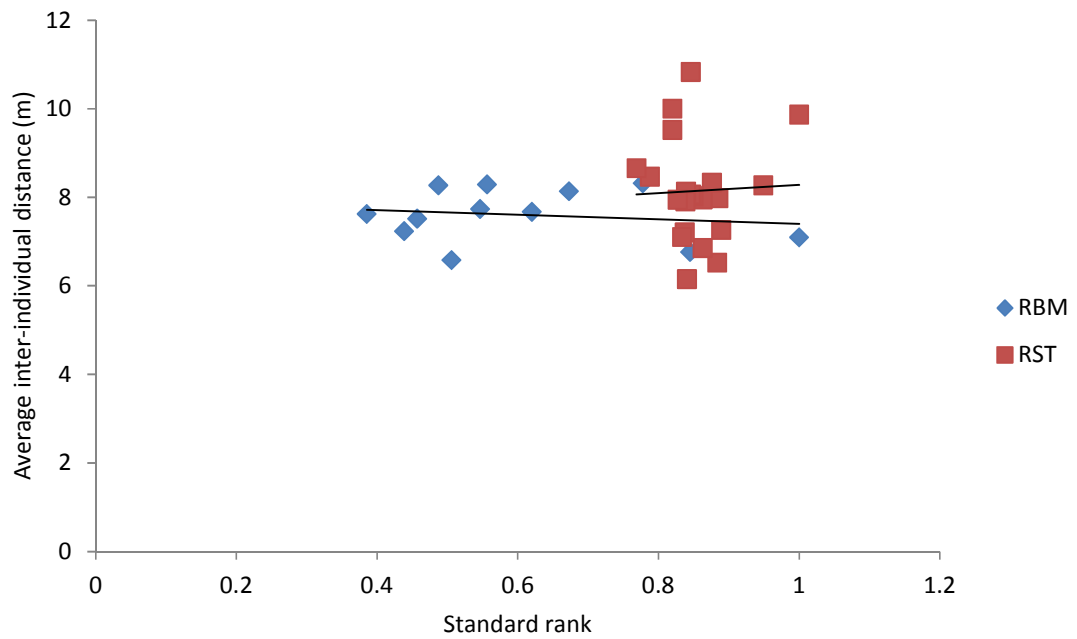
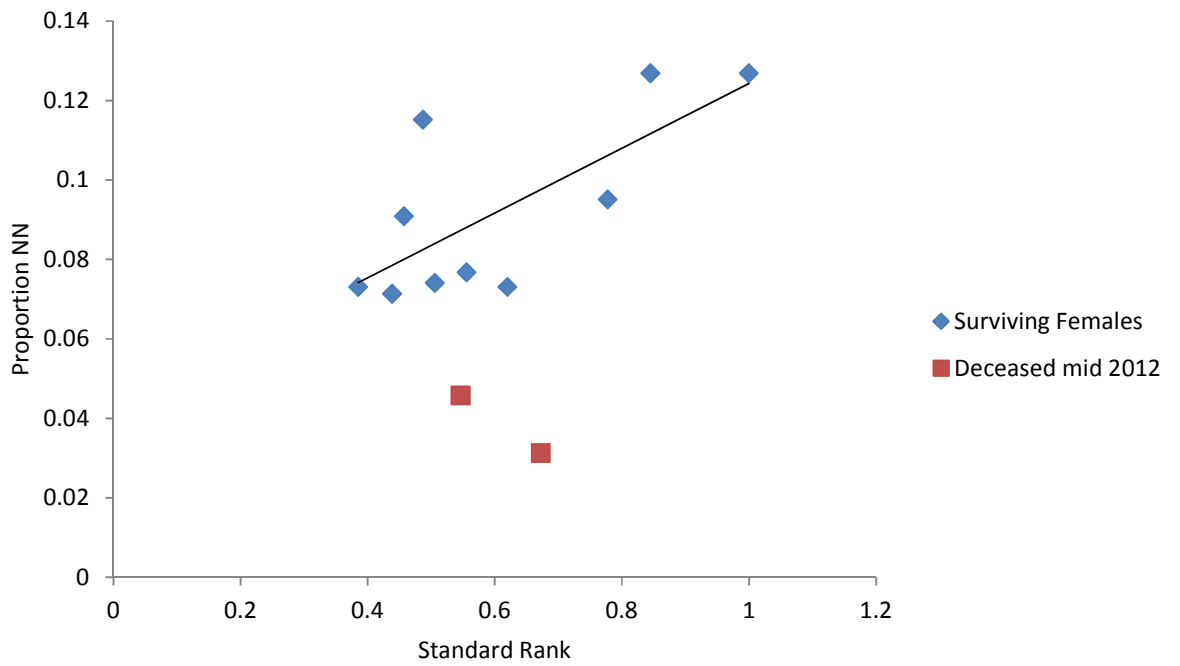


Figure 3.16 Relationship between average inter-individual distance and standard rank.

Nearest neighbours and rank: In line with prediction, RBM showed a strong relationship between rank and the total proportion of nearest neighbours ($r = .722$, $p = 0.018$, $N = 10$), while RST did not $r = -.078$, $p = 0.783$, $N = 15$, (Figure 4.11).

RBM



RST

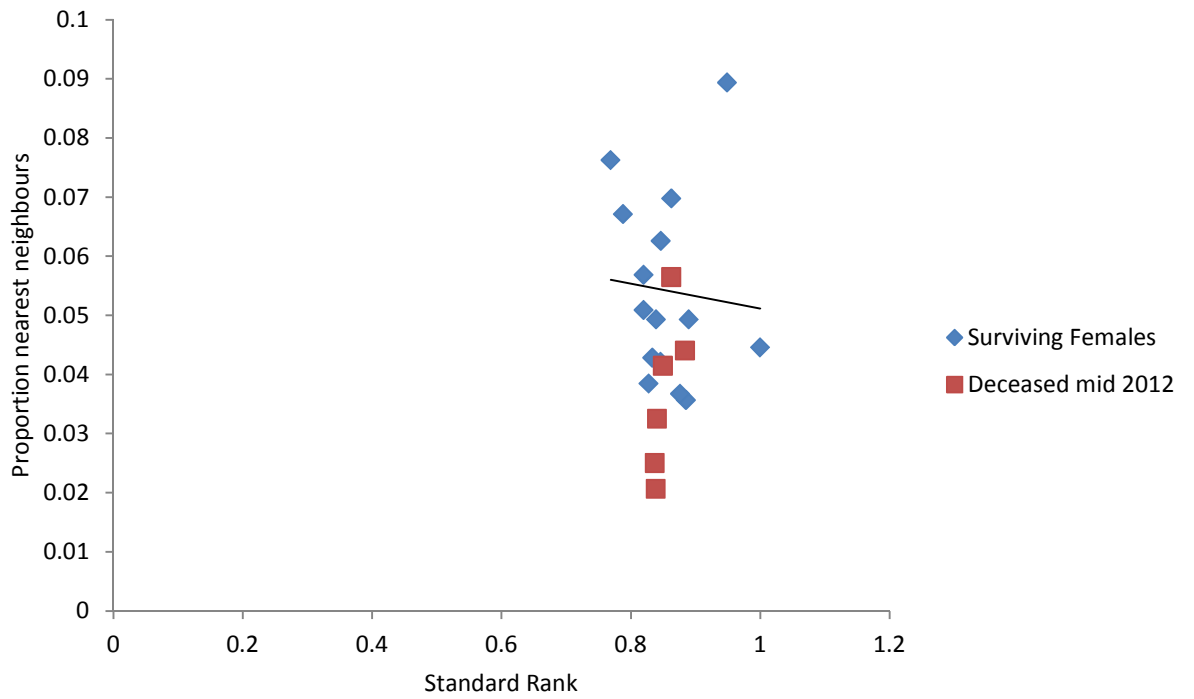


Figure 3.17 Overall proportion of nearest neighbours and rank in RBM and RST.

4.4 DISCUSSION

Vigilance behaviour in the Samara females did not seem to be driven primarily by predation pressure, as females did not scan more frequently when they were at most risk, i.e., on the ground and in the open. There was actually very little differences in their scanning locations, statistically. However, the numbers when taken as pure frequency do show the majority of scanning occurring when in the trees. Being high in a tree gives the monkey a good vantage point to spot predators, and they are also less likely to encounter an aggressive female. That being said they were often scanning while foraging in the trees and so they were constantly aware of their surroundings and keeping watch for a higher-ranking female. This result seems to mean that scanning is done where visibility distance is the best, to keep track of the group in a general sense and to watch for predators when time is available, meaning both predation and social pressures are driving scanning. Rank does have an effect on the amount of scanning a female performs. The results show a strong negative relationship between rank and proportion of scans in which vigilance was observed, which is in line with other research performed on baboons (Caine & Marra, 1988). Group size also had an effect on overall rates of scanning among females: the smaller troop (RBM) had individual rates of scanning that were higher than the larger troop (RST).

The distance at which a female was vigilant toward another was not affected by the rank distance between them in RBM, but it was in RST. This result is interesting and may be an effect of group size. As discussed in the previous chapter, increasing cohort

size results in an overall increase in the power differentials between females. This could have translated into their vigilance behaviour, as detecting more highly ranking females at a greater distance may be more advantageous in terms of avoiding a potential aggressive interaction that a lower ranking female is more likely to lose when power differentials are that much higher. The distance a female moved in response to the approach of another female was not affected by rank distance, however. For RST, this result seems to contrast with the earlier result regarding detection distance and rank distance. This suggests that a safe distance to move in avoidance of a potentially aggressive female is not influenced by power differentials across the female cohort. Perhaps early detection of a potentially aggressive female is more advantageous than moving a greater distance. It is also important to note that, although detection distance was affected by rank overall, when the comparison was limited to only the incidences when the female moved in response, the relationship was no longer significant.

The maximum observed detection distance was less than 15m for RBM but was 15m for RST. These maximums, however, were only recorded once for both groups of females. The majority of detection distances were at 5 meters or less. This contributes to our understanding of the next result, which shows there is no relationship between vegetation density and detection distance. The highest density measure was estimated at a maximum of 10m from the focal subject. If the majority of detections occurred at 5 meters or less then it makes sense that density will not influence this. The fact that females do not often detect individuals at greater than 5 meters suggests this

parameter in Evers et al., (2012) is not realistic and should be restricted to a closer range.

Females who are competing for spatial positions within the center of the group should experience more aggression overall than those who are living on the periphery. If rank also increases towards the center of the group because dominant females are more successful at contesting these positions, then the proportion of aggression in which a female is involved should also increase. This, combined with the fact that food sources on Samara are evenly distributed, suggests that females are competing for safe spatial positions. However, two things should be true if the pattern holds. The first is that the females who are most often nearest neighbours should be relatively close in rank. The second is that if dominant females are in the center and subordinate females are on the periphery, dominant females should have less distance between them and their nearest neighbours on average. In contrast to these predictions, females in both troops showed no relationship between how frequently a pair of females was recorded as being nearest neighbours, and the rank distance between them. They also showed no relationship between average nearest neighbour distance and rank. This suggests that pattern whereby the highest ranking females remain at the center and the lowest ranking females are found on the periphery is not strictly true in this population. Females may be using some other criteria to decide how they will associate spatially.. In line with prediction, however, dominant females in RBM did show a relationship between rank and the total proportion of nearest neighbours observed overall. This

effect was not shown in RST, and is likely a result of group size, as discussed in the previous chapter.

In this study, females lived in an environment with evenly distributed food sources (Pasternak et al., 2013) and so our analysis of spatial position within the group can be assumed to be as a result of predation pressure and competition for safe spatial positions. The results do not indicate that the females show the spatial pattern seen in other primate studies, as there appear to be no rank effects associated with the identity of a female's nearest neighbours, nor is there a relationship between rank and inter-individual distance. One reason that the Samara females differ from the agent-based model could be an effect of group size. The model operated with 30 individuals on the same dominance scale. Even the larger of the two troops in this study had a female cohort of just 15 females. Using Evers et al. (2012) avoidance model in NetLogo 4.0.5, and adjusting the parameters to an avoidance detection distance of 5m with a cohort of 15 individuals, it was found that the encounter rate, distance to the group center, and distance to nearest neighbours do not differ greatly across ranks. I have added Figure 4.12 to clarify this result. The graph on the left shows each female's average distance to the center of the group, and on the right shows the distances to all neighbours. The X axis of both graphs represents the dominance of the agents in the model from low-ranking on the left to high-ranking on the right. Both graphs are very flat, showing little rank difference in these two variables.

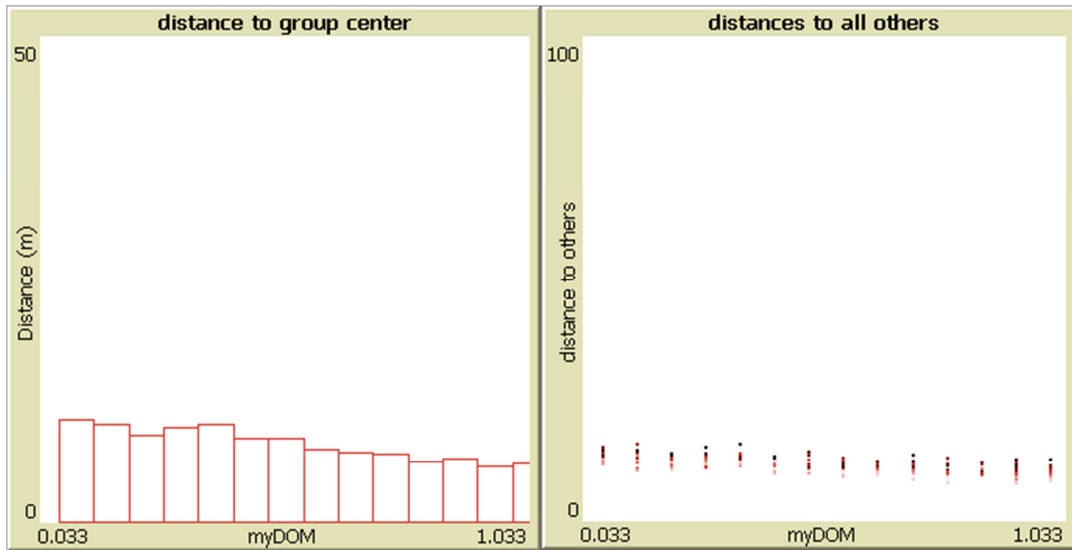


Figure 4.12, NetLogo 4.0.5 simulation results, with an avoidance distance of 5m and 15 individuals on the same dominance gradient.

Group size seems to affect scanning behaviour as predicted. A larger group will have more eyes to scan for predators overall, thus reducing the individual scanning costs of each member of the group. This corresponds with other research suggesting that in environments where predation pressure is high, a larger group is favoured (Cowlshaw, 1998; Treves, 1999). Because the analysis of nearest neighbours shows that there is little evidence for the dominant-center, subordinate-periphery pattern, it can be concluded that the parameters outlined by the Evers et al., (2012) model is not producing the expected results in this population and that the effects of environment and predation pressure are the likely cause. However, there still existed a strong relationship between rank and scanning frequency, with a female of low rank spending more time scanning her surroundings than a female of high rank. If this is not due to pressures from predation and competition for spatial position, then it must be

concluded that, because lower ranking females have more potential aggressors in their environment, their overall vigilance rates need to be higher, and they must scan more often to avoid injury. This also suggests that it is internal vigilance that is causing this differentiation, and that predation scanning is most likely equal amongst females. This is reasonable to assume because it was concluded earlier that a combination of predation and social scanning is driving the behaviour. Since there is no spatial pattern, and high and low ranking females are just as likely to be on the periphery, then the differences in scanning rates must be due to the internal social pressure, as predation scanning should be relatively equal. Unfortunately, since this study did not differentiate scanning for conspecifics and scanning for predators, we cannot reach that conclusion decisively.

For RBM, there was no effect of rank on the detection distance of an approaching female, but for RST the greater the rank distance between two females, the greater the physical distance at which the approaching female was detected. The correlation was not extremely strong, at $r = 0.30$, but it was still statistically significant. One explanation for this difference could be the greater power differentials in a larger female cohort, but results presented in the previous chapter already stated that RST had a shallower dominance slope than RBM, meaning relative power differences between females were actually smaller in RST. This result could then be from the instability that exists within this female cohort, where any female could start aggression to make a gain in the dominance hierarchy, and as such they were attending more to females around them

Aggression rates in both groups also correlated strongly with rank. Keeping in mind that females in these troops do not seem to form the predicted pattern of spatial arrangement, and that females of all different ranks encounter one another relatively equally, this suggests that aggression in this troop has less to do with competing for spatial position, and is more likely a strategy used by high-ranking females to reinforce the dominance hierarchy. A similar conclusion was drawn in the previous data chapter regarding coalition formation. High ranking females engage in more aggression overall to enforce the dominance hierarchy and keep others “in their place” so to speak. This also supports the previous result of lower ranking females having a higher vigilance rates than high ranking females.

When it comes to the real life applicability of the model proposed by Evers et al. (2012), it seems that it performs fairly well, despite existing in an environmental vacuum. My findings suggest that the maximum avoidance distance at which one female detects and chooses to avoid another is approximately 3 meters, with the majority of detections occurring at 5 meters or less. This means that the model needs to adjust this aspect, but it also confirms that density measures have little effect on the model’s parameters. My results indicate that vegetation density does not have an effect on the distance at which a female is detected. This makes sense as a detection distance of 5 meters or less is well within the highest vegetation density measure of a maximum visual range of 10 meters.

A conclusion about terrain cannot be reached as easily. Evers' et al. (2012) model produced a pattern of spatial arrangement that this population does not seem to show. Therefore the fact that most scanning in this population was performed from the trees may not have any relevant impact on the model. For the sake of argument, it could be stated that Evers' model would not produce the observed pattern if an effect of terrain was somehow added to it, but that is beyond the scope of this study. The conclusions that can be drawn from my results relate more to our understanding of the reasons why females scan at all. As demonstrated earlier, the differentiation of scanning frequency across female ranks is primarily driven by added social vigilance rates. That females scan more often from the trees, where they can see further, and observe more of their surroundings, rather than when on the ground in the open where predation risk is highest, also suggests that social vigilance rates influences where scanning occurs.

Suggestions for future research: To determine whether there exists a consistent level of predation scanning and an inconsistent level of social scanning across the female ranks, a study where the two types of scans are more clearly differentiated would be useful. If the rates of predator scanning turn out to be mostly equal across all ranks of females, then it will support the conclusions I arrived at in this study regarding the reasons these females do not show the dominant-center, subordinate-periphery pattern. The ability of this agent-based model to test various conditions in a simulated setting is a useful tool and more work should be done to improve models of this type. By integrating more complex environmental and behavioural features into the program, a more accurate depiction of what may occur in the field is possible. If the dominance

differentiation between males and females could be integrated into the model then even more interesting real life questions about how troops behave spatially could be more accurately modelled.

CHAPTER FIVE: GENERAL DISCUSSION

5.1 Key Findings

In this study I examined the effect that demographic conditions have on patterns of female social behaviour in two large groups of free-ranging vervet monkeys. The spatial pattern of this social organization, along with an analysis of their scanning and vigilance behaviour was also examined in an attempt to better understand the underlying factors contributing to these behaviours. In Chapter Three, a direct comparison was made with previous research conducted on this population under different ecological conditions. Lower levels of demographic stress in the present study resulted in a decrease in overall levels of competition and aggression amongst females in these two troops. A decrease in the level of demographic stress was shown to have little effect on how females interact in grooming relationships based on dominance; however, there was a significant change in their preferred spatial associates. Whereas in the previous study they did not associate with their top grooming partners preferentially (Henzi et al., 2013), in this study they spent most time in proximity to their grooming partners. In addition, despite the drop in demographic stress, females still capped their grooming cliques at a threshold size. The findings in this chapter serve to reiterate that grooming behaviour is a persistent part of female social relationships and that the behaviour remains largely unchanged despite changes in environment and group size. It also shows that the reasons behind female-female grooming relationships and whom they choose to groom and why, is still unclear.

Chapter Four was an exploration of how females utilize space, with measures of scanning and social vigilance were examined to help understand how these females organized themselves in relation to other individuals. Most scanning behaviour was performed while the animals were in trees, suggesting that scanning their surroundings is a behaviour not entirely driven by the threat of predation. A larger proportion of scanning was performed by females of low rank, suggesting that their increased vigilance rates may reflect the added factor of internal social vigilance, where a female must watch for aggression from all females of higher rank. An individual's total vigilance rates were also influenced by troop size. The larger group showed more vigilance overall but the rates for each individual were lower, suggesting that rates can decrease when they are distributed over a larger number of individuals.

An exploration of spatial relationships was tested using an agent-based model developed by Evers et al. (2012). They proposed a dominant-center, subordinate-periphery spatial pattern arises from simple decisions each female makes based on detecting and avoiding one another in relation to their dominance rank. Females in the two troops detected the approach of another female most often at a distance of 5 meters or less. This close distance means that vegetation density has little influence over the distance at which a female detects another, as the highest level of vegetation density was measured as being a visual range of 10 meters around the subject. Females did not produce the predicted spatial pattern, as females that were closest in rank did not spend the highest proportion of time as nearest neighbours. There was also no evidence that lower ranking females were, on average, at a greater distance from their

nearest neighbours than higher ranking females. This suggests females are not competing for foraging space or for safe spatial position in the group. There was a significant relationship between increasing rank and increased proportion of aggression, however, and this suggests that high ranking females are acting aggressively most likely to reinforce the dominance hierarchy, rather than contesting a resource with a subordinate female.

Social organization in these females seems to not be heavily influenced by changing ecological conditions. Though females in both troops failed to groom all other females, group social cohesion did not seem to be affected. Though females still displayed some level of competition, they did not seem to be competing for grooming partners, or for safe spatial positions within the group. With a low level of demographic stress and widely distributed favourable foods, there was little feeding competition among these females. The fact that dominance interactions did persist, but without evidence that females were competing for anything in particular, it can be concluded that aggression in these females was most likely orchestrated by high ranking females in an attempt to reinforce the dominance hierarchy.

5.2 Limitations and Problems

With a large number of females, I was unable to focal sample all females in both troops. Additionally, five of the original ten females from one troop died before the end of the study and needed to be replaced. In order to even out the total number of focals on each female, the individuals that were added mid-study may have had slightly

different seasonal influences as they were observed only through winter and spring, and not fall as well. Also the need to sample them more than once a day could have added bias; though this bias was controlled by ensuring that focals performed on the same day were not sampled within the same three hour time of day block.

An analysis of spatial positioning within a group would be ideally measured with GPS data. However, even with GPS data, there exists a level of error and uncertainty in the interpolation of points, and an accurate portrayal of spatial position in a group is difficult to produce. Resorting to nearest neighbour proportions and average distances is a relatively inaccurate way of measuring the position of females in relation to one another, so though the data presented here does not suggest these females are not producing the dominant-center, subordinate-periphery pattern, this could be because the data collected was not sensitive enough to truly detect it.

Finally, a more detailed approach to measuring specifics of social vigilance may improve our understanding of what drives scanning behaviour in these monkeys. First a better differentiation between a social scan and a predator scan would be helpful in determining what females primarily attend to in their environment. Though it was beyond the scope of this study, a better measure of whether a female is peripheral or not could also assist in differentiating these two types of scanning.

5.3 Future Research Suggestions

To better understand the factors that drive grooming and social interaction in females, an accurate measure of kinship among these females would be very revealing.

If we could say with confidence who was related to whom, the choices females make with regard to their grooming partners would likely become clearer. When it comes to competition and aggression, to better understand exactly what females are competing for, a better measure of the details of an agonistic interaction could be helpful. The activity that both females are engaged in before interacting and how they behave afterwards would also assist in determining what it is they are competing for or whether they are competing for resources at all.

An examination of what the true purpose of coalition formation does for the monkeys would perhaps clarify the results found in this study. There were slight changes in coalition formation among these females with a change in demographic stress, but overall coalition formation is a small portion of their behaviour, and it doesn't seem to contribute much to their social relationships. Better parameters are needed to study coalitions, including detecting whether the coalition is true or if the partner was dragged into the fight by being in proximity. This method may help tease out the true reasons why they do it, who they do it with and better understand what purpose it actually serves to females.

REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 227-267.
- Barrett, L, Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market Forces Predict Grooming reciprocity in Female Baboons. *Proceedings: Biological Sciences*, 266(1420), 665–670.
- Barrett, Louise, & Henzi, S. P. (2006). Monkeys , markets and minds : biological markets and primate sociality. In *Cooperation in Primates and Humans* (pp. 209–232). Springer Berlin Heidelberg.
- Barton, R. A., Byrne, R. W., & Whiten, A. (1996). Ecology , feeding competition and social structure in baboons, (April 1994), 321–329.
- Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons, (*Papio anubis*). *Animal behaviour*, 46, 777–789.
- Bastock, M., Morris, D., & Moynihan, M. (1953). Some Comments on Conflict and Thwarting in Animals. *Behaviour*, 6(1), 66–84.
- Busse, C. D. (1984). Spatial structure of chacma baboon groups. *International Journal of Primatology*, 5(3), 247–261. doi:10.1007/BF02735760
- Caine, N. G., & Marra, S. L. (1988). Vigilance and social organization in two species of primates. *Animal Behaviour*, 36(3), 897–904. doi:10.1016/S0003-3472(88)80172-6
- Chance, M. R. A. (1967). Attention Structure as the Basis of Primate Rank Orders. *Man*, 2(4), 503–518.
- Chapman, C., & Fedigan, L. M. (1984). Territoriality in the St Kitts Vervet, *Cercopithecus aethiops*. *Journal of Human Evolution*, 13, 677–686.
- Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom Dispersal in Free-Ranging Vervet Monkeys : Social and Genetic Consequences. *The American Naturalist*, 122(3), 392–412.
- Cheney, D. L., & Seyfarth, R. M. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541–543.
- Cheney, D. L., & Seyfarth, R. M. (1989). Redirected Aggression and Reconciliation among Vervet Monkeys , *Cercopithecus aethiops* Author (s): Dorothy L . Cheney and

Robert M. Seyfarth Published by : BRILL Stable URL :
<http://www.jstor.org/stable/4534796> . *Behaviour*, 110(1), 258–275.

Cowlshaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53, 667–686.

Cowlshaw, G. (1998). The Role of Vigilance in the Survival and Reproductive Strategies of Desert Baboons. *Behaviour*, 135(4), 431–452.

De Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71(3), 585–592.
doi:10.1016/j.anbehav.2005.05.015

Di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal behaviour*, 54(1), 199–211. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9268450>

Dunbar, R I M, Korstjens, a H., & Lehmann, J. (2009). Time as an ecological constraint. *Biological reviews of the Cambridge Philosophical Society*, 84(3), 413–29.
doi:10.1111/j.1469-185X.2009.00080.x

Dunbar, R.I.M. (1992). Time : a hidden constraint on the behavioural ecology of baboons. *Behavioral ecology and sociobiology*, 31(1), 35–49.

Evers, E., de Vries, H., Spruijt, B. M., & Sterck, E. H. M. (2012). Look before you leap - individual variation in social vigilance shapes socio-spatial group properties in an agent-based model. *Behavioral ecology and sociobiology*, 66(6), 931–945.
doi:10.1007/s00265-012-1342-3

Fairbanks, L. a, & McGuire, M. T. (1985). Relationships of vervet mothers with sons and daughters from one through three years of age. *Animal Behaviour*, 33(1), 40–50.
Retrieved from [http://dx.doi.org/10.1016/S0003-3472\(85\)80118-4](http://dx.doi.org/10.1016/S0003-3472(85)80118-4)

Fairbanks, L. A. (1980). RELATIONSHIPS A M O N G ADULT FEMALES IN CAPTIVE VERVET MONKEYS : TESTING A MODEL OF RANK-RELATED ATTRACTIVENESS. *Animal Behaviour*, 28, 853–859.

Fedigan, L., & Fedigan, L. M. (1988). *Cercopithecus aethiops*: a review of field studies. In *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge (pp. 389–411).

Hall, C. L., & Fedigan, L. M. (1997). Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, 53(December 1995), 1069–1082.

- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of theoretical biology*, 31(2), 295–311. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/5104951>
- Hemelrijk, C. (2000). Towards the integration of social dominance and spatial structure. *Animal behaviour*, 59(5), 1035–1048. doi:10.1006/anbe.2000.1400
- Hemelrijk, C. K. (1998). Spatial Centrality of Dominants Without Positional Preference . In *Artificial Life VI: Proceedings of the Sixth International Conference on Artificial Life*. CambridgeMass: MIT Press. (pp. 307–315).
- Henzi, S P, Lycett, J. E., & Piper, S. E. (1997). Fission and troop size in a mountain baboon population. *Animal Behaviour*, 53(3), 525–535. Retrieved from <http://linkinghub.elsevier.com/retrieve/pii/S0003347296903024>
- Henzi, S Peter, & Barrett, L. (1999). The Value of Grooming to Female Primates University of Natal University of Liverpool, 40(January), 47–59.
- Henzi, S Peter, Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts, 1–16.
- Henzi, S., Lycett, J., & Weingrill, T. (1997). Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour*, 54(5), 1235–43. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9398376>
- Henzi, S.P., Barrett, L., Gaynor, D., Greeff, J., Weingrill, T., & Hill, R. a. (2003). Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Animal Behaviour*, 66(5), 931–938. doi:10.1006/anbe.2003.2244
- Horrocks, B. Y. J., Hunter, W., Hill, C., & James, S. (1983). MATERNAL RANK AND OFFSPRING RANK IN VERVET MONKEYS : AN APPRAISAL OF THE MECHANISMS OF RANK ACQUISITION monkeys (Cercopithecus aethiops sabaesus) in, (Lancaster 1971), 772–782.
- Hutchins, M., & Barash, D. P. (1976). Grooming in Primates: Implications for Its Utilitarian Function. *Primates*, 17(2), 145–150.
- Isbell, L A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2(2), 143–155. Retrieved from <http://beheco.oxfordjournals.org/cgi/content/abstract/2/2/143>
- Isbell, Lynne A, & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys , and their implications for group living. *Behavioral ecology and sociobiology*, 32(6), 377–385.

- Johnson, G. A. (1982). Organizational Structure and Scalar Stress, 389–421.
- Kappeler, P. M., & Schaik, C. P. Van. (2002). Evolution of Primate Social Systems. *International Journal of Primatology*, 23(4), 707–740.
- Koenig, A. (2002). Competition for Resources and Its Behavioral Consequences Among Female Primates, 23(4), 759–783.
- Lehmann, J., Korstjens, a. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, 74(6), 1617–1629.
doi:10.1016/j.anbehav.2006.10.025
- McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Original article Social monitoring in a primate group : the relationship between visual attention and hierarchical ranks. *Animal Cognition*, (1), 65–69.
- Melnick, D. J. (1987). The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. *Genetica*, 73, 117–135.
- Noë, R., & Hammerstein, P. (1994). Biological markets : supply and demand determine the effect of partner choice in cooperation , mutualism and mating. *Behavioral ecology and sociobiology*, 35, 1–11.
- O'Brien, T. G. (1993). Allogrooming behaviour among adult female wedge-capped capuchin monkeys. *Animal Behaviour*, (46), 499–510.
- Parr, L. A., Matheson, M. D., Bernstein, I. S., & De Waal, F. B. M. (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, *Cebus apella*. *Animal behaviour*, 54(2), 361–7. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9268468>
- Pasternak, G., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L., & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe - African Protected Area Conservation and Science*, 55(1), 1–9.
doi:10.4102/koedoe.v55i1.1078
- Rasmussen, D. R., & Farrington, M. (1994). Relationships Between Position in the Central-peripheral Structure , Age , and the Dominance Index in the Tanaxpillo Colony of Stumptail Macaques (*Macaca arctoides*), 35(October), 393–408.
- Robinson, J. G. (1981). STRUCTURE IN FORAGING GROUPS OF WEDGE - CAPPED CAPUCHIN MONKEYS *CEBUS NIGRIVITTATUS*, 29, 1036–1056.

- Rowell, T. E., & Olson, D. K. (1983). Alternative Mechanisms of Social Organization in Monkeys. *Behaviour*, *86*(1), 31–54.
- Rubenstein, D. I. (1978). On Predation, Competition, and the Advantages of Group Living.
- Seyfarth, R. M. (1977). A Model of Social Grooming Among Adult Female Monkeys.
- Seyfarth, R. M. (1980). THE DISTRIBUTION , OF GROOMING AND RELATED BEHAVIOURS AMONG ADULT FEMALE VERVET MONKEYS. *Animal behaviour*, *28*, 798–813.
- Silk, J. B. (1982). Altruism among Female *Macaca radiata* : Explanations and Analysis of Patterns of Grooming and Coalition Formation. *Behaviour*, *79*(2), 162–188.
- Silk, J. B., Alberts, S. C., & Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, *67*(3), 573–582. doi:10.1016/j.anbehav.2003.07.001
- Snaith, T. V., & Chapman, C. a. (2007). Primate group size and interpreting socioecological models: Do folivores really play by different rules? *Evolutionary Anthropology: Issues, News, and Reviews*, *16*(3), 94–106. doi:10.1002/evan.20132
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–309. doi:10.1007/s002650050390
- Struhsaker, T. T. (1967a). Ecology of Vervet Monkeys (*Cercopithecus Aethiops*) in The Masai-Amboseli Game Reserve , Kenya. *Ecological Society of America*, *48*(6), 891–904.
- Struhsaker, T. T. (1967b). Social Structure among Vervet Monkeys (*Cercopithecus aethiops*). *Behaviour*, *29*(2), 83–121.
- Tappen, N. C. (1960). Problems of Distribution and Adaptation of the African Monkeys. *Current Anthropology*, *1*(2), 91–120.
- Terborgh, J., & Janson, C. H. (2013). THE SOCIOECOLOGY OF PRIMATE GROUPS. *Annual Review of Ecology and Systematics*, *17*(1986), 111–136.
- Treves, A. (1999). Has Predation Shaped the Social Systems of Arboreal Primates ?, *20*(1), 35–67.

- Trusina, A., Maslov, S., Minnhagen, P., & Sneppen, K. (2004). Hierarchy Measures in Complex Networks. *Physical Review Letters*, 92(17), 178702. doi:10.1103/PhysRevLett.92.178702
- Turner, T. R., Anapol, F., & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology*, 103(March 1996), 19–35.
- Van Schaik, C. P. (1983). Why Are Diurnal Primates Living in Groups ? *Behaviour*, 87(1), 120–144.
- Van Schaik, C. P., & van Noordwijk, M. A. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, (206), 533–549.
- Van Schaik, C. P., & van Noordwijk, M. A. (1988). Scramble and Contest in Feeding Competition among Female Long-Tailed Macaques (*Macaca fascicularis*). *Behaviour*, 105(1), 77–98.
- Van Schaik, C. P., van Noordwijk, M. A., Boer, R. J. De, & Tonkelaar, I. Den. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral ecology and sociobiology*, 13(3), 173–181.
- Vehrencamp, S. L. (1983). Optimal Degree of Skew in Cooperative Societies. *Integrative and Comparative Biology*, 23(2), 327–335. doi:10.1093/icb/23.2.327
- White, D. R. (2003). Social Scaling: From scale-free to stretched exponential models for scalar stress, hierarchy, levels and units in human and technological networks and evolution.
- Willems, E. P., & Hill, R. a. (2009). A critical assessment of two species distribution models: a case study of the vervet monkey (*Cercopithecus aethiops*). *Journal of Biogeography*, 36(36), 2300–2312. doi:10.1111/j.1365-2699.2009.02166.x
- Wrangham, R. W. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*, 75(3), 262–300.
- Wrangham, R. W., & Waterman, P. G. (1981). Feeding Behaviour of Vervet Monkeys on *Acacia tortilis* and *Acacia xanthophloea*: With Special Reference to Reproductive Strategies and Tannin Production. *Journal of Animal Ecology*, 50(3), 715–731.