

SOCIAL AND SPATIAL STRUCTURE OF VERVET MONKEY TROOPS

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ABSTRACT

This thesis explores the female social structure of free ranging vervet monkeys and how social structure affects spatial positioning of individuals in the troop. The effect of dominance hierarchies on female grooming interactions within troops on Samara Game Reserve has historically been quite dissimilar to patterns found in a population at Amboseli. Since the initial analysis of Samara cohorts, the troop sizes at Samara have decreased providing the opportunity to test whether the differences can be attributed to group size. These changes are argued to be due to dominance not being as influential a factor in large troops. In many primate groups dominance is a strong predictor of spatial position. However, since the Samara troop members tend to benefit from social integration but not necessarily dominance, I tested whether this is also the case in predation exposure. Broad social integration predicted lower levels of predation exposure whereas dominance did not.

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CHAPTER ONE: GENERAL INTRODUCTION

1.1 Social Structure of Animal Groups

The social structure of a troop is the synthesis of how individuals interact with each other (Whitehead, 2008). A description of social structure should be reflective of the actual structure of social interactions in a group, and general enough to allow comparison across animal groups. Fulfillment of both conditions is necessary in order to measure phenomenon relevant to the animals, and yet prove useful as a tool to compare between animal groups, populations and species.

Animal social systems can be characterized either by quantifying qualities of societies (Wilson, 1975) or by building metrics from dyadic interactions (Hinde, 1976). Animal societies can be qualified using any or all of the ten qualities of animal societies: “group size, demographic distributions, cohesiveness, amount and pattern of connectedness in communication, permeability or movement between social groups, compartmentalization or the degree to which the population contains distinct social units, differentiation of roles, integration of behavior, information flow, and fraction of time devoted to social interactions” (Whitehead, 2008, pp. 7). Though informative on group level phenomena, this method does not offer descriptions of how individual animals within a group differ. An alternate approach, developed by Hinde (1976), is to measure the interactions between individuals and abstract types of relationships between individuals from those interactions. Group social structure is a further abstraction from the relationship types between dyads. In this way varying types of relationships can be typified: such as, mother-daughter, subordinate-dominant, juvenile-adult, male-female, etc. The social structure of the whole group can be constructed from the type and strength of each dyadic pair relationship.

Though the social structure is constructed from measures of interactions, there is no *a priori* reason to believe that social structure does not affect relationships, or interaction types and frequency. Rather, it is quite likely that there is a dynamic interplay between social structure, relationships and interactions where each affects the other (Figure 1.1).

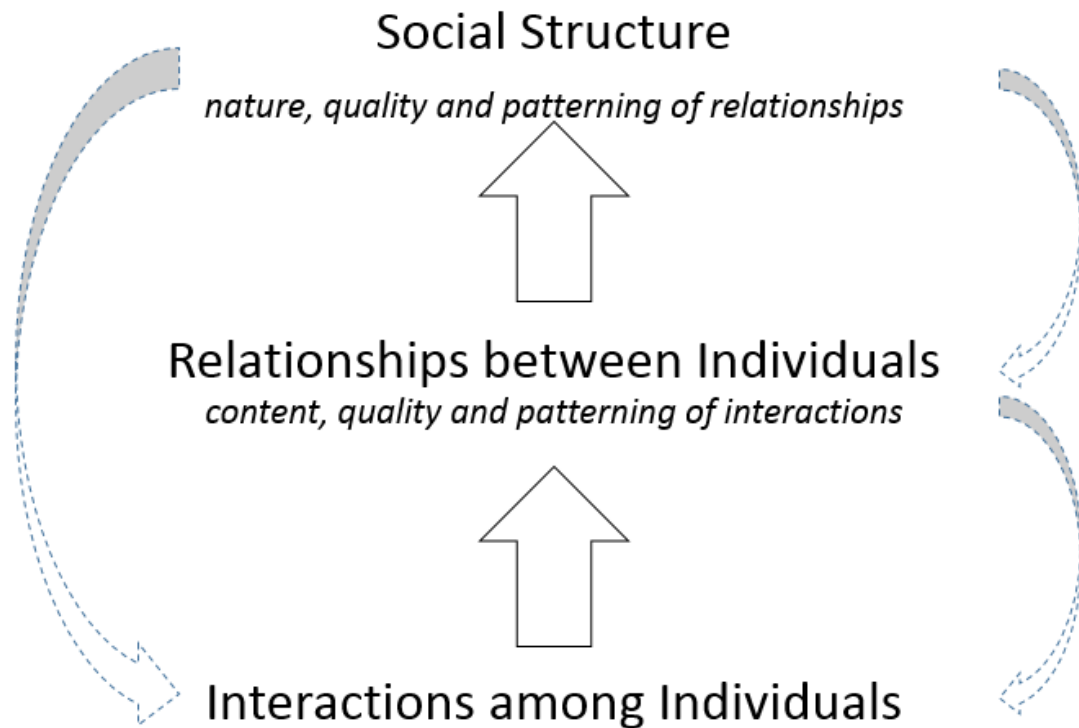


Figure 1.1 Whitehead's (2008) schematic of Hinde's (1976) framework for analysing animal society. An understanding of the relationships between individuals is developed from the interactions between individuals, and the social structure is derived from all the relationships between individuals. Theoretically the social structure affects the relationships between individuals and both the social structure and relationships between individuals affect low level interactions among individuals.

Both the general assumptions and the general application of Hinde's model have been criticized (Barrett & Henzi, 2002). The general assumption built into the model is that the structure so measured is actually relevant to the animals in the society. However, the animals may very well not conceptualize their relationships in the way that human researchers do but, instead, understand each interaction as a local, discrete interaction with an individual (Barrett & Henzi, 2002). This is not a problem for the model as long as researchers do not use it to attempt to draw conclusions about how the individuals in a group understand the group structure. Furthermore, researchers must be aware that if interactions are a result of local discrete interaction, the optimal engagement strategy for individuals may change according to changes in the social group and changes in the ecology. Therefore, generalizations of social structure constructed from interactions measured across changing circumstances must be interpreted cautiously. A second critique is that in application, social structure is generally constructed from grooming interactions alone, ignoring other kinds of social interaction, and this may not be reflective of actual social structure (Barrett & Henzi, 2002). Again, this critique does not mean Hinde's theoretical model should not be used, but if only grooming is used to measure patterns in the relationship in a dyad, those patterns might not be representative of the overall relationship between those two individuals.

In this thesis I focus on the grooming patterns of vervet monkeys (*Chlorocebus pygerythrus*). Though, as noted, grooming behavior is just one aspect of social behavior, it is an undeniably important part of vervet social interactions (Fairbanks, 1980; Henzi & Barrett, 1999; Seyfarth & Cheney, 1984). The patterns of social engagement of the vervets in Samara (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013; Matlock, 2013) have

historically been distinctly different from those of a population from Amboseli (Seyfarth, 1980). My primary objective with this analysis is to determine whether changes in troop composition—decreased troop size—has changed the grooming patterns of the Samara vervet monkeys to be more similar to those found in Amboseli.

1.2 Social Niche Construction

Niche construction is an extension of the standard theory of natural selection to incorporate the changes that animals themselves enact on their environments as a significant factor in the determination of the traits that are subsequently selected (Odling-Smee, Laland, & Feldman, 2003). As an organism changes its ecological surroundings to increase certain resource availability, the traits that used to optimize the survival of that animal might no longer be optimal, while other traits may increase in survival value. A beaver, by damming a river, not only creates its ecological niche of a pond, but actively participates in creating an environment where strong swimming and the ability to fell and move trees are selected for. This results in a 'loopy' ecological theory that functions on an evolutionary time scale. Organisms change their environments, and adapt to the change, in a cause and effect loop that changes over time.

Similarly, social animals can be understood to inhabit social niches. An animal's ecological niche is composed of the resources that affect survival and reproductive success (prey availability, nest construction material, etc.) while its social niche is composed of its set of social and behavioral connections (Flack, Girvan, de Waal, & Krakauer, 2006). Each animal's social niche comprises the social connections between itself and the other animals in the group and depends on the type, strength and quantity of those social connections.

The question I address in the fourth chapter of this thesis is: how do social niches affect a particular aspect of fitness, namely predation avoidance? I investigate whether vervets that invest more time in maintaining social connectivity benefit from decreased exposure to predation. In this way I test the effect of social niches on survival indirectly.

CHAPTER 2: GENERAL METHODOLOGY

2.1 Study Animal

2.1.1 Ecology and characteristics

Vervet monkeys (*Chlorocebus pygerythrus*) are a semi-terrestrial, female philopatric species of Old World monkey that inhabits closed savanna woodlands (Enstam & Isbell, 2007) and narrow riparian zones (Isbell, Pruettz, & Young, 1998; Pasternak, 2011). The second most widely distributed African non-human primate after baboons, vervets are found as far south as the tip of South Africa and north from Ethiopia to Senegal (Struhsaker, 1967).

Vervets live in multi-male multi-female troops with membership as low as 7 and as high as 72 individuals, and move within home-ranges that are defended from incursion by other vervet troops. Adults are sexually dimorphic: adult males weigh between 5-6.5kg and adult females 2.5-4kg (Bolter & Zihlman, 2003; Kagira, Ngotho, Thuita, Maina, & Hau, 2007; Pasternak et al., 2013). Vervets are generally divided into four age categories, infant, juvenile, sub-adult and adult. Sub-adult and adult males transfer from their natal group and often transfer to additional troops every few years (Henzi & Lucas, 1980), while females remain in their natal troop their entire lives.

2.1.2 Social Organization

Vervets are highly social animals who interact regularly with many group mates (Seyfarth, 1980). Their interactions vary from aggression, such as supplanting, chasing, or fighting, to affiliative actions such as grooming, or alloparenting. Dominance in females is matrilineally inherited, with young adult females tending to achieve a rank directly below their mother and above their older sisters. If the dominant female dies before her youngest daughter reaches adulthood, the next dominant female will take the highest rank (Fairbanks & McGuire, 1985). Males transfer out of their natal troop removing the possibility of the mother conferring

status on her son (Henzi & Lucas, 1980). Instead, dominance hierarchies among males are best predicted by physical size and fighting ability (Cheney & Seyfarth, 1989).

2.2 Study Site

Data were collected on Samara Private Game Reserve, a 27,000ha protected area near Graaff-Reinet, Eastern Cape, South Africa (Figure 2.1), from January through May 2014. The broader ecosystem is semi-arid karoo, but the home ranges of the troops reported in this study inhabit riverine woodlands that straddle a non-perennial river. Though the river does not flow during the dry winter season, small water holes dispersed along the riverbed generally allow year round access to water, as was the case during my study.

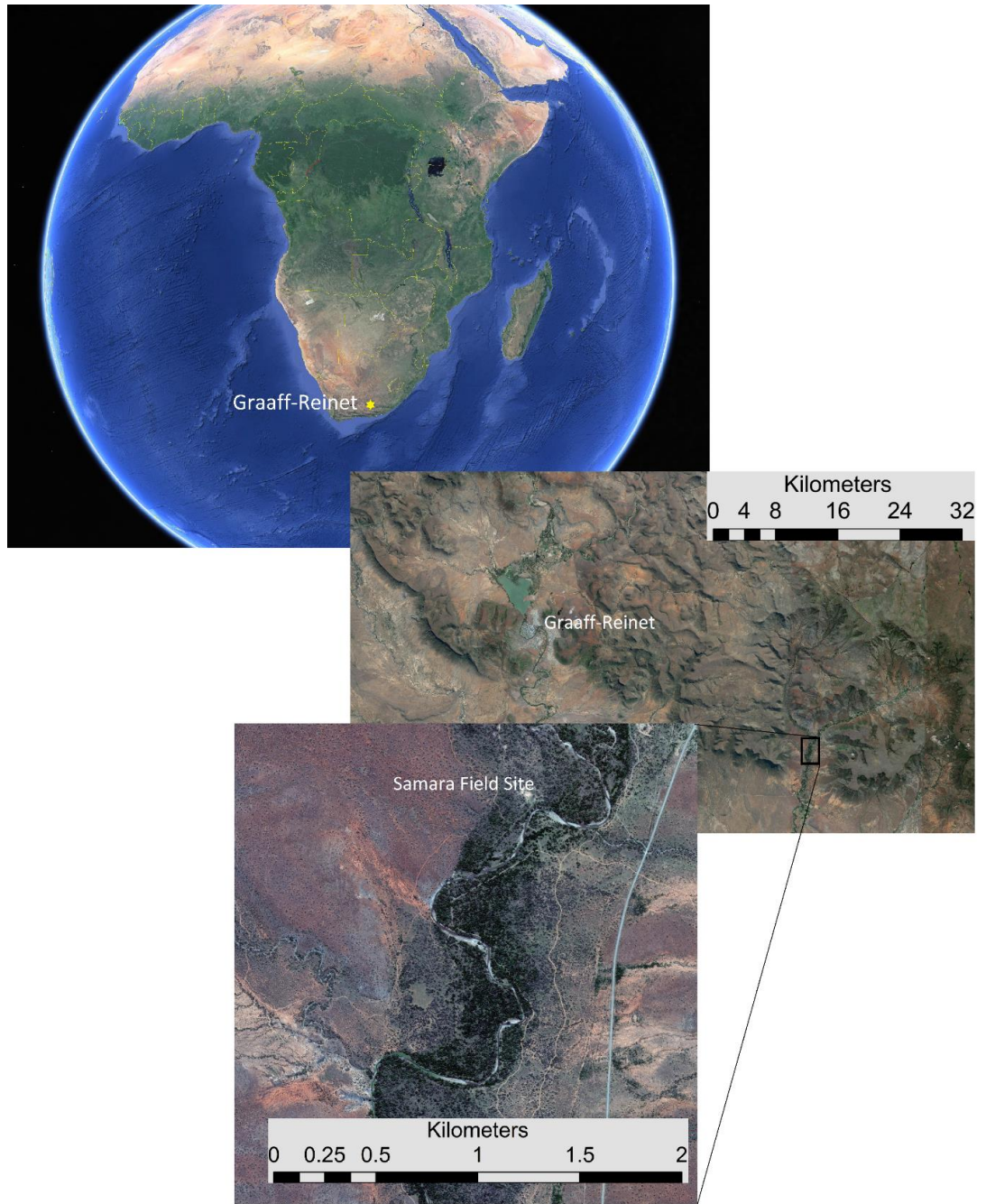


Figure 2.1 Location of the Samara field site's position in Africa and in relation to Graaff-Reinet

2.2.1 Flora and Fauna

Vervets at this field site consume as many as 30 different species of plant (Pasternak et al., 2013). Insect foraging comprises 7% of all foraging, while the other five most foraged species were all plants, vachellia karroo (*Acacia karroo*) 33.8%, Australian saltbush (*Atriplex semibaccata*) 15.33%, dunal (*Lycium oxycarpum*) 6.47%, peppercorn tree (*Schinus molle*) 5.44% and wolfthorn (*Lycium cinereum*) 4.72%, provided for 65.76% of all foraging effort (Pasternak et al., 2013). All of these plants are well represented and distributed within the monkey home ranges (Pasternak, 2011), suggesting that if food competition exists within this population it is likely to be scramble competition – where individuals who find a resource will be able to consume it – rather than contest competition – where whoever can monopolize a food site benefits from it the most (Hirsch, 2007; Janson, 1985).

Vervets at this field site fall prey to two classes of predators, avian and large land predators, and suffer mortality from poisonous snakes. Avian predators include Verreaux's eagle (*Aquila verreauxii*), martial eagle (*Polemaeus bellicosus*), Giant eagle owl (*Bubo lacteus*) and Cape eagle owl (*Bubo capensis*). Land predators are caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*) and black-backed jackal (*Canis mesomelas*). Though poisonous snakes do not actively prey on vervets, if they are not avoided they will deliver a lethal bite. Poisonous snakes on Samara include boomslang (*Dispholidus typus*), puff adder (*Bitis arietans*), ring-necked spitting cobra (*Hemachatus haemachatus*) and cape cobra (*Naja nivea*) (Pasternak, 2011).

2.2.2 Climate

Samara Game Reserve is subject to strong seasonal changes. Rainfall is heaviest during the austral summer months with very little precipitation during the winter months (Figure 2.2). Temperatures during the peak of summer range from a mean high of 32°C to mean low of 16°C

and during the coldest winter month range from a mean high of 18°C to a mean low of 2°C (Figure 2.3).

In spite of the high temperatures (Figure 2.3), sometimes reaching 43°C, the vervets in this population are not under as much heat stress as they are under cold stress (Lubbe et al., 2014; McFarland et al., 2015).

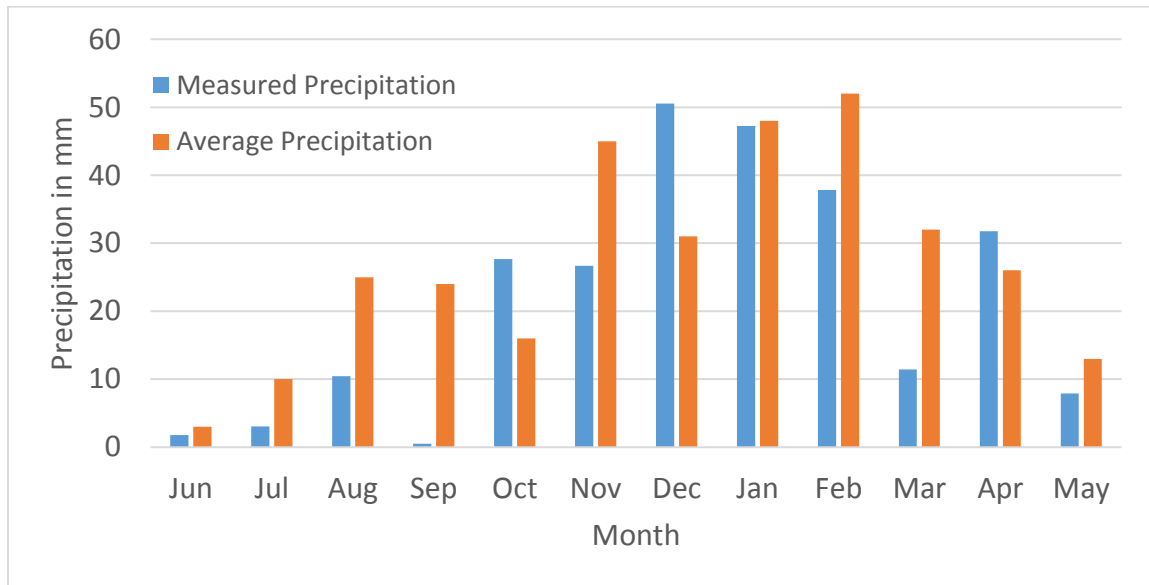


Figure 2.2 Monthly precipitation (mm) recorded in Graaff-Reinet located 33km from the field site seven month prior to, and five months during data collection.

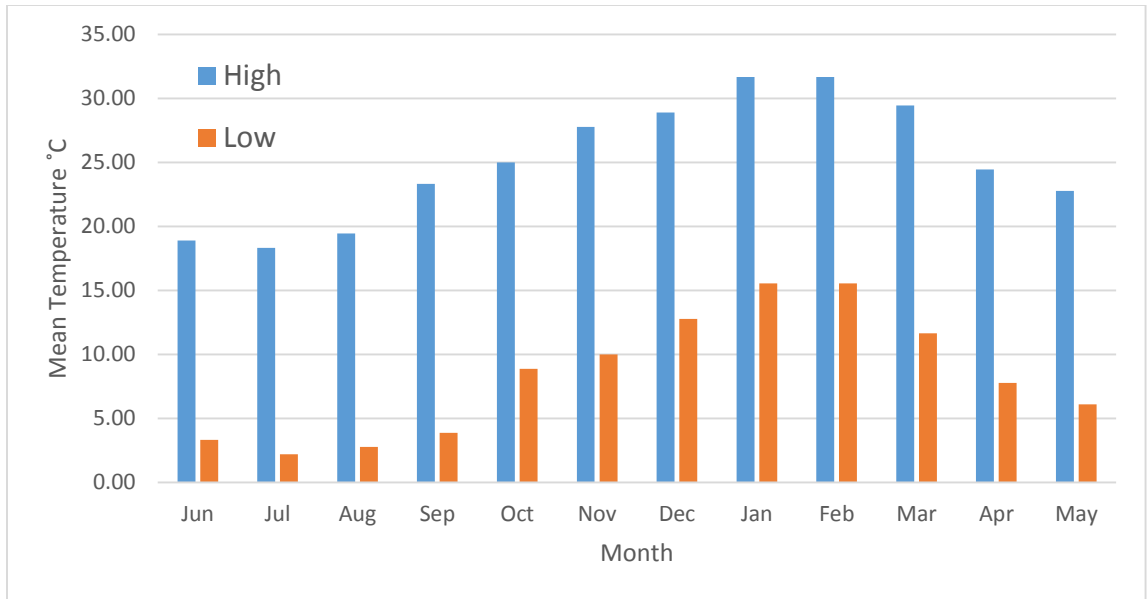


Figure 2.3 Average monthly maximum and minimum temperature (°C) recorded in Graaff-Reinet located 33km from the field site seven months prior to, and five months during data collection

2.3 Study Troops

The data were collected on three troops of free ranging vervet monkeys. Two of the troops, River Bend Mob (RBM) and River Side Troop (RST) have been under continuous study since September 2008 while Picnic Troop (PT) has been studied since August 2012. All three troops were fully habituated prior to data collection. The troops shared home range borders along the Milk River with overlap between all three troops. Home range size varied from 7.5 ha for PT, to 14.6 ha for RST and 26.8 ha for RBM (Figure 2.4). During the study period every troop encountered the other two troops as well as other non-study troops along the river.

Daily travel distance within the home range depends on the local availability of water (Pasternak, 2011). Though differing significantly in distance moved, sometime traveling as little as several hundred meters in a day, the average daily distance travelled for troops in Samara in 2009 was 2-3km (Pasternak, 2011).

2.3.1 Demography

RBM, consisted of 43 animals: 8 adult males, 10 adult females, 8 sub-adult males, 1 sub-adult female, 4 juvenile males, 2 juvenile females and 9 infants. PT had 25 members: 5 adult males, 8 adult females, 1 sub-adult male, 3 juvenile females and 8 infants. RST consisted of 46 non-infant individuals: 8 adult males, 16 adult females, 2 sub-adult males, 4 juvenile males, 4 juvenile females and 12 infants.

One adult male immigrated to PT mid-February and one sub-adult male, and one adult male emigrated from RBM at the end of April, and one adult male emigrated from RST in mid-March. All three males were included in the counts of their respective troops. The sub-adult male immigrated to RST but is only included in RBM analysis due to his short duration in RST before the end of the study. There were no other births, deaths, immigrations or emigrations recorded during the study interval.

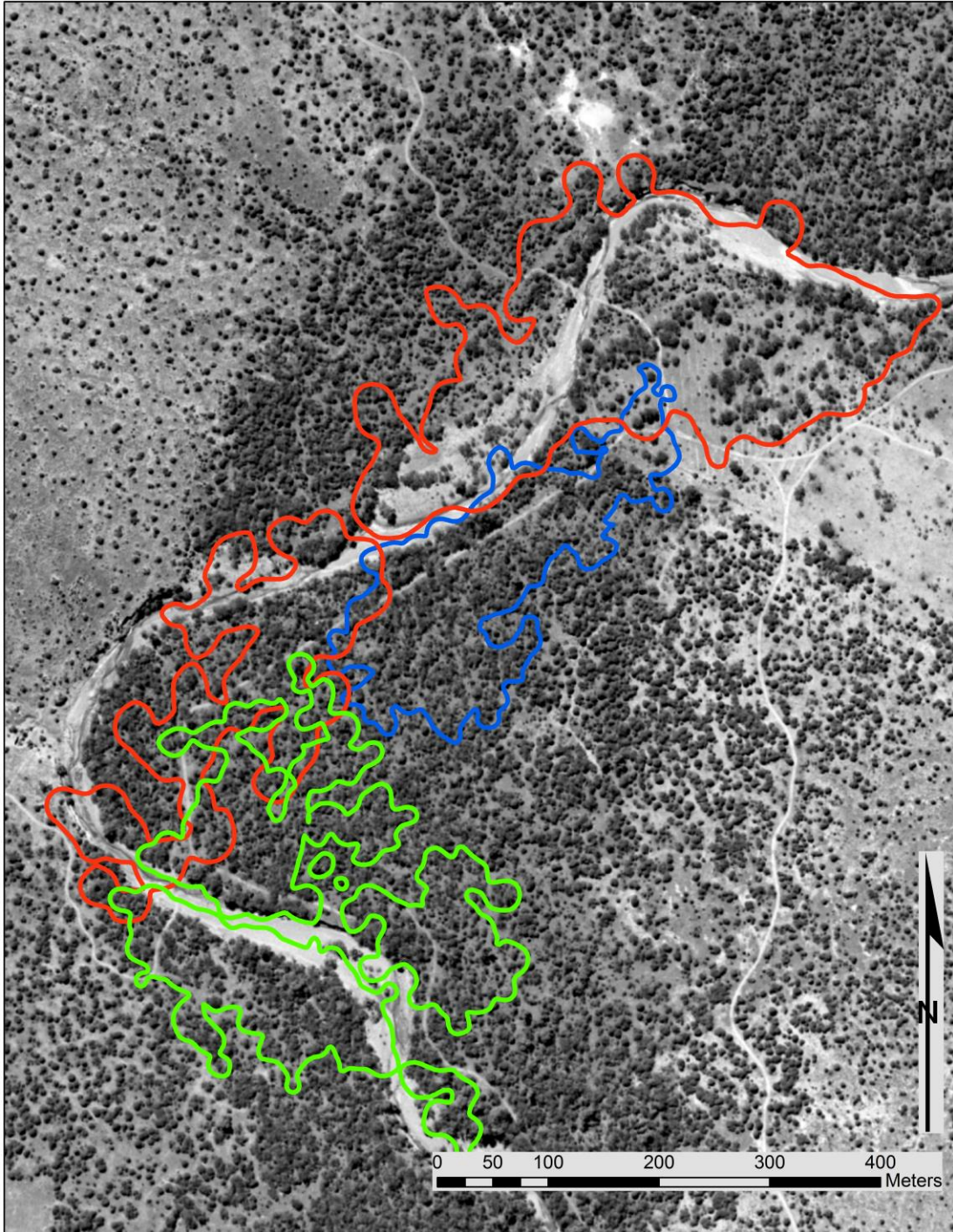


Figure 2.4 Home range of the three troops, RBM in red, PT in blue and RST in Green. GPS points of group center (N=4324) were used to create home range boundaries. Boundaries are isopleths with 90% of points observed within the boundaries constructed with geospatial modelling environment (Beyer, 2012).

2.4 Data Collection

I followed the monkeys at a distance of 1-6 meters depending on the comfort level of the monkeys. If they showed signs of distress, hyper-alertness towards me, or signs of running away, the following distance was increased until these indications disappeared. Individual monkeys were recognized by a variety of natural markings including ear-nicks, facial markings, tail types and broken phalanges.

2.4.1 Instantaneous Data Collection

Behavioral data were collected on all adult and sub-adult individuals using instantaneous scan samples at 30 minute intervals (J. Altmann, 1974). Instantaneous scans were taken of every visible adult and sub-adult during a ten-minute period. Three measures recorded in this way are used in this thesis: activity, vigilance and nearest neighbor distances (Table 2.1). Information was recorded using hand-held computing devices loaded with Pendragon Forms 5.1 software. Over the course of the study, 23,796 instantaneous scans were collected. The number of scans/troop/month are provided in Table 2.2. Point scans were collected with the assistance of Nicola Guthrie, Jonathan Jarrett, and Marta Fincias.

Table 2.1 Definition of information collected during scans

Category	Definition
Time	Time and date of instantaneous scan
Identity	Identity of the scanned individual
Activity	
<i>Foraging</i>	Actively gathering, or ingesting of food items.
<i>Moving</i>	Continuous movement greater than one body length
<i>Allo-Groomer</i>	Actively grooming another individual

<i>Allo-Receiver</i>	Actively receiving grooming from another individual
<i>Autogroom</i>	Actively grooming self
<i>Resting</i>	Not Moving, foraging or grooming
<i>Aggression</i>	Engaging in an interaction including fights, chases, threats
<i>Other Social</i>	Playing or copulating
Social Partner	Identity of activity partner
Vigilance	
<i>Human</i>	Alertly monitoring researchers movements
<i>Social</i>	Alertly scanning in the direction of conspecifics
<i>Predator</i>	Alertly scanning environment at areas not occupied by conspecifics
<i>Unknown</i>	Alert scanning behavior, but the object of scanning is indiscernible
<i>Not Vigilant</i>	Not alertly monitoring surrounding area
Nearest Female	Identity of and meter distance to nearest female
Nearest Male	Identity of and estimated meter distance to nearest male

Table 2.2 Days and number of scans per troop per month

Month	PT Days	PT Scans	RBM Days	RBM Scans	RST Days	RST Scans
Jan	9	1121	11	1338	9	975
Feb	14	1374	12	1268	12	1038
Mar	19	1863	19	2400	15	1612
Apr	21	2172	21	2961	18	1856
May	12	1054	16	1479	13	1274
Total	75	7584	79	9446	67	6755

2.4.2 Sweep Data

In order to create a 'snapshot' of the position of every non-infant individual within the troop in relation to all the other individuals, I conducted a ten-minute 'sweep' during which I determined the spatial location of individuals within two of the study troops (PT, RBM). At approximately 8:00AM and 4:00PM each day, all the data collectors in the field met at the location of either PT or RBM. After determining the spatial location of the majority of the troop, half the researchers present positioned themselves at the front of the troop and the other half at the rear. At a signal transmitted by hand-held radio, the researchers at either end of the troop walked towards the center identifying and creating GPS points for each non-infant individual found. After the initial walk through, the researchers circulated around and in the troop until ten minutes was up at which time a signal to stop was given. During the sweep, as many individuals as possible were located and, in order to assess the general movement direction of the troop, resampling of individuals' position was prioritized.

A total of 147 sweeps were completed ($N_{\text{RBM}}=73$, $N_{\text{PT}}=74$) with an mean \pm SD of 51.7 ± 16.5 and 31.8 ± 9.5 points taken for RBM and PT respectively. The mean number of individuals identified per sweep was 25.6 ± 4.0 for RBM and 14.4 ± 1.9 for PT. Rarely were all of the individuals located within any given sweep. In order to check whether individuals were missing at rates greater than predicted by chance I applied Pearson's Chi-squared test to each troop. The rates of finding individuals within each troop did not differ significantly from chance (PT: $\chi^2_{16}=14.25$, $p=0.58$; RBM: $\chi^2_{32}=27.22$, $p=0.71$).

2.5 Social Measures

2.5.1 Dominance Hierarchy

Vervet dominance hierarchies are linear and transitive. Linear hierarchies means that the dominance difference between the most dominant individual and the second most

dominant individual is roughly equivalent to the dominance difference between the second and third most dominant individuals, which is equivalent to the difference between the third and fourth most dominant individuals, etc. Hierarchies are transitive when, if A is dominant to B and B is dominant to C, A is also dominant to C (de Vries, 1998).

Decided agonistic interactions were recorded *ad libitum* (J. Altmann, 1974) on all non-infant individuals in the two study troops, and used to construct dominance hierarchies ($N_{RBM}=419$, $N_{PT}=376$). Because males' larger body sizes allow them to defeat females in dyadic agonistic interactions, separate hierarchies were calculated for each sex. Dominance was calculated using David's Score, a measure which is constructed from wins and losses weighted for the relative strength of opponents (David, 1987; de Vries, 1998). The formula to calculate David's scores is

$$DS = w + w_2 - l - l_2$$

$w = \sum P_{ij} (j = 1 \dots N: j \neq i)$, where P_{ij} is i 's proportion of wins, the number of wins divided by the number of encounters, with the j th individual in the group. w_2 represents the sum of i 's proportion of wins weighted by the w values of its aggression partner; $w_2 = \sum w_j P_{ij} (j = 1 \dots N: j \neq i)$. l is the sum of the proportion of i 's losses with the j th individual (P_{ji}); $l = \sum P_{ji} (j = 1 \dots N: j \neq i)$. l_2 is the sum of i 's P_{ji} weighted for the l value of its interaction partner; $l_2 = \sum l_j P_{ji} (j = 1 \dots N: j \neq i)$ To adjust for the number of individuals in each hierarchy, I used normalized David's scores (NDS), which gives information on the steepness of the hierarchy. NDS are calculated by adding the maximum David's score possible to the measured David's score and dividing by the number of individuals in the hierarchy (de Vries, Stevens, & Vervaecke, 2006). To standardize for troop size (StdRank), NDS was again divided by the number of individuals in the hierarchy resulting in a

hypothetical maximum and minimum score of 1 and 0, though those scores will only result from a perfectly steep linear hierarchy.

2.5.2 Grooming Centrality

Using behavioral data, I constructed weighted grooming interaction matrices from individual grooming interactions ($N=54\pm 37SD$). In addition to an undirected grooming matrix, I also constructed a directed grooming matrix where grooming given and received was taken into account. The value for each dyad (A,B) was calculated as:

$$\frac{N_G}{N_A + N_B}$$

Where, N_A+N_B is the sum of the number of scan recorded for A and B and N_G depending on whether it was a directed matrix or not, is the number of occasions A groomed with B, the number of occasions A groomed B or the number of occasions B groomed A (Table 2.3).

Table 2.3 Directed grooming matrix. Columns represent receivers, rows represent groomers. The sum of the columns or rows represent that individual's grooming (Groom Out) or receiving (Groom In). An undirected matrix is the addition of both grooming and receiving occasions.

	Brie	Daff	Glad	Herm	Lisa	Puzz	Trac	Tyva	GroomOut
Brie	0	0	0	0.0016	0.0020	0.0009	0.0027	0.0009	0.0081
Daff	0.0025	0	0.0041	0.0023	0.0064	0.0073	0.0008	0.0032	0.0266
Glad	0	0.0041	0	0.0032	0	0.0017	0.0017	0	0.0107
Herm	0.0049	0.0038	0	0	0.0018	0.0095	0.0047	0.0031	0.0278
Lisa	0.0110	0	0.0029	0.0018	0	0.0057	0.0058	0.0037	0.0309
Puzz	0.0044	0.0016	0.0051	0.0032	0.0144	0	0	0.0100	0.0386
Trac	0.0284	0.0000	0.0026	0.0016	0	0	0	0.0017	0.0342
Tyva	0.0121	0.0008	0.0008	0.0008	0.0028	0.0100	0.0133	0	0.0405
GroomIn	0.0634	0.0103	0.0155	0.0143	0.0273	0.0351	0.0290	0.0225	

In social network terms, the sum of an individual's measure of dyadic grooming rates is its grooming centrality strength score. A graphical representation of a grooming

network demonstrates how an individual can have either a high out-centrality, or a high in-centrality strength without necessarily having a high, undirected centrality strength score (figure 2.5). Because of this, the measures are often uncorrelated and can be used to answer a variety of different questions. In the remainder of this thesis I will refer to the undirected grooming centrality score as GroomCent, the directed grooming given centrality score as GroomOut or social effort, and the receiving centrality score as GroomIn or popularity.

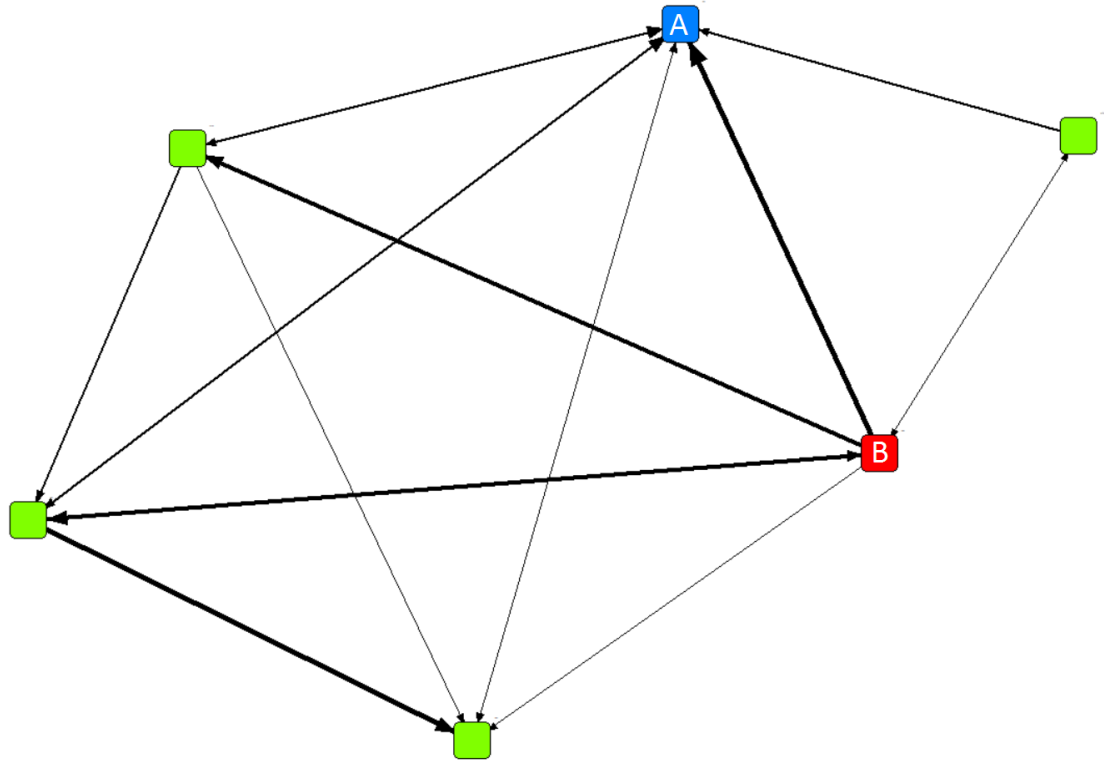


Figure 2.5 Directed social network. Arrow size represents the strength of a directed interaction. Individual A received grooming from all individuals and has a high in-centrality strength while individual B has high out-centrality strength. Both A and B have relatively high undirected centrality strength when compared to the other individuals in the network.

CHAPTER 3: THE STRUCTURE OF FEMALE VERVET SOCIAL GROOMING

3.1 Hypothesized Model for Structure of Social Interactions

The most influential model in understanding female vervet social structure is one developed by Seyfarth (1977), in which he made a number of assumptions about the social preferences of female vervets and, drawing from those assumptions, made several predictions about the structure of social interactions. His main assumptions can be outlined as follows: 1. vervets receive two main benefits from engaging in grooming; ectoparasite removal, and coalitionary support from grooming partners in consequent aggressive interactions. The first benefit is well documented in the literature (Saunders, 1988; Tanaka & Takefushi, 1993), but the second was self-admittedly as yet a hypothetical conjecture with little support found for it since (Barrett, Gaynor, & Henzi, 2002; Matlock, 2013). 2. Assuming that all individuals are equally skilled at removing parasites, but are not all equally valuable as coalition partners, more dominant individuals are more valuable because they are more likely to be successful as a part of a coalition. 3. Individuals should consequently attempt to maximize the benefit they receive from grooming encounters by engaging with high-ranking individuals.

Using these assumptions, he created a list of predictions about which individuals are likely to be preferred grooming partners, and the level of reciprocity to be expected between any two individuals. His predictions concerning who is most likely to be a preferred grooming partner draw from the assumption that an individual's attractiveness will be derived from the potential benefit she can offer others. Consequently female vervets will attempt to interact as much as possible with high-ranking individuals because they are assumed to offer the most benefit in terms of coalitionary support. However, due to a

further prediction that members of the troop will behave with a significant level of synchrony, i.e., move, forage, rest and groom at roughly the same time, not all individuals will have the time to optimize their grooming partners. In other words, if all grooming interactions occur in a limited time frame, and dominant animals will more easily access highly attractive grooming partners, there will not be enough time for subordinate animals to also access those attractive grooming partners. Because of the time factor and the competition for high-ranking grooming partners, there will be a tendency to groom both up the hierarchy *and* individuals of similar rank. To illustrate this last point more clearly, imagine a dominance hierarchy where individual A is the highest rank, and B is the second highest, followed by C etc. A is the most attractive grooming partner, but, whenever B is grooming, she will be able to realize her attraction to groom A by monopolizing her from subordinates. If B is not engaged in grooming activities, and C is in need of a grooming partner, she will be able to monopolize A as a grooming partner, etc. The resulting pattern is that dominant females receive more grooming, and that most individuals will only be able to access the non-monopolized individuals of similar rank.

Seyfarth's predictions extended to include elements of dyadic relationships. He predicted that the greater the power differential between two individuals, the less likely it is that grooming interactions are reciprocal. This is predicted because the attractiveness of a social partner is dependent on her dominance rank, so though a dominant female may be willing to receive grooming from a low ranking animal, she is less likely to reciprocate because the added benefit as a coalition partner is small. Because of this, it is also predicted that dominant animals will have a higher ratio of grooming received to grooming given.

3.2 Model Critique

Female-bonded primate groups, where females remain in natal troops throughout their lives, have often been studied using the model outlined in Section 3.1 (Fairbanks, 1980; O'Brien, 1993; Silk, 1982). However, there are several criticisms of the basic assumptions of the model, of which the most salient may be that female primates rarely show coalitionary support against other females (Hemelrijk, 1990; Henzi & Barrett, 1999; Schino, 2001). In his empirical test of his model, Seyfarth (1980) found that 70% of female coalitions in a population of vervets were against males, and there was evidence in only two of the three troops studied of a significant correlation between grooming and alliance formation; in these two troops, though significant, the correlation was not high, ($r=0.3$). There was no analysis indicating whether there was a correlation within alliances formed only against females, and without such an analysis it is unclear whether this correlation remains when only anti-female coalitions are formed. It is also unclear whether dominant individuals are more valuable as coalition partners. Though this is assumed by Seyfarth, it is just as likely that even two low ranking females together can defeat any other individual in the troop. And, since rates of coalitions constituted only 3% of female aggression instances at Amboseli, the value of developing alliances with high ranking females is questionable. This and other evidence (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Silk, 1982) suggests that coalition formation cannot be the driving factor behind the pattern of grooming interactions found in vervet troops.

Not only has coalitionary support not been found to be a significant factor in female primate social engagement, several tests of predicted grooming patterns showed patterns not predicted by the model. In brown capuchin monkeys (Parr, Matheson, Bernstein, & de

Waal, 1997) and wedge-capped capuchin monkeys (O'Brien, 1993) females tended to groom down the dominance hierarchy. These studies conclusively showed that dominance does not have the same effect on grooming patterns in all primate groups.

An additional critique of the assumptions of Seyfarth's grooming model is that it assumes the social benefit of being a recipient of a grooming bout is equivalent to that of being the groomer. In most studies which use grooming interactions as a measure of pro-social behavior, the direction of grooming is ignored and only total grooming interactions are measured (O'Brien, 1993; Seyfarth, 1980; Seyfarth & Cheney, 1984; Silk, 1982; Silk et al., 2010). However, there is no *a priori* reason to believe that direction is irrelevant, nor is there any empirical evidence to support the conjecture that they are socially equivalent. The assumption plays an important role in the Seyfarth's model because it supports the claim that it is always more advantageous to be the recipient than the groomer (Seyfarth, 1977, pp 680). However, without this assumption, in theory, if an animal is able to trade grooming given for a resource it finds more valuable than receiving grooming, it may be a better strategy to groom than be groomed. In other words, if an animal receives a social benefit from grooming another individual greater than the benefit it would receive from parasite removal, it should choose to groom over receiving grooming.

Perhaps the strongest criticism of Seyfarth's basic model is that it assumes a static preferences in the ratio of giving to receiving grooming within each animal, and that grooming interactions have a constant value. However, if, as is likely, females can trade grooming for other resources, such as short term tolerance at a feeding site (Barrett et al., 2002; Henzi et al., 2003), the value of grooming relative to the value of tolerance will change as foraging conditions vary. This perspective, known as the biological market

hypothesis (Noë & Hammerstein, 1994, 1995), suggests that since grooming can be traded for grooming, and can also be traded for other resources, as the availability of those other resources change, so will the relative value of grooming. The biological market model expands standard reciprocal altruism theory in which two individuals trade and the only decision available is to offer service or not to offer services (Trivers, 1971), to include a market wherein individuals of different classes possess resources not available to individuals of the other class. In the context of a vervet monkey troop, dominant individuals conceivably have a higher resource holding potential (RHP); they possess resources unavailable to lower ranked individuals, i.e., access to feeding sites, or spatial location in the troop. Lower ranking individuals can therefore trade their grooming effort for tolerance from dominant individuals, thereby gaining access to those resources.

Support for the biological markets explanation of grooming patterns in primates comes from several studies and experiments on primate groups (Barrett & Henzi, 2002; Barrett et al., 1999; Fruteau, Voelkl, Van Damme, & Noë, 2009; Gumert, 2007a, 2007b). Comparing two populations of chacma baboons (*Papio hamadryas ursinus*), Barrett et al. (1999) found that in the population at De Hoop, with high rates of intra-troop aggression, grooming bouts were less reciprocal within dyads, and with large rank differences, lower-ranking individuals groomed higher-ranked individuals more than the other way around. In the other population, where agonism was rare, grooming within dyads was much more reciprocal. This phenomenon was explained in terms of biological markets, where, in the absence of aggression, individuals had little to trade other than grooming itself, while, in the more aggressive population, dominant individuals were able to trade other commodities, such as tolerance at feeding sites, for grooming. In another study of the same population at

De Hoop, the baboons varied their grooming behavior as market conditions changed (Barrett et al., 2002; Barrett & Henzi, 2002) suggesting that grooming patterns do not simply function to maintain consistent, long lasting social bonds, but instead reflect changing market conditions.

The biological markets model has been shown to apply to grooming patterns in vervet monkeys. In an experimental setting, Fruteau et al. (2009) manipulated the number of food sources available to troops of wild vervets at the Loskop Dam Nature Reserve (South Africa). The researchers provided a food container accessible only to a low ranked individual selected to be the “food provider”. Before the introduction of the food container, the food provider had a low receiving to grooming ratio, but when the food site was introduced, the provider’s grooming ratio shifted to higher than average. When the researchers introduced a secondary food provider, the effect of being a food provider on grooming ratio decreased because the increased supply of food resulted in a lower relative value. When there were two food providers, they could not demand as high a price in terms of grooming for priority access to the food sites. This finding supports the application of biological markets model to vervet troops in general and grooming behavior in particular. Grooming is likely to be a traded commodity that varies in value as the market conditions change.

3.3 Model Modifications

Seyfarth’s model is a sort of proto-biological markets model. The model maintains that females will trade grooming for coalitionary support, and supposes that the relative value of grooming to coalitionary support is constant. However, the full biological markets model incorporates predictions about trading patterns when market conditions change.

Recent work supports the claim that Seyfarth's static model of female grooming patterns may not be applicable to all vervet troops, or even populations, but elements of his model may be incorporated into a biological markets model. Henzi et al (2013) and Matlock (2013) analyzing data collected on two Samara troops in 2009 and 2012 respectively, found no propensity for females to groom up the dominance hierarchy, nor did they find that females had a propensity to groom similarly ranked individuals. Additionally they found lower rates of aggression than Seyfarth (1980), suggesting that dominance may not play as important a role in the Samara troops as in Amboseli troops. However, grooming clique size, the number of grooming partners, remained the same in Samara as in Amboseli. This last finding is surprising because in both periods, the troop sizes at Samara were much larger than those at Amboseli. The consistency in grooming clique size was explained by Henzi et al. (2013) as a part of the renormalization process necessary with larger grooming cohorts. The grooming clique size of ~7 individuals, also found in Japanese macaques (Nakamichi & Shizawa, 2003) and baboons (Silk, Seyfarth, & Cheney, 1999), is similar to the point at which humans also restructure social groups. This may be because of an inherent, non-linear increase in complexity associated with increased group size (Johnson, 1982). The consistency of clique size despite changes in cohort sizes suggests that some sort of renormalization of grooming patterns dependent on cohort size may be occurring.

The similarities and differences suggest that changes in social dynamics may be driven by group size and, if this is the case, a modification to Seyfarth's model to account for changing market dynamics is necessary. One possible adjustment might be that, as a group increases in size, dominance may not play as large a role in large troops (Henzi et al., 2013). This could result from the increased ability to evade aggressive individuals while still

remaining within a tolerable distance of others. If this is the case one should expect a weakened effect of dominance on both grooming allocation and RHP in large troops. Conditions in Samara at the time of my study provide an excellent opportunity to test this proposition. Since 2012, both troops under long-term observation have decreased in size while a third troop, of comparable size to the Amboseli troops, was added to the study population.

3.4 Predictions

1. Seyfarth's model, predicated on high levels of competition for grooming partners, assumes high levels of behavioral synchrony. If most of the individuals groom at the same time, they are less likely to be able to groom with their optimally preferred grooming partner due to increased competition. However, because of increased difficulty in coordinating in large groups, I predict that increased groups size will predict lower levels of behavioral synchrony. If there is a decrease as group size increase in behavioral synchrony, it provides evidence that there are changes in the market that may have significant effects on grooming patterns.

2. In the smaller Amboseli troops dominance hierarchies were significantly steeper than those at Samara in 2009. I therefore predict that as grooming cohort size increases, the steepness of the dominance hierarchy will decrease.

3. In the Amboseli troops dominance predicted levels of grooming received but at Samara in 2009 dominance was not correlated with grooming rates. Grooming rates are therefore likely to be predicted by dominance only in smaller troops. Since at Amboseli there was no relationship found between dominance and grooming given, I also predict that these patterns will only apply to overall grooming rates, and rates of grooming received, but

that there will be no relationship between grooming given and dominance in any of the troops.

4. As rank distance increases, vervets at Amboseli were less likely to be grooming partners, while there was either no relationship, or the reverse relationship in the vervets at Samara in 2009. If this pattern is due to changes in grooming cohort size I predict that as the cohort increases in size, the rank distances between grooming partners will, on average, also increase.

5. Dominant vervets at Amboseli tended to receive more grooming than they gave, that is, they had a higher receive to grooming ratio than subordinates. Henzi et al. (2013) did not report whether or not this was the case at Samara in 2009. However, considering there was no relationship between rank and rate of grooming, it is not likely that there would have been a rank effect on grooming ratio. I predict that as grooming cohort size increases, dominance will have less of an effect on grooming ratio. Also, since grooming ratio within dyads were not predicted by rank distance in the vervets at Amboseli, I predict that rank distance will have no effect on receiving to grooming ratio within dyads.

6. Vervets at Amboseli were reported to groom individuals they were most often in spatial proximity to. This was not the case at Samara in 2009, where the vervets tended to groom most often with individuals that were not often spatially proximate. Again I predict that as grooming cohort size increases, grooming patterns will reflect what was found at Samara in 2009. If grooming cohort size decreases, the prediction is that grooming patterns will be more like those found in the troops at Amboseli.

7. Grooming clique size was not significantly different between the two study sites. Therefore, I predict that grooming clique size will not vary with changes in grooming cohort size.

3.5 Methods

In addition to the *ad libitum* dominance data, and scan data outlined in Chapter 2, I used 2012 data from Samara analyzed by Matlock (2013) (same collection method), and, where applicable, I compared results to those reported by Seyfarth (1980) on three troops in Amboseli and Henzi et al. (2013), on data collected in 2009 in Samara. The size of each troop is given in Table 3.1.

Table 3.1 Size of the female grooming cohorts by year and troop. Within troops at Samara female grooming cohort size has decreased since 2009.

Location	Troop	Year	Females	Total
Amboseli	A	1977	8	29
Amboseli	B	1977	7	17
Amboseli	C	1977	8	29
Samara	PT	2014	8	25
Samara	RBM	2009	15	48
Samara	RBM	2012	13	38
Samara	RBM	2014	11	43
Samara	RST	2009	23	72
Samara	RST	2012	21	54
Samara	RST	2014	16	46

The general rationale for the structure of the following models is to construct models to best test the effect of change in cohort size on grooming patterns. Entering grooming cohort, that is, each troop-year, as a factor variable, would only provide information on whether there are significant differences between grooming cohorts. Since it is the structure of those differences that are of interest, particularly whether changes in cohort size predict the changes in grooming patterns, I fitted the models with numerical cohort sizes. To control for repeated measures of individuals within troops and years, I used mixed effect models with ID nested in Troop cross classified with Year. An overview of all the models is given in Table 3.2 in Section 3.5.8.

3.5.1 Behavioral Synchrony

I used instantaneous behavioral scan data from the three troops followed in 2014 to determine the synchrony of the monkeys' activities; grooming, foraging, moving or resting. For each individual scan, I measured the proportion of other individuals observed engaged

in each activity within a 10-minute window. I then tested whether the proportion of group-mates engaged in an activity predicted the individual's observed activity with a generalized linear mixed effect model; with *troop size* as a control variable, individual *ID* nested in *Troop* as random effects, a binomial error distribution and logit link function.

3.5.2 Steepness of Dominance Hierarchy

The steepness of each dominance hierarchy is the slope of a regression line of *normalized David's score* (NDS) against *ordinal rank* and ranges from 1, most steep, to 0 completely egalitarian (de Vries et al., 2006). I also assessed the linearity of each hierarchy by the R^2 of a linear fit. After calculating the steepness and linearity of the hierarchy for each troop, I fitted a linear model predicting the *steepness of the dominance hierarchy* from the *grooming cohort size*.

3.5.3 Rank Effect on Total Grooming

To test whether dominant individuals engage in grooming interactions more than subordinates do, I used grooming centrality strength (measure description in Chapter 2) to fit a linear mixed effect model predicting the *rate of grooming interactions* according to *StdRank* and *grooming cohort size*. I fitted *ID* nested in Year cross classified with *Troop* as random effects. Considering that Seyfarth's theory predicts that subordinate individual benefit more from any given grooming interaction, and that, according to theory, receiving grooming (*Groom In-Strength*) is more beneficial than giving, I also test whether dominants receive more grooming than subordinates. The model also predicts that dominant animals also groom more because they are regarded as highly attractive partners, so I tested whether this is the case by fitting a model with only grooming given (*Groom Out-Strength*) as a dependent variable.

3.5.4 Rank Distance Effect on Grooming Proportion

Rank distance can be conceptualized in two distinct ways, one is how easily one individual can defeat another, and the other is the relative distance within a dominance hierarchy two individuals are. The statistic StdRank difference does a good job at measuring the first way, but is not providing useful results at the second way. Consider a situation in which the dominance hierarchy is steeper in one group (ranges from 0-1) than in the other (ranges from 0.4-0.6). If the steepness of the hierarchy is correlated with a variable of interest, and both troops are included in the same regression model, it will appear that the variable of interest has a significant effect that is actually caused by the necessarily low rank distances in the shallow dominance hierarchy troop. To make this example even more concrete, my prediction is that dominance hierarchy will be steeper when grooming cohorts are smaller and that individuals are more likely to groom others of similar rank in small troops. If the first prediction is correct, then larger grooming cohorts will generally have smaller rank differences between any two individuals than small grooming cohorts. This will make it appear that interactions occur more often between closely ranked individuals in large troops than in small troops, when it may not be the case. To correct for this, before calculating rank distance, I normalized each hierarchy so that the lowest ranking individual has a score of 0 and the highest has a score of 1 (NormRank).

Proportion of grooming (P_G) given was calculated for each female dyad:

$$P_G = \frac{N_{AB}}{N_A}$$

Where N_{AB} is the number of times A groomed B and N_A is the number of times A was observed grooming. Following Henzi et al. (2013), I only used dyads in which grooming

interactions occurred. Since the dependent variable had a binomial distribution, I fitted a generalized linear mixed effect model with a binomial error distribution and logit link function. *Absolute NormRank difference* and *cohort size* with an interaction term were a fixed effects predicting P_G and *ID* nested in *Year* cross classified with *Troop* were entered as a random effects.

3.5.5 Rank Effect on Grooming Proportion

To determine whether dominant females received more grooming than they gave, I calculated a receiving-to-giving ratio for every individual:

$$\frac{G_r - G_g}{G_t}$$

Where G_r is grooming received, G_g is grooming given and G_t is total grooming. The measure effectively standardizes the ratio which would otherwise have a $[0, \infty)$ distribution, and is centered on zero with positive number signifying higher rates of receiving than giving. I then fitted a linear mixed effect model with *StdRank* and *grooming cohort size* as a predictor of *grooming ratio* with *ID* nested in *Year* cross classified with *Troop* a random effect.

To test whether the receiving to grooming ratio increased as rank distance increased, I calculated the ratio for every dyad. I used a measure similar to individual receiving to grooming ratio based on the difference of grooming effort in the dyad:

$$\frac{G_S - G_D}{G_S + G_D}$$

Where G_S is the grooming given by the subordinate partner and G_D is grooming given by the dominant partner. The measure is a standardized version of the ratio centered on zero, with more extreme deviations from zero signifying greater unevenness in grooming rates. I fitted a linear mixed effect model with *grooming effort difference* as the dependent variable and *NormRank* distance and *cohort size* with an interaction term as the independent variables. Both *ID* of the giver and receiver were entered as random effects nested in *Troop* cross Classified with *Year*.

3.5.6 Spatial Association Effects

To test whether spatial association predicts rates of grooming interaction I calculated the proportion of time a grooming partner was the groomer's nearest neighbor. I then fitted a linear mixed effect model predicting the *proportion of grooming given* according to *spatial association* and *grooming cohort size*. *ID* was nested in *Year* cross classified with *Troop* for random effects.

3.5.7 Grooming Clique Size

I tested whether grooming clique size, the number of individuals a female groomed or was groomed by, varied dependently on cohort size. I determined grooming clique size by fitting a linear regression model with *grooming clique size* as the dependent variable and *grooming cohort size* as the fixed effects. *ID* nested in *Year* cross classified with *Troop* were random effects.

3.5.8 Models Overview

Table 3.2 Overview of models described in this methods section. The Results Section in which each model's results can be found are specified. For description of each model see corresponding section in methods.

Test (Section)	Dependent Variable	Fixed Effects	Random Effects	Model Type
Behavioral Synchrony (3.6.1)	Activity	Other's Activity, Group Size	ID nested in Troop	Generalized Mixed Effect Model (Binomial)
Steepness of dominance Hierarchy (3.6.2)	Normalized David's Score	Ordinal Rank		Linear Model
	Steepness of Dominance Hierarchy	Cohort Size		Linear Model
Grooming Up the Hierarchy (3.6.3)	Total Grooming	Cohort size, StdRank	ID nested in Year and Troop	Mixed Effect Model
	Grooming Received	Cohort size, StdRank	ID nested in Year and Troop	Mixed Effect Model
	Grooming Given	Cohort size, StdRank	ID nested in Year and Troop	Mixed Effect Model
Rank Distance Effect on Proportion of Grooming Given (3.6.4)	Proportion of grooming interactions	Cohort Size, NormRankDifference	ID Groomer and ID Reciever both nested in Year and Troop	Generalized Mixed Effect Model (Binomial)
Rank Effect on Grooming Ratio (3.6.5)	Grooming Ratio	Cohort size, StdRank	ID nested in Year and Troop	Mixed Effect Model
	Grooming Ratio within Dyad	Cohort Size, NormRankDifference	ID Groomer and ID Reciever both nested in Year and Troop	Mixed Effect Model
Spatial Association Effects (3.6.6)	Proportion of grooming given	Cohort Size, Spatial Association	ID Groomer and ID Reciever both nested in Year and Troop	Mixed Effect Model
Grooming Clique Size (3.6.7)	Grooming clique size	Cohort size	ID nested in Year and Troop	Mixed Effect Model

All models were fitted using R statistical software version 3.2.0 “Full of Ingredients” (R Core Team, 2014). Mixed effect models were fit using lme4 package (Bates, Maechler, Bolker, & Walker, 2014) and frequentist estimates were computed using the lmerTest

package (Kuznetsova, Brockhoff, & Christensen, 2014). Statistical significance was determined from parameter estimates. All linear models conformed to model assumptions of homoscedasticity and normal residual distribution.

3.6 Results

3.6.1 Behavioral Synchrony

The four generalized linear mixed effect models predicting individual activity from group activity were significant for each activity type. Though the moving and resting synchrony were lower in the larger troops, for all behavior types in every troop behavior was strongly synchronous. Results in Table 3.3 and Figure 3.1 indicate significant positive relationships between the observed behavior of an individual and that of others at the same time.

Table 3.3 Results of model predicting behavior from proportion of group mates engaged in that behavior. Results are for each model fitted for each behavior type. Animal identity nested within Year cross classified with Troop were entered as random effects to control for repeated measures.

	β (Log Odds)	SE (Log Odds)	Z	P	95% CI (Log Odds)	
a. Moving Synchrony						
AveMoving	4.603	0.248	18.54	<0.001	4.117	5.089
TroopSize	0.039	0.007	5.61	<0.001	0.025	0.053
AveMoving:TroopSize	-0.056	0.01	-5.38	<0.001	-0.076	-0.036
Intercept	-2.902	0.165	-17.542	<0.001	-3.225	-2.579
b. Resting Synchrony						
AveResting	3.406	0.202	16.86	<0.001	3.010	3.802
TroopSize	0.006	0.005	1.13	0.259	-0.004	0.016
AveResting:TroopSize	-0.029	0.009	-3.275	0.001	-0.047	-0.011
Intercept	-1.753	0.133	-13.146	<0.001	-2.014	-1.492
C. Foraging Synchrony						
AveForaging	3.827	0.232	16.51	<0.001	3.372	4.282
TroopSize	-0.006	0.006	-1.00	0.316	-0.018	0.006
AveForaging:TroopSize	0.000	0.010	-0.001	0.996	-0.020	0.020
Intercept	-2.18	0.135	-16.146	<0.001	-2.445	-1.915
b. Grooming Synchrony						
AveGrooming	5.018	0.381	13.15	<0.001	4.271	5.765
TroopSize	0.001	0.008	0.06	0.954	-0.015	0.017
AveGrooming:TroopSize	0.007	0.016	0.39	0.691	-0.024	0.038
Intercept	-3.215	0.192	-16.747	<0.001	-3.591	-2.839

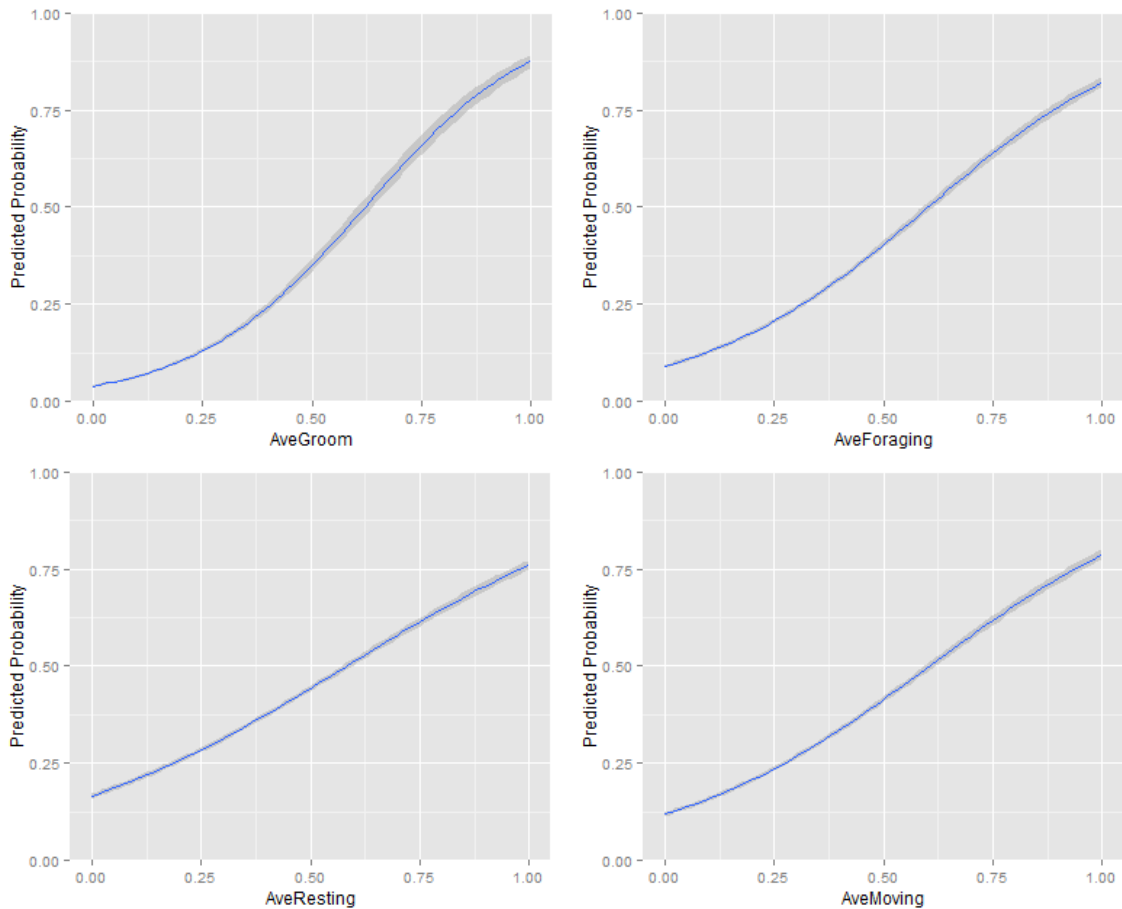


Figure 3.1 Predicted probability, with 95% confidence interval, of an individual engaging in an activity as predicted by the average rate of other troop members engaged in that activity in the same time period. Predicted probability values are converted from linear log-odds values.

3.6.2 Steepness of Dominance Hierarchy

The dominance hierarchy in all female cohorts were well described by a linear model: all R^2 were above 0.97 (Table 3.4). A linear model predicting NDS with an interaction term between ordinal rank and troop/cohort as a factor was the best fit (Table 3.5), indicating significant differences in the slope of the dominance hierarchy between female

cohorts (Figure 3.2). A linear model predicting steepness of dominance hierarchy from cohort size was significant ($B = -0.06$, $SE = 0.01$, $p = 0.01$). As cohort size increases, the steepness of the dominance hierarchy decreases (Figure 3.3).

Table 3.4 The linearity of the hierarchy is given by the R^2 which from the fit of a linear model to each hierarchy. Intercept and slope of dominance hierarchies are from the best fit model in Table 3.5.

Troop	Cohort Size	R^2	Intercept	Slope
12RBM	13	0.9	8.77	0.42
12RST	21	0.8	10.92	0.08
14PT	8	1.0	7.72	0.94
14RBM	11	0.9	8.22	0.55
14RST	16	1.0	10.40	0.34

Table 3.5 The best fit model included an interaction term between ordinal rank and troop. Best fit was determined by AIC.

Model	AIC	ΔAIC
NDS~Ordinal Rank	472.09	
NDS~Ordinal Rank+Troop	310.11	162.0
NDS~Ordinal Rank*Troop	88.95	383.1

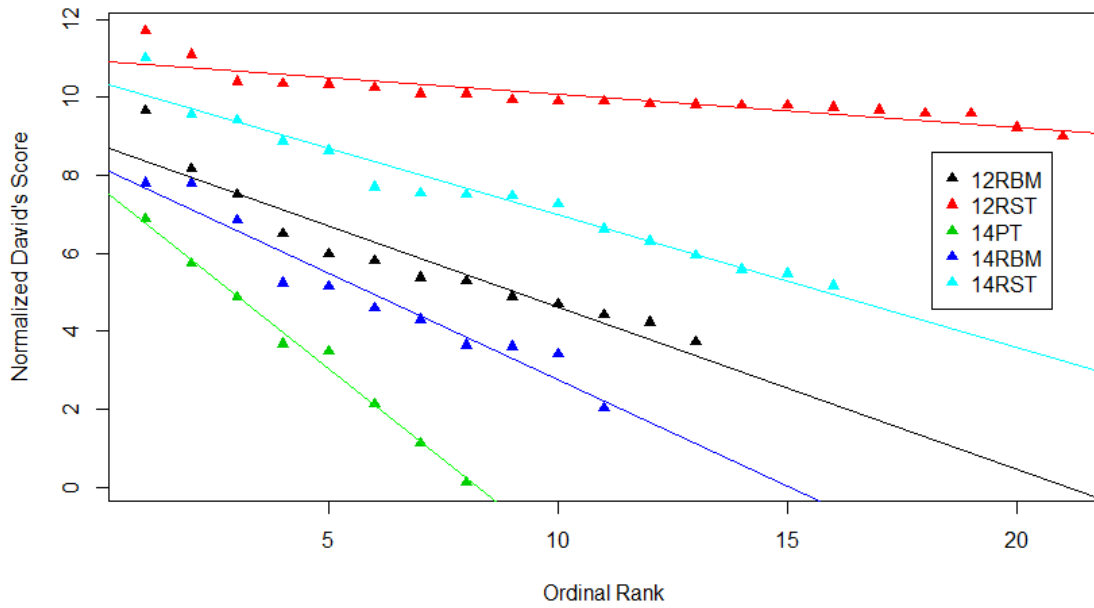


Figure 3.2 Hierarchy steepness estimated by the slope of Normalized David's Score regressed on Ordinal Rank. Each troop/cohort hierarchy was regressed as a separate factor in a linear model with an interaction term between troop/cohort and ordinal rank.

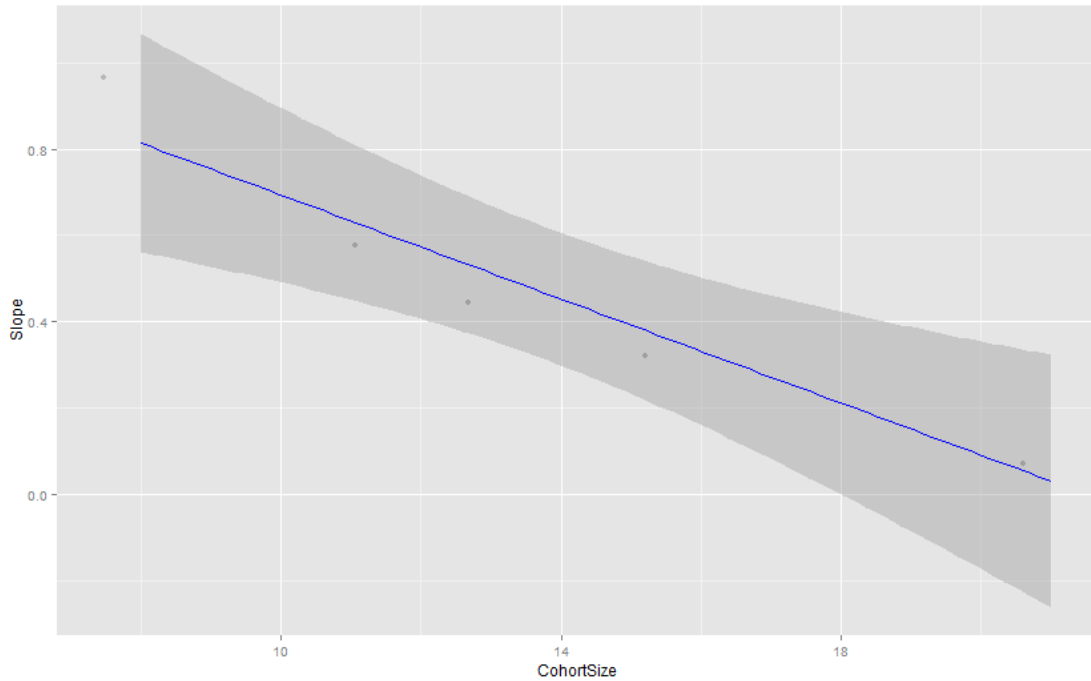


Figure 3.3 Steepness of the dominance hierarchy slope (shown in Figure 3.2), with 95% confidence interval, predicted by cohort size.

3.6.3 Rank Effect on Total Grooming

The fitted model predicting grooming centrality strength from dominance rank showed that overall, dominant individuals engaged in more grooming than subordinates (Table 3.6a, Figure 3.4). This effect was significantly less strong in larger troops, in line with predictions, as the grooming cohort size increased, the effect of StdRank on strength-centrality decreased. Table 3.6b shows the result of the fitted model predicting grooming In-Strength. More dominant individuals had higher levels of In-Strength (Figure 3.5), and this effect was not significantly different between troops of varying cohort size. The third model,

results in Table 3.6c, showed no significant difference predicted by dominance in groom out-strength (Figure 3.6).

Table 3.6 Results of model predicting grooming patterns from rank and grooming cohort size.

Model a predicted overall grooming strength-centrality. Model b predicted in-strength centrality, and Model c predicted out-strength centrality. Animal identity nested within Year cross classified with Troop were entered as random effects to control for repeated measures.

	B	SE	t	P	95% CI	
a. Grooming all-Strength						
StdRank	12.914	4.593	2.81	0.006	3.912	21.916
CohortSize	0.416	0.216	1.92	0.059	-0.007	0.839
StdRank: CohortSize	-1.017	0.419	-2.42	0.017	-1.838	-0.196
Intercept	-1.133	3.059	-0.371	0.722	-7.129	4.863
b. Grooming In-Strength						
StdRank	6.787	2.951	2.3	0.024	1.003	12.571
CohortSize	0.18	0.139	1.29	0.199	-0.092	0.452
StdRank: CohortSize	-0.433	0.269	-1.61	0.112	-0.960	0.094
Intercept	-0.97	1.786	-0.543	0.595	-4.471	2.531
C. Grooming Out-Strength						
StdRank	6.105	4.108	1.48	0.142	-1.947	14.157
CohortSize	0.222	0.193	1.15	0.254	-0.156	0.600
StdRank: CohortSize	-0.581	0.374	-1.55	0.126	-1.314	0.152
Intercept	0.026	2.279	0.010	0.991	-4.441	4.493

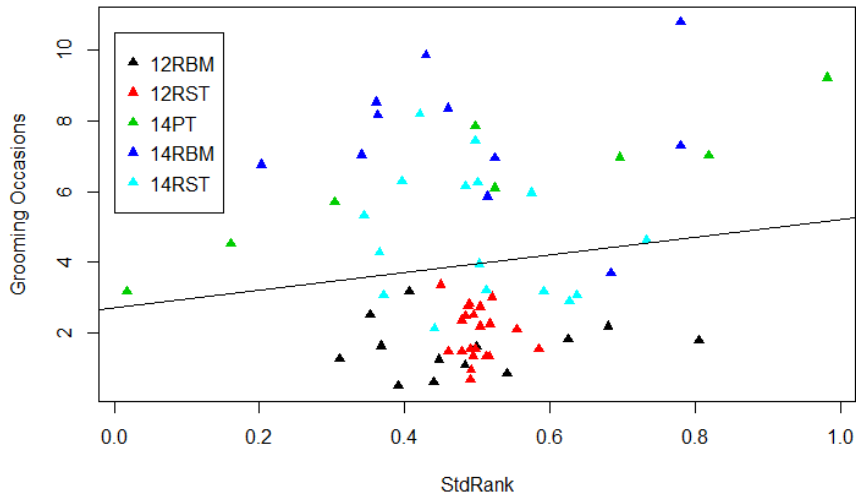


Figure 3.4 Fitted regression line predicting the overall grooming centrality strength for individuals from their standard rank. Observed values (point) colors are by troop and year.

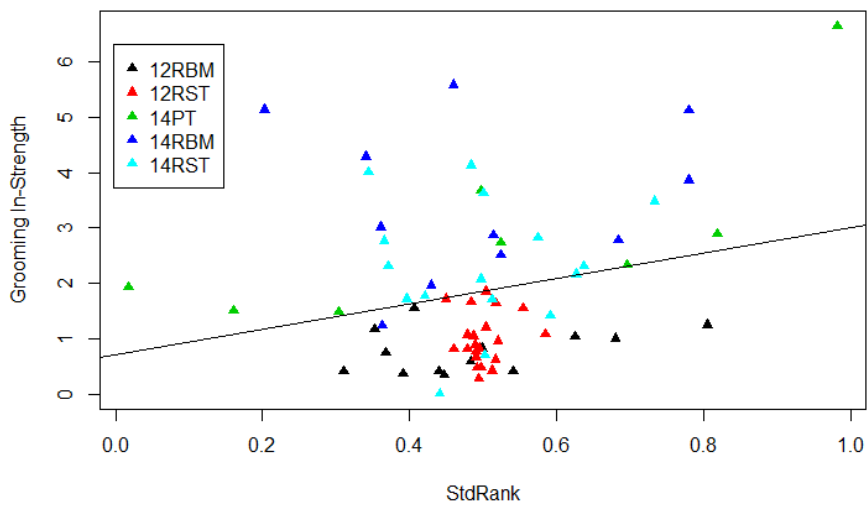


Figure 3.5 Fitted regression line predicting the grooming in-strength for individuals from their standard rank. Observed values (point) colors are by troop and year.

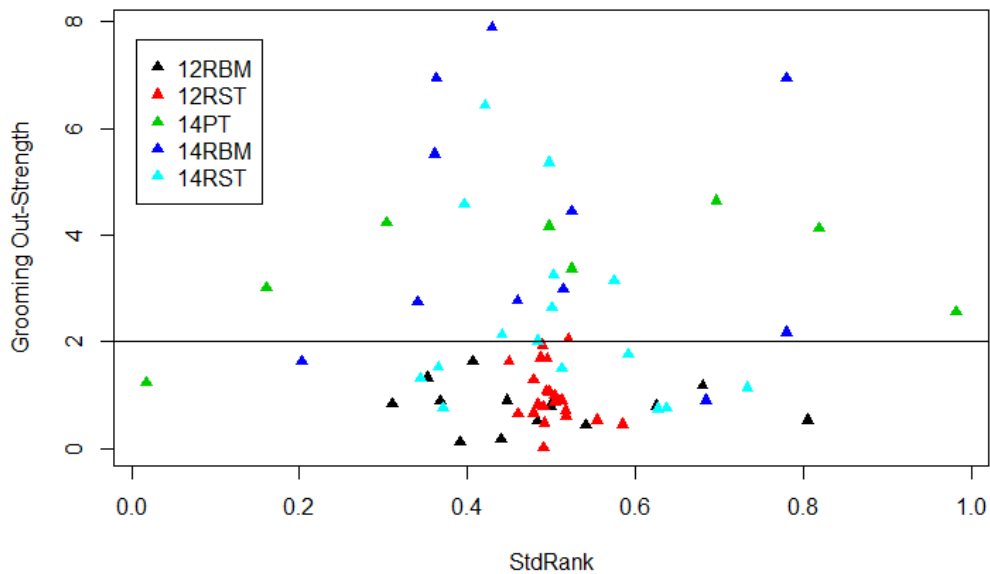


Figure 3.6 Fitted regression line predicting the grooming out-strength for individuals from their standard rank. Observed values (point) colors are by troop and year.

3.6.4 Rank Distance Effect on Proportion of Grooming

The model predicting proportion of grooming given from rank difference shows that, as rank distance within a dyad increases they are less likely to engage in grooming behavior (Table 3.7, Figure 3.7). This is similar to what was reported by Seyfarth (1980) but different to what was reported at Samara by Henzi et al. (2013). In 2009 one troop showed no propensity to groom with similarly ranked individuals, and the other groomed more with individuals of different rank. The significant interaction term between NormRank differences and grooming cohort size shows that as cohort size increases, individuals show less propensity to groom similarly ranked individuals.

Table 3.7 Results of model predicting proportion of grooming (Pg) from normalized rank differences and cohort size. Animal identity of each dyad were nested within Year cross classified with Troop and entered as random effects to control for repeated measures.

	β (Log Odds)	SE (Log Odds)	Z	P	95% CI (Log Odds)	
NormRank Difference	-3.05	0.505	-6.03	<0.001	-4.040	-2.060
CohortSize	-0.127	0.19	-0.67	0.503	-0.499	0.245
NormRank Difference:CohortSize	-0.971	0.417	-2.33	0.02	-1.788	-0.154
Intercept	0.103	0.247	0.420	0.676	-0.381	0.587

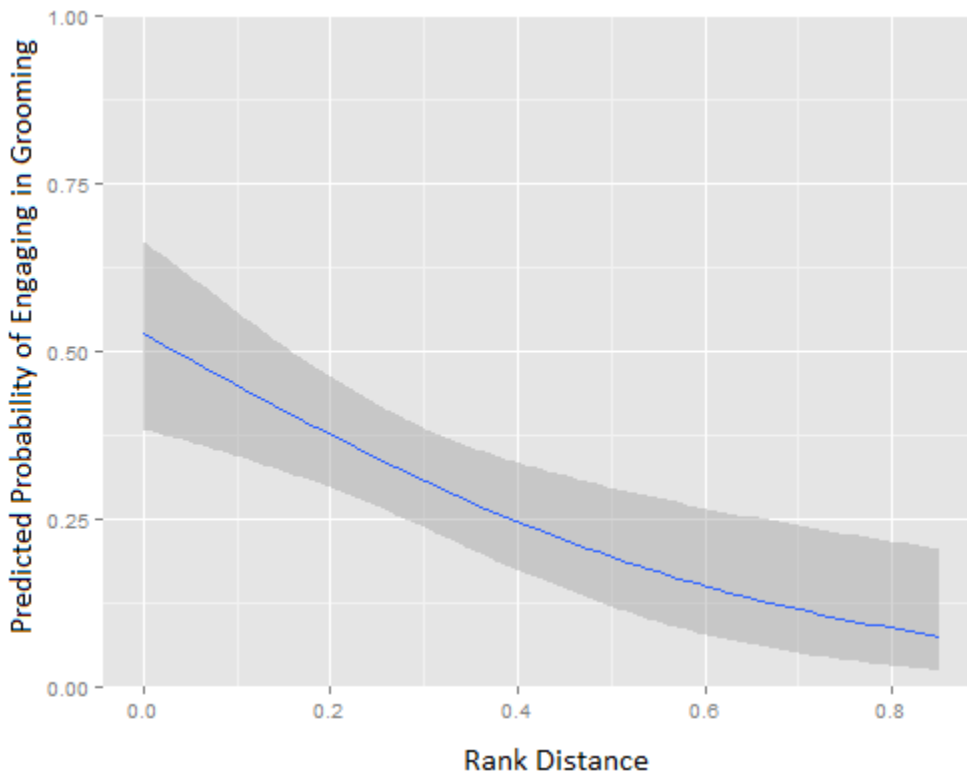


Figure 3.7 Predicted probability of engaging in grooming within a dyad as a function of rank distance with 95% confidence interval shown. As rank distance increases, dyads are less likely to engage in grooming interactions. Predicted probability values are converted from linear log-odds values.

3.6.5 Rank Effects on Grooming Ratio

A model predicting the receiving to grooming ratio from dominance showed no significant result from either standard rank or grooming cohort size (Table 3.8a, Figure 3.8). Dominant vervets at Amobseli did tend to have a higher receiving to grooming ratio (Seyfarth, 1980) while historically dominance did not have an effect at Samara (Henzi et al. 2013). Since there was no relationship found between increased grooming cohort size and the effect of dominance, it appears that the difference is due to something other than the size of the grooming cohort.

Predicting the receiving to grooming ratio within dyads showed no significant effect of rank distance (Table 3.8b, Figure 3.9). There was no effect for rank distance or cohort size. This is a similar finding to that reported by Seyfarth (1980), who determined a relationship between rank distances and grooming ratio within dyads.

Table 3.8 Fitted models predicting a. rank's and cohort size effect on grooming ratio and b. rank distance and cohort size effect on grooming ratio within dyads. In model a. animal identity nested within Year cross classified with Troop were entered as random effects to control for repeated measures and in model b. Animal identity of each dyad were nested within Year cross classified with Troop and entered as random effects to control for repeated measures.

	β	SE	<i>t</i>	P	95% CI	
a. Rank Effect on Grooming Ratio						
StdRank	0.113	0.592	0.19	0.849	-1.047	1.273
CohortSize	0.006	0.02	0.30	0.768	-0.033	0.045
StdRank: CohortSize	0.008	0.041	0.19	0.848	-0.072	0.088
Intercept	0.092	0.612	0.150	0.880	-1.108	1.292
b. Rank Distance Effect on Grooming Ratio						
NormRank Difference	0.498	0.638	0.78	0.437	-0.752	1.748
CohortSize	0.000	0.014	0.01	0.996	-0.027	0.027
StdRank Difference:CohortSize	-0.046	0.052	0.88	0.382	-0.148	0.056
Intercept	0.205	0.196	1.049	0.299	-0.179	0.589

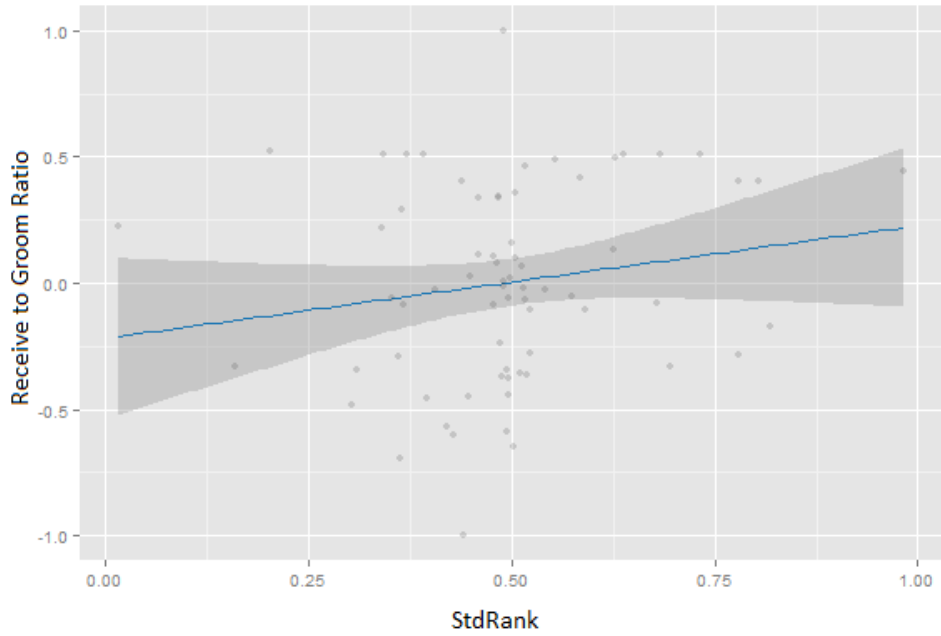


Figure 3.8 Fitted (line with 95% confidence interval) and observed (points) values of receive to groom ratio as a function of StdRank. No significant effect of rank.

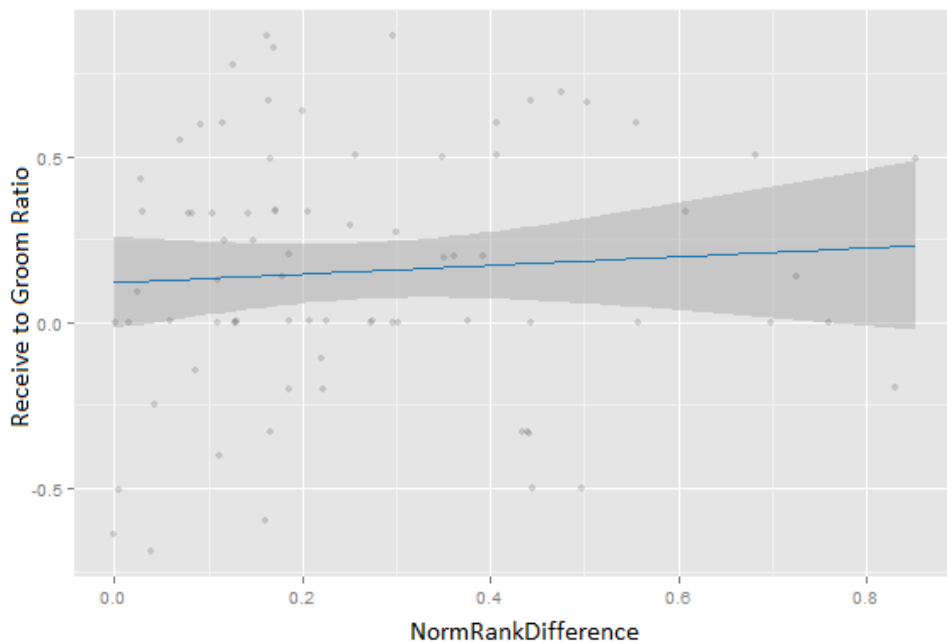


Figure 3.9 Fitted (line with 95% confidence interval) and observed values (points) for receive to grooming ratio as rank difference increases. No significant effect of rank distance.

3.6.6 Spatial Association Effects

A generalized linear mixed effect model indicated that spatial association did predict the proportion of grooming interactions. The more time that individuals spent in close proximity, the more grooming interactions they engaged in (Table 3.9). There was a significant interaction term between spatial association and cohort size; as cohort size increases, individuals are less likely to groom those with whom they spend the most amount of time. In Amboseli there was a high correlation between grooming and spatial proximity, but at Samara in 2009 females more often groomed with individuals who were less often in spatial proximity. The result that individuals groom their spatial partners less as the grooming cohort size increases fits with the overall prediction that grooming patterns in small troops will fit with patterns observed at Amboseli.

Table 3.9 Results of model predicted log odds of engaging in grooming activity from spatial rank and cohort size. Animal identity of each dyad were nested within Year cross classified with Troop and entered as random effects to control for repeated measures.

	β (Log Odds)	SE (Log Odds)	Z	P	95% CI (Log Odds)	
Normalized Spatial Rank	3.931	0.160	24.57	<0.001	3.617	4.245
CohortSize	-1.243	0.131	-9.44	<0.001	-1.500	-0.986
Normalized Spatial Rank:CohortSize	1.114	0.147	7.54	<0.001	0.826	1.402
Intercept	-0.317	0.288	-1.110	0.267	-0.881	0.247

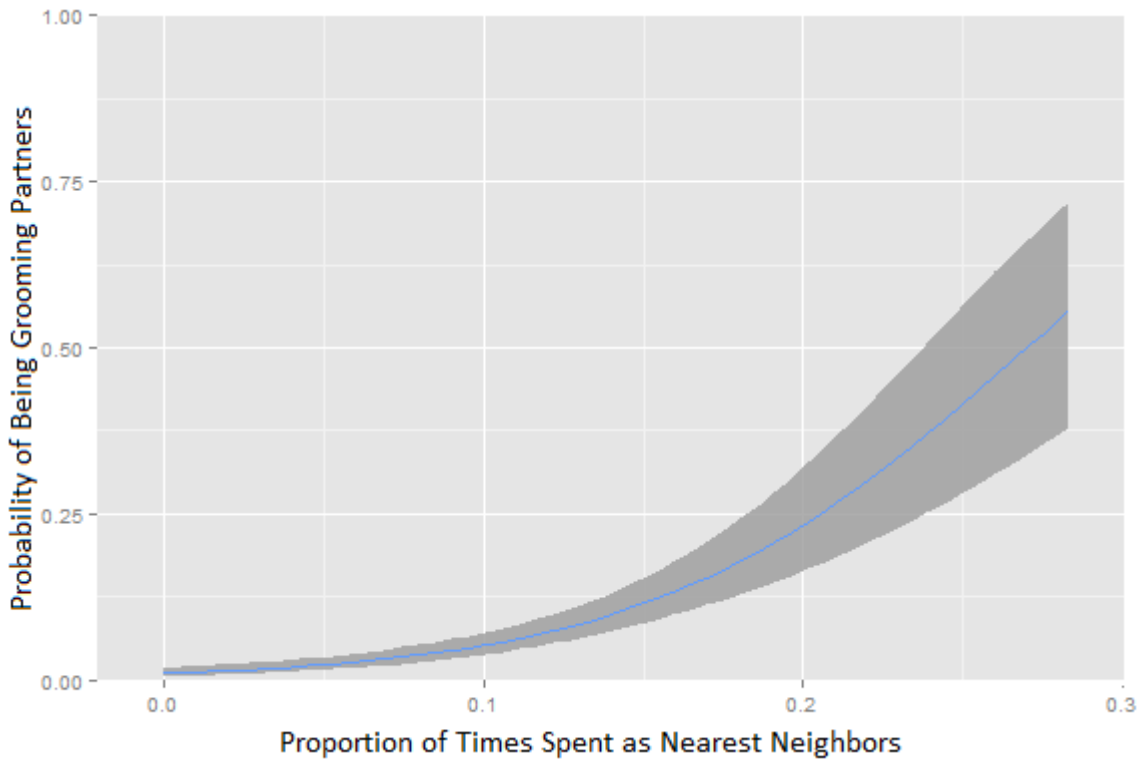


Figure 3.10 Fitted (line with 95% confidence interval) values for model predicting probability of being a grooming partners based on time spent as a nearest neighbor. Predicted probability values are converted from linear log-odds values.

3.6.7 Grooming Clique Size

Fitting a linear model mixed effects model predicting clique size from cohort size showed no significant difference as cohort size increased (Table 3.9, Figure 3.10). This is as predicted since at both Amboseli and Samara in 2009 grooming cliques sizes were similar (Table 3.11).

Table 3.10 Estimated values of model predicting grooming clique size from cohort size. Animal identity nested within Year cross classified with Troop were entered as random effects to control for repeated measures.

	β	SE	<i>t</i>	P	95% CI	
CohortSize	0.05	0.058	0.86	0.395	-0.06368	0.16368
Intercept	6.054	0.921	6.572	<0.001	4.24884	7.85916

Table 3.11 Average clique size for individuals in each female cohort with associated range. Though grooming cohort size changed, grooming clique size remained relatively stable.

Cohort Size	Troop	Clique Size
15	09RBM	6.3
23	09RST	5.3
13	12RBM	6.3
21	12RST	7.4
8	14PT	6.5
11	14RBM	7.5
16	14RST	6.1
8	A	7.0
7	B	6.0
8	C	7.0

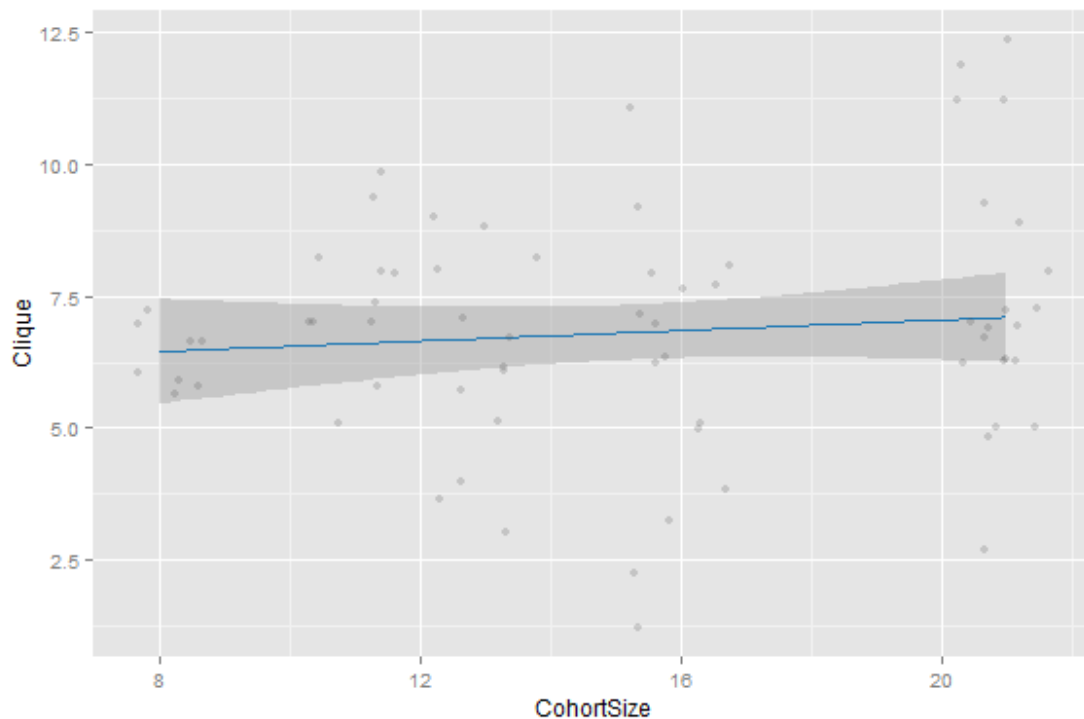


Figure 3.11 Fitted (line with 95% confidence interval) and observed (points) values of grooming clique size as a function of cohort size. Points are offset from actual cohort size values (jittered) to better show distribution.

3.7 Discussion

Grooming cohort size did predict trends consistent with the differences found between Amboseli and Samara in 2009. Dominance was not as strong a predictor of grooming rates in larger troops, smaller rank distance did not predict probability of engaging in grooming as well in larger troops as in smaller troops, and grooming was given to those most often in spatial proximity more in the smaller troops than in the larger troops. These results strongly support the hypothesis that grooming cohort size fundamentally changes the status of the grooming market in female vervet cohorts.

However, though I predicted that in smaller troops high ranked individuals would receive more grooming than they gave, rank did not predict grooming ratio in individuals in troops of any size. Also, even though behavioral synchrony of moving and resting was lower in larger troops, levels of grooming and foraging synchrony did not differ depending on troop size. The failure to reject the null hypotheses of no effect of group size in these instances suggests that there may be other, unmeasured variables that affect grooming patterns. One likely variable may be differences in the ecology between Amboseli and Samara. If grooming is being traded for other resources, then differences in defensibility of foraging sites should affect the biological market in the grooming cohorts.

The finding that rank distance does not predict inequality in grooming dyads while at the same time dominance does predict overall rates of grooming implies that rank distance does not factor into the relationship, the only thing that matters in a dyadic interaction is who is dominant. Seyfarth's model depended on the coalition value of the grooming partner; higher ranked females were assumed to be more valuable, so rank distance would reflect the relative value of each grooming partner. However, if instead of grooming, lower ranked females are trading for other resources such as tolerance at a foraging site, the only thing that matters within each dyad is whether the other female is capable of winning a contest between the two. The power differential is irrelevant because the dominant will always be able to defeat the subordinate. If trading for resources is what is occurring in these grooming interactions, and dominant animals do have a higher RHP, dominant females will still be more attractive grooming targets because they are attractive to more individuals as grooming partners; not because each individual prefers to interact with

individuals of increased positive rank difference but because dominant individuals will have more subordinates, all of whom are attracted to them.

To illustrate this point, imagine a simple hierarchy of three individuals A, B and C. Seyfarth's model would assume that the most dominant individual A is more attractive to the lowest ranking individual C than the individual B. However, consider when a defensible resource desirable to C is present, there are a number of possibilities: A monopolizes resource; A tolerates B but rejects C; A tolerates both B and C, but B rejects C; A rejects B but tolerates C; A does not care for the resource but B monopolizes and rejects C; A does not care for the resource B tolerates C; or both A and B don't care for the resource and C is able to access the resource freely. In this scenario, the difference between C's attraction toward A and B depends entirely on whether A will reject B, only then will C not have to depend on the tolerance of B, which minimizes the difference in attractiveness of A and B to individual C. Overall though, A will be an attractive grooming partner to twice as many individuals – both B and C – as individual B – only individual C. The difference in attractiveness of dominants as grooming partners is even less when the number of defensible resources increases proportionally to the cohort size. If there are two defensible resources and individual A and B each monopolize one, individual C only needs to gain access through one of those individuals so they are equally attractive as interaction partners.

If this line of reasoning is correct, it not only explains that rank distance does not predict inequality in grooming relationships, it also explains the phenomenon whereby smaller troops have a larger correlation between dominance rank and grooming received. In a hierarchy of three, the dominant individual is highly attractive as a grooming partners to

two others and the second most dominant individual to one other, a ratio of 2:1. In a hierarchy of four, the dominant individual is attractive to three and the second most dominant is highly attractive to two, a ratio of 3:2. If the number of individuals attracted to dominant individuals is what is driving the correlation between dominance and grooming received, then it would explain why the correlation only exists in smaller cohorts where the ratio differs significantly from 1.

A finding not fully explained by this model adaptation is that dominance has no effect on the amount of grooming given. Conceivably, if dominant females were trading other resources for grooming, they would have no need to reciprocate grooming. The biological markets hypothesis, though it does postulate that animals can trade one type of resource for another, does not necessitate that different types of resources must be traded. A likely explanation is that dominant females do trade certain amounts of grooming for grooming, but that they also have the option to trade other resources as well.

The result that across all cohort sizes females tend to groom similar rank individuals more may seem at odds with the argument that increased cohort size decreases the importance of dominance. However, there are two possible explanations for this phenomenon, one unrelated to the theory, and one predicted by the theory. The unrelated explanation is that, in vervets, the dominance rank of female offspring is directly related to the mother's dominance. Consequently the propensity to groom similarly ranked individuals could simply be due to kin preference. An alternate explanation is that even if subordinate females have no preference which dominant animal they groom, more dominant females will still prefer to groom up the hierarchy rather than down. Considering that the model assumptions of behavioral synchrony and partner competition still stand, this will result in

more dominant females grooming other, even more dominant females, and subordinate females grooming whoever is left, other subordinate females.

The decreased steepness of the dominance hierarchy as cohort size increases may also be explained by the decrease in the value of being dominant. The decreased steepness reflects that though the hierarchies are still transitive, the certainty that in any interaction dominant A will defeat subordinate B decreases. Since agonistic interactions can be costly in terms of suffering injury, if dominance status is not as valuable a commodity, A may simply not invest in maintaining strict despotism. Henzi et al. (2013) provided a further reason for the decreased value of dominance, arguing that in larger troops, subordinate individuals are able to avoid aggression while satisfying conditions required to avoid being the target of predation, i.e. remain within a tolerable distance of other troop members. More individuals occupy a larger area so more food sites are encompassed by the troop, further decreasing the value of being the most dominant individual.

Though I did not collect aggression rate data, the aggression rates found in the large Samara troops have been significantly lower than the rates found at in the smaller Amboseli troops (Henzi et al., 2013; Matlock, 2013). Though between 2009 and 2012 aggression rates also dropped significantly (attributed to decrease in ecological stress (Matlock, 2013)), the overall lower aggression rates may be a result of the decreased importance of dominance and consequent value in engaging in an aggressive encounter. More data on aggression rates in different ecological conditions with varying cohort sizes is required to tease apart the effects of ecological stress and group size.

Henzi et al. (2013) suggested that differences found in the social structure between the Samara and Amboseli troops were likely due to a renormalization of social interactions.

Their hypothesis as to what drove the renormalization is primarily the previously mentioned ability to avoid higher ranked individuals in a larger troop. However, this hypothesis does not predict their finding that dominance hierarchies were shallower in the larger Samara troops, which is explained by the decreased importance of dominance in larger groups.

CHAPTER 4: SOCIAL FACTORS AFFECTING INTRATROOP LOCATION OF VERVETS

4.1 Introduction

4.1.1 Predation Exposure

The hypothesis that animals receive anti-predation benefit is the primary explanation for why animals live in groups (Van Schaik, 1983). Hamilton (1971) developed the selfish herd theory that animals decrease predation risk by clustering with conspecifics. Predation exposure, or, in Hamilton's terms domain of danger (DoD), is defined as the area in which an animal is closer to a predator than any other individual. If an animal is surrounded by conspecifics, their DoD is much smaller than if the animal is solitary, or on the edge of a group. The animals are, in effect, able to hide behind each other. Animals should preferentially occupy areas of decreased predation exposure, and this should increase their probability of survival, and convey fitness benefits.

The selfish herd theory is just one mechanism by which individuals gain anti-predator benefit from living in groups. The dilution effect is the name of the hypothesis that each individual in a group shares the risk of being the target of predation and hence has a smaller chance of being eaten than a lone animal encountering a predator (Turner & Pitcher, 1986). Additional benefits are that groups are quicker to detect predators than are individuals, and that groups are able to defend against a predator either by confusion or mobbing. Quinn and Cresswell (2006) found that redshanks (*Tringa tetanus*) near the main body of the flock reacted to predators more quickly than stragglers. In a study on the predation abilities of three-spined stickleback (*Gasterosteus aculeatus*), Milinski (1977) discovered that the stickleback made fewer successful bites at swarming flees when biting at the center when compared to biting at stragglers and hypothesized the effect was due to confusion. An

extreme defensive behavior, mobbing a predator, can be seen in many avian species attempting to protect their young, e.g., American robins (*Turdus migratorius*) (Shedd, 1982), song birds and hummingbirds (Altmann, 1956), European blackbird (*Turdus merula*) (Curio, Ernst, & Vieth, 1978).

Of all the possible reasons for animals to live in groups, only the selfish herd theory predicts differential benefits for group members. According to the theory, those with a larger domain of danger will suffer higher rates of predation. Several empirical studies directly support the selfish herd theory. Using a flotilla of seal decoys, De Vos and O'Riain (2010) were able to manipulate the fake seals' intra-individual distances. They determined that the area of a seal decoy's DoD predicted its chance of being targeted by predatory sharks. Quinn and Cresswell (2006) found that redshanks, a wader bird that forages in large open swamps, were more likely to be targeted by their primary predator, sparrowhawks (*Accipiter nisus*), if they were a greater distance from their nearest neighbors than others in the flock. In a troop of Chacma baboons (*Papio ursinus*) Ron, Henzi, and Motro (1996) found that dominance rank was positively correlated with positions near conspecifics and negatively correlated with predation mortality. All three studies show that within groups, the degree of predation exposure is a contributor to individual survival.

The fitness differential between peripheral – more exposed – and central– less exposed – individuals, coupled with the limited number of central positions makes central positions a scarce resource. Predicted differential fitness naturally leads researchers to investigate determinants of spatial position within a troop.

Primatologists have developed numerous techniques to measure intra-troop spatial position (Table 4.1). A common method is to define central and peripheral individuals

according to their distance from the group center (Hall & Fedigan, 1997; Heesen, Macdonald, Ostner, & Schülke, 2014; Janson, 1990; Robinson, 1981; Sugiyama & Ohsawa, 1982; Teichroeb, White, & Chapman, 2015; Wada & Matsuzawa, 1986). Using distance to group centroid as a measure of centrality/periphery, dominants were shown to be more central in white-faced, brown, and wedge-capped capuchins (*Cebus capucinus*, *Cebus paella*, and *Cebus olivaceus*) (Hall & Fedigan, 1997; Janson, 1990; Robinson, 1981), Japanese macaques (*Macaca fuscata*) (Sugiyama & Ohsawa, 1982) and Assamese macaques (*Macaca assamensis*) (Heesen et al., 2014), though no effect was found in vervet monkeys (*Chlorocebus pygerythrus*) (Teichroeb et al., 2015). The breadth and consistency of the result, despite a variety of data collection methods, suggests that distance from group centroid is a measure sensitive to primate troop socio-spatial structure. However, distance from group center is not an ecologically relevant measure. In many primate groups, foliage obstructs an individual's ability to monitor the location of every other individual in the troop and, in order to position themselves in relation to the center of the group, members must be able to determine and maintain knowledge of the centroid. Both of these requirements offer significant challenges to any animal's mental abilities. Distance from group centroid may indirectly measure predation exposure, but a more direct, theoretically and ecologically relevant, measure is desirable.

A stronger, alternative to measuring distance from the group center is to directly measure Hamilton's proposed DoD. An animal's DoD is a polygon with edges equidistant between the focal animal and its nearest neighbors in all directions (Figure 4.1). The result is that if a predator is in an individual's polygon, that individual is closer to the predator than any other individual in the troop. However, in order to measure the DoD it is necessary to

record the distance and direction from the focal animal to each individual near enough to affect the DoD. It is nearly impossible for researchers to instantaneously determine and record all the necessary variables to measure an individual's domain of danger. Busse (1983) attempted to collect instantaneous data on DoD in a troop of chacma baboons by estimating the area from data collected on the two individuals who defined the largest area of the polygon of any two neighbors (Figure 4.2). Busse's estimation of DoD is the best attempt to date at developing an ecologically relevant predation exposure measurement.

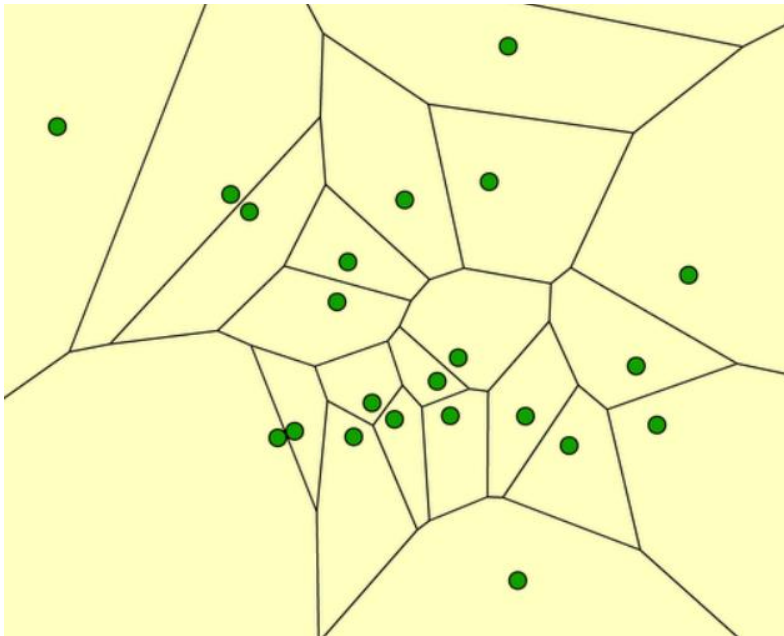


Figure 4.1 Example domains of danger for a group of animals. The sides of each polygon are equidistance from the two nearest points.

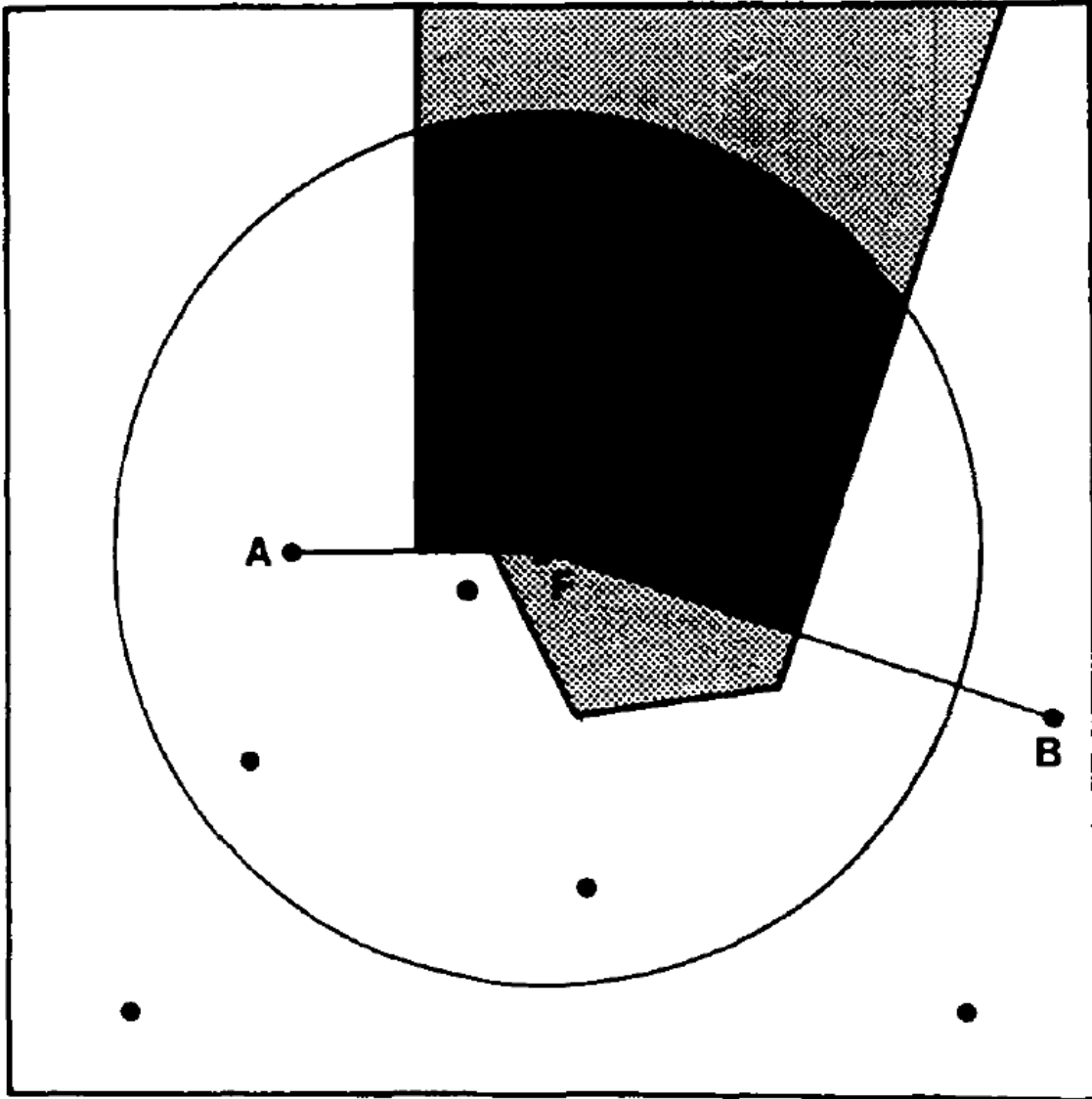


Figure 4.2 Estimation of domain of danger from Busse (1983). Shaded area represents actual domain of danger defined by Hamilton. Black area represents estimated domain of danger using two neighbors which result in largest area calculated. Circle represents arbitrary distance of 50m.

An alternate method to measure domain of danger, often used in conjunction with other predation exposure measures, is to record the distance to nearest neighbor, or the number of neighbors within an arbitrary distance (Busse, 1983; Collins, 1984; Cowlshaw, 1999; Quinn & Cresswell, 2006; Robinson, 1981; Ron et al., 1996). Collins (1984) found a positive correlation between dominance and clustering in female yellow baboons (*Papio cynocephalus*) and Busse (1983) and Ron et al. (1996) each found a correlation between number of nearest neighbors and dominance rank in chacma baboons (*Papio ursinus*), but Cowlshaw (1999) found no correlation. Other studies have found a positive correlations between distance to nearest neighbor and spatial centrality, and a decrease in predator vigilance (Robinson, 1981), or as a predictor of predation (Quinn & Cresswell, 2006). See Table 4.2 for a complete overview of studies investigating predation exposure and a comparison of their methods.

Table 4.1 References, methods and results for all papers dealing with factors predicting predation exposure.

Reference	Species	Methods	Results
Heesen, Macdonald, Ostner, & Schülke, 2014	Assamese Macaque (Macaca assamensis)	GPS group scans used to measure distance from group center	Both Male and Female Dominants more central, infants and juveniles more central than adults
Robinson, 1981	Wedge crested capuchin monkeys (Cebus olivaceus)	Cross section walk through of troop noting distance from center and front	Dominant adults were spatially central. Animals tolerated by dominant female were spatially central, no effect by dominant male's tolerance
Busse, 1984	Chacma Baboon (Papio ursinus)	Calculated domain of danger by measuring the angle of the two near neighbors that would result in the largest domain of danger at 50m	No dominance effect for males, dominance effect for females, dominant individuals were less exposed to predation, except when each troop were correlated separately
Collins, 1984	Yellow Baboon (Papio cynocephalus)	Instantaneous scan classified as front, side, reare, or in a cluster	Dominant females were more likely to be in a cluster than sub-dominants, no effect within males.
Teichroeb, White, & Chapman, 2015	Vervet (Chlorocebus pygerythrus)	Plotted each individuals position relative to the troop using a clock orientation and distance from group center	Males were more peripheral than females. Dominant individuals were more often in the front section while moving. No effect when not moving
C. L. Hall & Fedigan, 1997	White Faced Capuchin (Cebus capucinus)	Plotted each individuals position relative to the troop in one of 7 predetermined position types	Dominants were more central, but not more frontal. During dry seasons dominants were in front of the center of the group, but not fully in front, no effect during wet season.
Janson, 1990	Brown Capuchins (Cebus paella)	Plotted each individuals position relative to the troop in one of 5 predetermined position types	Dominant male and female were more front/front center
K. R. L. Hall & DeVore, 1965	Chacma and olive baboons (Papio ursinus, P. anubis)	Unspecified	Mothers with infants near center, dominant males central except when threat perceived they moved towards the front

Washburn & DeVore, 1961	Baboon (species unspecified)	Unspecified	Mothers with infants near center, dominant males central, lower ranking males peripheral, when threat perceived females retreat leaving males between them and threat
Sugiyama & Ohsawa, 1982	Japanese Monkey (<i>Macaca fuscata</i>)	Measured female distance from center of the group	"Almost Coincides" that dominant female have a more central score
Yamada, 1966	Japanese Monkey (<i>Macaca fuscata</i>)	Scanned and classified individuals as peripheral or central	Dominant individuals more likely central
Wada & Matsuzawa, 1986	Japanese Monkey (<i>Macaca fuscata</i>)	Mapped troop from position across a valley	Females and infants more central than peripheral, males randomly distributed
Cowlshaw, 1999	Chacma Baboon (<i>Papio ursinus</i>)	Measured distance to nearest neighbor	No significance for dominance, though females were more aggregated when they had an infant
Rasmussen, D. R. & M. Farrington, 1994	Stumptail Macaques (<i>Macaca arctoides</i>)	Created an index to measure how much individual movements differed from average group movements	Dominant animals differed less from average group movements than subordinates
Ron, Henzi & Motro, 1996	Chacma Baboon (<i>Papio ursinus</i>)	Measured number of neighbors less than five meters distant	Dominant females had more near neighbors and lower predation rates

4.1.2 Foraging Pressure

In spite of the significant anti-predator benefits that potentially accrue with central positions, such positions may impose foraging costs because peripheral individuals may acquire and deplete food resources before central individuals encounter them (Hirsch, 2007; Krause, 1994). Individuals on the edge, particularly the front moving edge, of a group first encounter food sources and therefore forage most efficiently. If food supply results in competition, the optimal foraging positions are the positions close to where new food items are discovered, that is, the edge in stationary troops and the front in moving troops (Hirsch, 2007). If food supply is so abundant that every individual is able to access food regardless of position within the troop then foraging pressure is not likely to determine spatial position.

4.1.3 Benefits of Dominance

After age/sex class, studies most often investigate the effect of dominance on the spatial structure of primate troops. Dominance is measured by rank-ordering individuals with respect to their ability to win aggressive contests. Testing for effect of dominance is a phenomenon not only prevalent in primatologists concerned with spatial structure, but also in primatologists investigating other costs and benefits associated with social status. In a large meta-analysis of 94 published primate studies investigating effect of dominance on fitness, Majolo, Lehmann, de Bortoli Vizioli, and Schino (2012) tested whether dominance affected female fecundity, feeding success and survivability of infants through their first years and male mating success and fecundity. Overall, the results showed that while there was no feeding benefit, dominance improved infant survivability for females, mating success for males, and fecundity for both males and females. In an older meta-analysis of 32

published studies on male primate reproductive success, Cowlshaw and Dunbar (1991) also showed that, despite variability, dominance did positively affect male primates' ability to reproduce.

The benefits of dominance extend to within-troop spatial position. Several studies have shown that dominant animals tend to be more spatially central, or less exposed to predators (Busse, 1983; Hall & Fedigan, 1997; Heesen et al., 2014; Janson, 1990; Rasmussen & Farrington, 1994; Robinson, 1981; Ron et al., 1996; Yamada, 1966). When foraging, dominants also take positions near the front, which maximizes their foraging potential (Hall & Fedigan, 1997; Janson, 1990; Teichroeb et al., 2015).

4.1.4 Benefits of Social Integration

Aggression is just one among many measurable interaction types (Barrett, Henzi, & Lusseau, 2012; Hinde, 1976). Though there are few studies that have examined how individual differences in sociality or prosocial behavior benefit individuals, what little has been done shows that, like dominance, high levels of sociality can be valuable for individuals. In a review of reproductive success across many mammalian species, Silk (2007) showed that offspring survival was directly related to the number of animals participating in infant caretaking. In baboons, females with strong affiliations both live longer (Silk et al., 2010) and produce more offspring who survive to reproductive age (Silk, 2009; Silk, Alberts, & Altmann, 2003). Vervets in the population reported in this study suffered less cold stress during winter nights if they had more affiliative bonds (McFarland et al., 2015).

In spite of evidence that sociality benefits primates, little work has been done to determine whether individual differences in sociality affects within troop spatial position. Seyfarth and Cheney (2012) postulated a set of questions about the correlates of high

sociability. Among questions already addressed in social primate literature, they asked whether increased sociability leads to decreased predation exposure. They predict that, if social animals spend more time in close proximity with other group members, their domain of danger will decrease.

As yet, only a limited number of studies have investigated the effect of social bonds on anti-predation behavior. Crested macaques (*Macaca nigra*) do not react any faster, but show longer reactions to playback predator warnings given by a closely-bonded individual than other troop members (Micheletta et al., 2012). The researchers suggested that all individuals react equally quickly to the stimulus because evasive action might be necessary, but closely bonded individuals react for longer because individuals often coordinate to mob predators: an activity which requires significant levels of cooperation. The only empirical study to investigate the effect of social affinity on spatial centrality is Robinson's (1981) study on wedge-capped capuchin monkeys (*Cebus olivaceus*). He tested whether individuals that were tolerated by the dominant male and female were more central. Since the dominant male and female had already been determined to be spatially central, he predicted that those tolerated by each of those individuals would be more spatially central regardless of their dominance rank. Though the dominant male's tolerance had no effect, those tolerated by the dominant female were closer to the center of the troop than those to which she directed aggression. This suggests that individuals may be able to exchange grooming for tolerance with influential troop members, thereby gaining access to scarce resources (see Chapter 3 for a more in-depth discussion on trading grooming for other resources).

4.1.5 Predictions

This population of vervet monkeys is characterized by high predation and large mean group size (Pasternak et al. 2013; Van de Ven et al. 2013; Ducheminsky et al. 2014). In these groups, the presence of strong, linear dominance hierarchies does not underpin social preference (Henzi et al. 2013; Matlock 2013, Chapter 3 of this thesis) and it is likely that the size and dispersion of these groups attenuates the influence of rank as a structuring force (Henzi and Barrett 2007) and instead promotes the benefits of broad social integration (McFarland et al. 2015). Here, I use spatially explicit data to test the prediction (i) that group members who give and receive more grooming, but not those that are high ranking, have smaller domains of danger and spend less time vigilant, which is the proximate index for predation risk (Robinson 1981). I also consider the possibility that safety seeking involves a trade-off against foraging efficiency (Krause 1994; Bumann et al. 1997) by drawing on recent evidence to suggest that high-ranking vervets accept increased exposure in order to forage more efficiently, which they do by leading the troop (Teichroeb et al. 2015. See also Janson 1990 for capuchin monkeys). Hence, I also test whether (ii) if not central, dominant animals are more likely to be in the group's vanguard.

4.2 Methods

4.2.1 Predation Exposure

During each troop-wide sweep (data collection described in Chapter 2), the troops often moved a significant distance ($RBM_{\text{Mean}}=36.8\pm 21.5\text{m}$; $PT_{\text{Mean}}=18.1\pm 12.6\text{m}$). To account for this in the mapping of each individual's position relative to other animals in each sweep, I utilized two methods: interpolation and group movement average extrapolation, to correct for time and individual movement differences to create a 'snapshot' of all individual

positions. Interpolation predicts the position of an individual at point “B” in time by its position at times “A” and “C” and the time distance from “A” to “B” and “B” to “C” (Figure 4.3). The assumption is that, if a small enough time has elapsed, individuals will have moved in a relatively straight line at a constant speed. For time intervals less than 5 minutes, this is a valid assumption with a small margin of error (Dostie, 2014). I therefore interpolated all individual’s position to the same point in time. Instead of using the median time in each snapshot, to maximize the number of interpolated individuals, I defined the snapshot time as that which produced the greatest number of interpolated points. Compared to using median snapshot time, optimized snapshot time increased the number of interpolated points for RBM from 9.7 ± 4.8 to 11.7 ± 4.7 and for PT from 7.3 ± 2.7 to 8.3 ± 2.5 .

Though interpolation uses stronger predictive methods than group movement average extrapolation, it can only be used when an individual is plotted on both temporal sides of the snapshot point. Non-interpolated individuals’ position was inferred using group movement average extrapolation by determining group movement velocity average and adding average movement to each individual’s point. I calculated group movement velocity (V_{Aver}) from the average movement of all individuals sampled more than once, by taking the sum of all those individuals’ movement (M_i) and dividing by the sum of all individuals’ time elapsed (T_i) (Figure 4.4). Extrapolated points were calculated from the original point P_{Origin} by multiplying the group movement velocity by the time to the optimal sweep time (Figure 4.5).

$$V_{Aver} = \frac{\sum M_i}{\sum T_i} \quad i = (1, 2, \dots, n)$$

$$P_{Extrap} = P_{Origin} + V_{Aver} * T_{Diff}$$

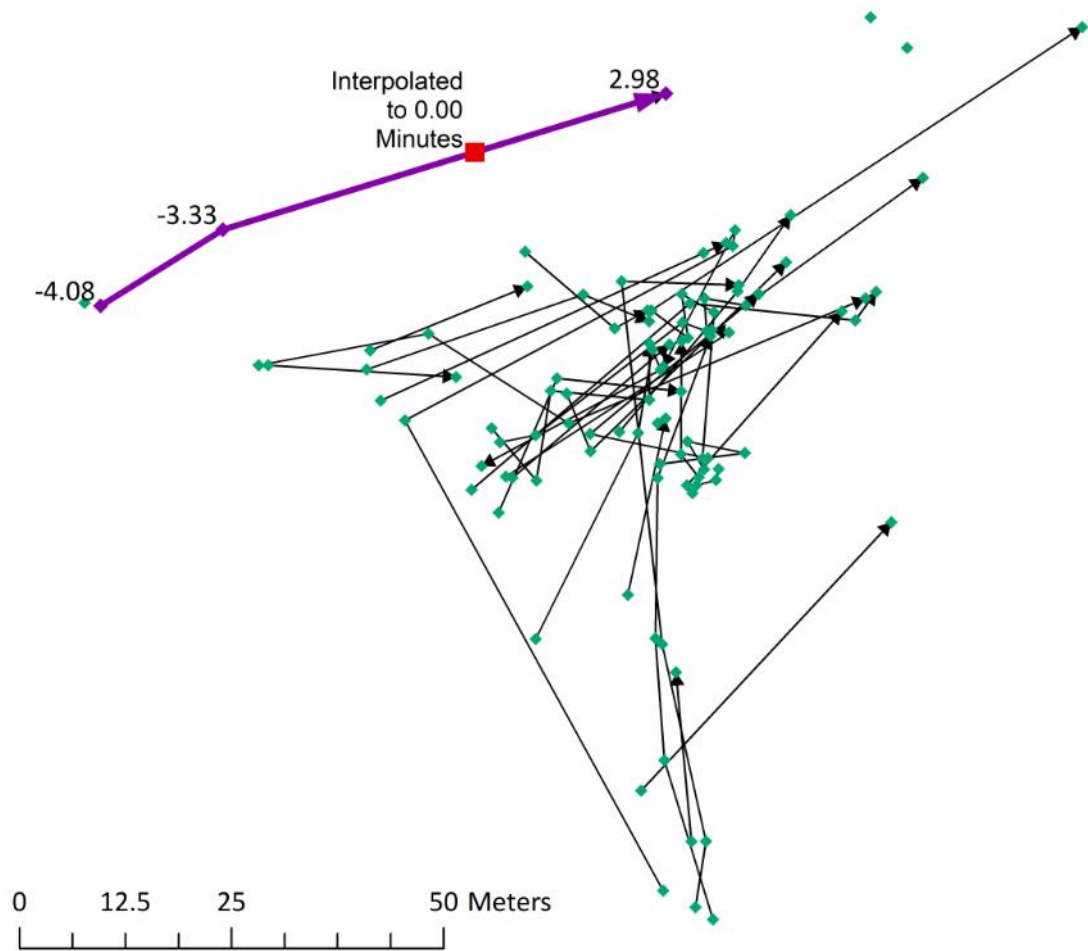


Figure 4.3 The square is the interpolated position of an individual at optimized sweep time. The point is positioned between the two points recorded before and after the optimized time. Large arrow represents movement of one interpolated individual, small arrows represent the movement of the remainder of the troop.

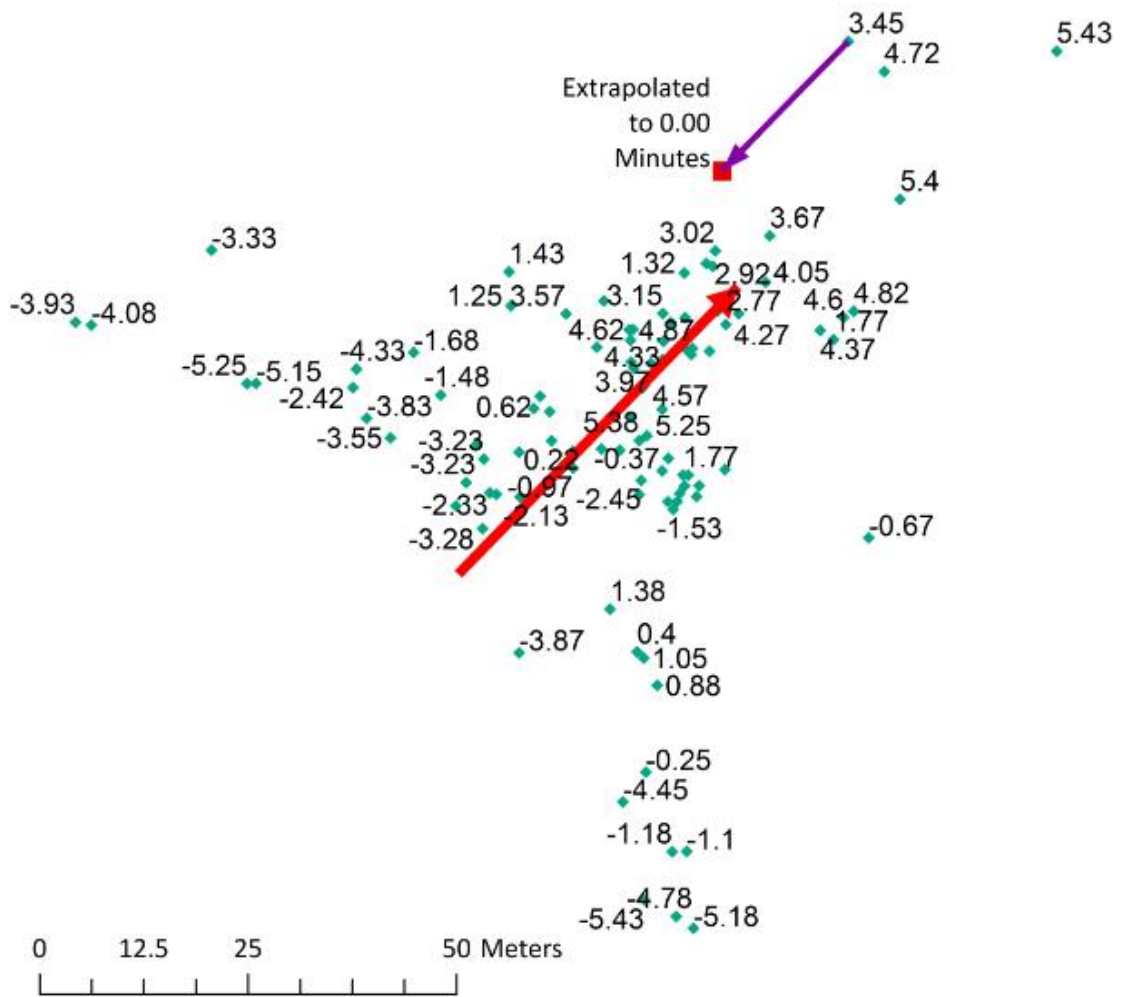


Figure 4.5 Extrapolated position of individual (square) at optimized sweep time. Position was determined by adding or subtracting the average group distance moved during the interval, in this case during the 3.45 minutes, to the original point.

To ascertain whether estimated position was more accurate using group movement extrapolation than the original point, I used extrapolation to predict positions of individuals with multiple points from one point to the point in time their second position was measured. Group movement velocities were calculated from average movement vectors of all individuals with multiple points measured excluding the individual whose position was

being predicted. For the relevant time interval, five minutes or less, group movement average extrapolation reduced error from an average of $20.2 \pm 17.0\text{m}$ to $19.2 \pm 16.3\text{m}$ for RBM ($t=4.41$, $p<.01$) and 12.6 ± 12.3 to 11.9 ± 12.1 for PT ($t=1.51$, $p>.05$).

To measure the domain of danger, I created Voronoi tessellations around each individual. A Voronoi tessellation is a polygon whose boundary is defined as being equidistant from the nearest two points. If a predator is in the Voronoi tessellation of an individual, the predator is nearer to, and assumed to be more likely to target that individual than any other animal in the troop. I used ArcGIS 10.2 software (ESRI, 2014) to create Voronoi tessellations for each sweep.

One problem with this domain of danger measurement is that for the individuals at the edge of the troop the DoD expand infinitely into space. To deal with this, a limit must be placed on the edge of an animal's domain of danger, and one solution is to use the distance at which predator target individuals (James, Bennett, & Krause, 2004). In previous work on predator alarm calls with this population, vervets first reacted to predators at a distance of 15m. Using 15m as a proxy for distance at which predators target the monkeys, I created a domain boundary at a minimum distance of 15m from every individual in the troop. I used the area of each individual's polygon resulting from the intersection of the Voronoi tessellations and "bubbly" buffer expressed in m^2 as a measure of predation exposure (Figure 4.6).

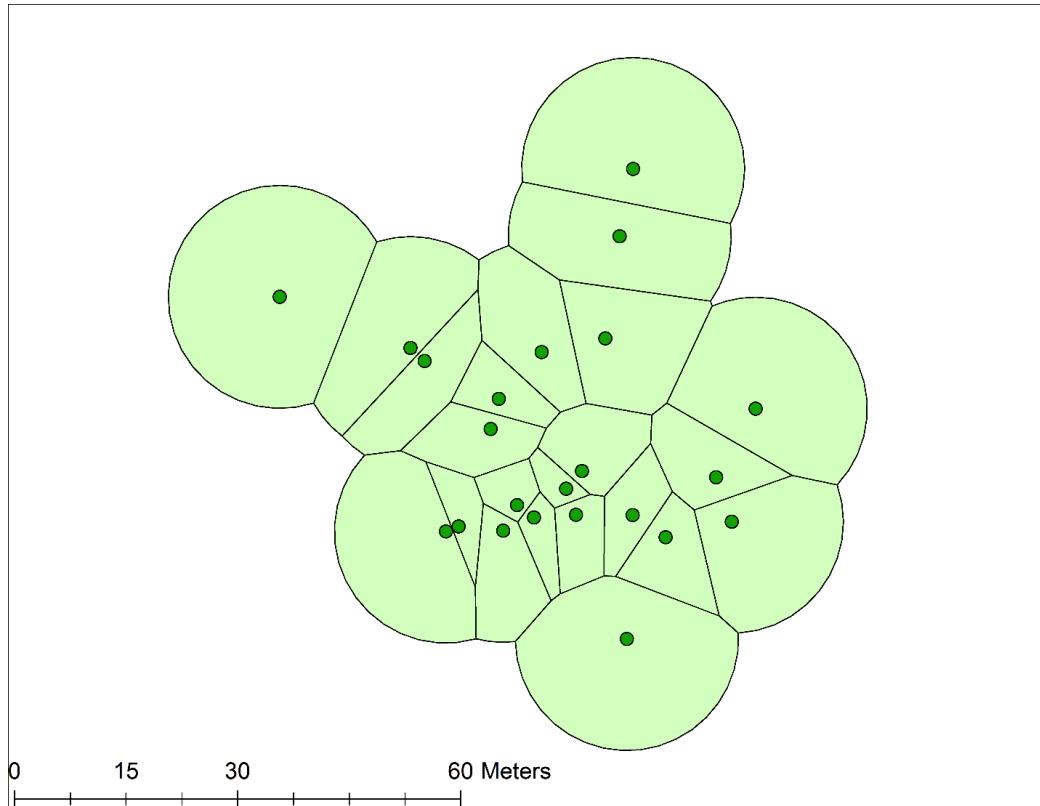


Figure 4.6 “Bubbly” buffer around voronoi tessellations provide area for limited domain of danger. The lines are equidistant from the nearest two points and the buffer around the troop is at least 15m from any individual’s point.

4.2.2 Front Position

In order to calculate distance from the front of the troop, I rotated each sweep on an XY plane so that the average direction of travel was down the y- axis. Distance from the front was calculated as distance from the individual with the highest Y value. Measures were then standardized to vary from 0, the frontal individual, to 1, the rear most individual (Figure 4.7).

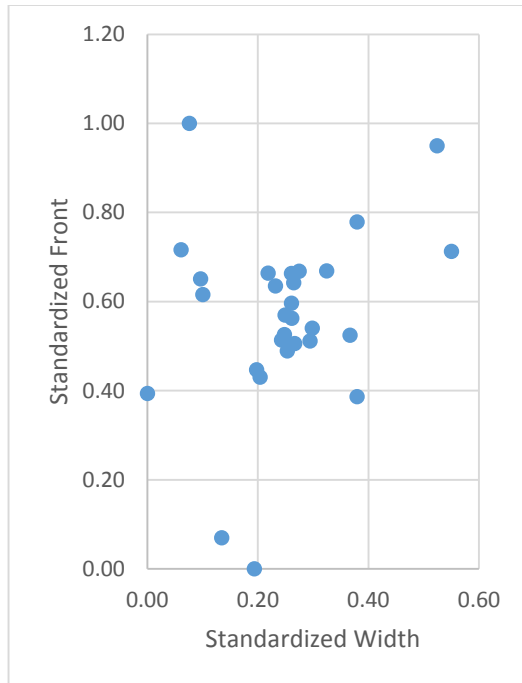


Figure 4.7 Rotated troop standardized distance to the front. Width is standardized by dividing distance from the left by the distance from the front to rear.

4.2.3 Activity

I used instantaneous scan samples (J. Altmann 1974), taken every 30 minutes, to record the activity of visible subjects ($N_{PT}=7584$ records, $N_{RBM}=9446$ records). I identified four behavioural states (foraging, moving, resting and grooming) as well as vigilance, recorded when an animal was visually scanning the environment beyond its immediate surroundings (Baldellou & Henzi, 1992). These data allowed me to estimate the proportion of time spent in each of these states by each subject over the study period. A subset, comprising those scans taken just prior to each sweep, was used to establish general activity schedules at the time of the sweep.

4.2.4 Statistical Analysis

I entered standardised dominance rank, grooming in-strength centrality and grooming out-strength centrality as fixed effects in each of two linear mixed models to assess the effects of sociability and dominance on (i) the extent of exposure and (ii) the probability of being in the vanguard of the troop. Troop identity and subject sex were entered as control variables. Subject identity was entered as a random effect. Following Barr, Levy, Scheepers, and Tily (2013), I specified random slopes for as many predictor variables as still allowed the model to converge.

In the absence of relevant data at the level of the sweep, I used single linear models to regress (a) mean exposure and (b) mean distance from the front of the group on foraging and vigilance aggregated across the study period. Mean exposure and mean distance from the front for each adult across the study period were entered as the criterion variables and the proportions of time that it spent foraging and vigilant as predictor variables, after determining that foraging and vigilance were not collinear ($r=-0.127$, $N=42$, $P=0.42$). I entered Troop and Sex as control variables.

As I had no a priori predictions for interactions, I ran each model with main effects and then, after testing whether they differed significantly from the control models, using the Akaike information criterion (AIC) and likelihood ratio tests to do so, I did the same to determine whether the models were improved by the addition of interaction terms. I evaluated the distributions of the response variables and the residuals of final models, and compared obtained standard errors to robust standard errors (King & Roberts, 2014). The models I report are those that best met the assumptions of normal error structure and were run using STATA 14 statistical software (StataCorp, 2015). I used Cohen's f^2 as a measure of

relative effect size (Selya, Rose, Dierker, Hedeker, & Mermelstein, 2012). Alpha was set at 0.05.

4.3 Results

4.3.1 Social influences on exposure

I ran the model with random slopes on both in-and out-strength centrality. While the main-effects model differed from the control model ($\Delta\text{AIC}: -10.12$, $X^2_3 = 16.12$, $P=0.001$), the two-way interaction model made no additional contribution ($\Delta\text{AIC}: 4.69$, $X^2_3 = 1.31$, $P = 0.727$). The whole model was significant (Log likelihood = -15702.103; Wald $X^2_5 = 40.51$; $P = 0.0001$) and differed from the equivalent linear model without random effects ($X^2_3 = 15.48$, $P = 0.017$). Parameter estimates for fixed effects (Table 4.2a) indicate significant negative relationships between degree of Exposure and both Grooming out-strength ($f^2 = 0.00033$) and Grooming in-strength centrality ($f^2 = 0.00011$. Figure 4.8), as well as for Troop identity. Examination of the pattern of ongoing activity indicates that these results were not a consequence of conducting the sweeps when the modal activity was grooming (Figure 4.9). While the overall distribution differed from expectation ($X^2_3 = 347.37$, $P = 0.000$), only grooming had an observed value that was lower than expected.

Table 4.2 Results from the linear mixed model analysis to test the fixed effects of dominance rank, grooming out-strength and grooming in-strength on exposure to risk and distance from the front of the troop. Animal sex and the troops to which they belonged were entered as control variables. Animal identity was entered as a random effect to control for repeated measures.

	β	SE	Z	P	95% CI	
a. Exposure to risk						
Sex (Ref: Female)	5.097	15.853	0.320	0.748	-25.974	36.167
Troop (Ref: PT)	-31.833	16.162	-1.970	0.049	-63.510	-0.157
Rank	-20.418	30.567	-0.670	0.504	-80.328	39.492
Grooming out-strength	-254.865	78.307	-3.250	0.001	-408.343	-101.387
Grooming in-strength	-141.073	71.987	-1.960	0.050	-282.165	0.018
Intercept	301.493	26.633	11.320	0.000	249.294	353.693
b. Distance from the front of the troop						
Sex (Ref: Female)	0.046	0.025	1.83	0.067	-0.003	0.095
Troop (Ref: PT)	-0.013	0.016	-0.82	0.411	-0.045	0.018
Rank	0.002	0.063	0.03	0.978	-0.121	0.124
Grooming out-strength	0	0.005	0.07	0.944	-0.01	0.011
Grooming in-strength	0.007	0.007	1.02	0.310	-0.007	0.021
Intercept	0.44	0.036	12.34	0.000	0.37	0.51

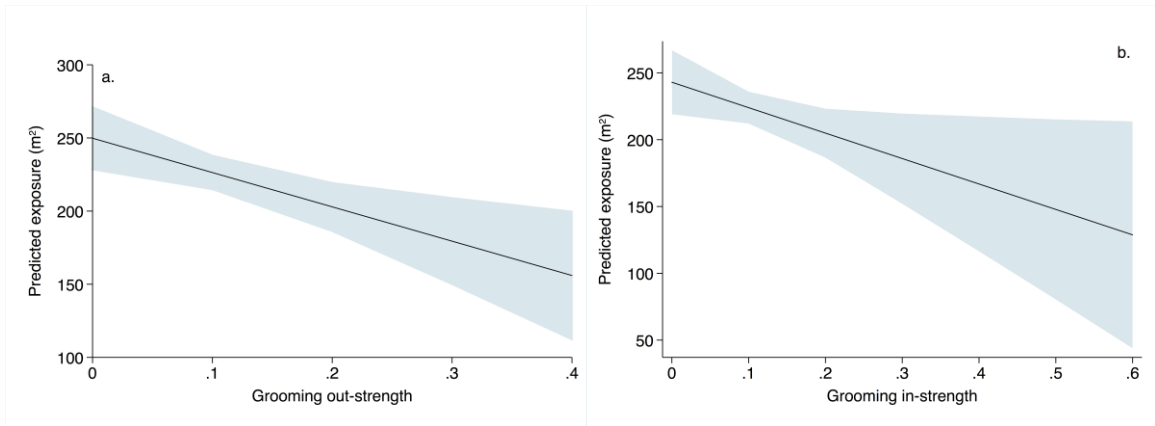


Figure 4.8 Predictive margins with 95% CIs for the relationship between exposure to risk and (a) grooming out-strength and (b) grooming in-strength for adult vervet monkeys.

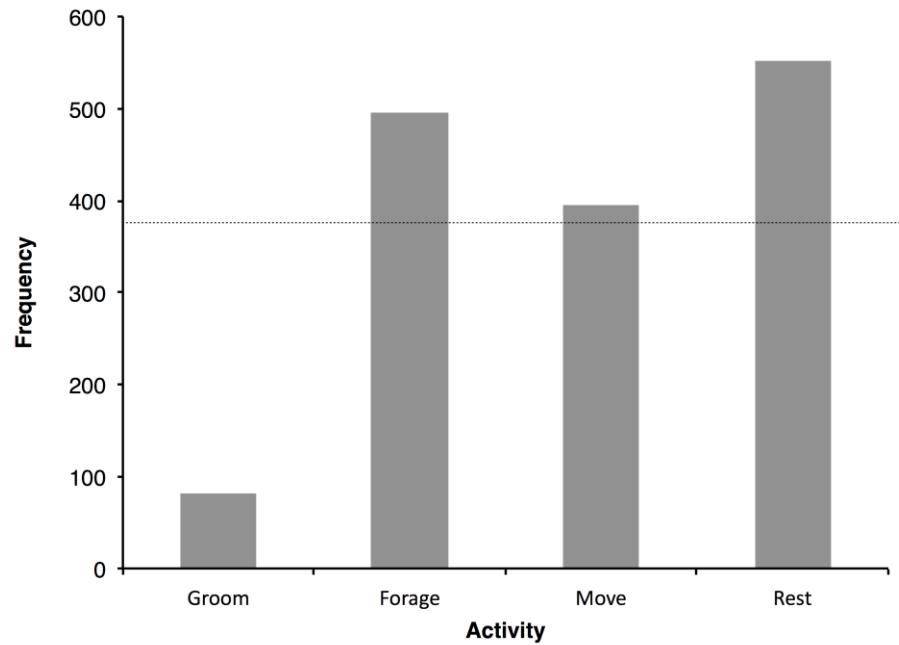


Figure 4.9 Activity at the times when animal spatial location was recorded. Activity budget estimates for all adult animals come from scan samples taken every 30 minutes. Data presented here come from scans of individual activity ($N_{\text{total}}=1524$; $N_{\text{groom}}=81$; $N_{\text{forage}}=496$; $N_{\text{move}}=396$; $N_{\text{rest}}=551$) recorded during the scan sample closest to the time at which each spatial sweep was conducted. Dashed line indicates frequencies expected from a uniform distribution.

4.3.2 Social influences on distance from the front

I standardised distance from the front of the troop by expressing it as a proportion of the distance between the front and back animals. I then ran the model with dominance and the social network measures as fixed effects, together with a random slope on out-strength centrality. I found no support for the prediction that dominant animals were closer to the front of the group (Table 4.2b). The model was not significant (Wald $X^2_5 = 6.68$, $P=0.245$)

and differed from neither the control ($\Delta\text{AIC}: 4.16, X^2_3 = 2.7, P = 0.441$), nor the null model ($\Delta\text{AIC}: 2.16, X^2_5 = 7.83, P=0.166$).

4.3.3 The effect of mean exposure on foraging and vigilance

The results of the regression are reported in Table 4.3a. While the main-effects model was significant ($F_{4,37} = 6.084, P = 0.0007, \text{Adj. } R^2 = 0.33$) and differed from the control model ($\Delta\text{AIC}: -6.28, X^2_2 = 10.27, P = 0.006$), the interaction model made no additional contribution ($\Delta\text{AIC}: +1.92, X^2_1 = 0.07, P = 0.79$). Parameter estimates indicate that while vigilance increased significantly with increasing exposure ($f^2 = 0.151$), foraging effort decreased ($f^2 = 0.116$).

Table 4.3 Results from the linear model to test the consequences of (a) the extent of mean exposure to risk and (b) mean distance from the front of the group on vigilance and foraging effort. Animal sex and the troops to which they belonged were entered as control variables.

	β	SE	t	P	95% CI	
a. Exposure to risk						
Sex (Ref: Female)	18.941	13.996	1.35	0.184	-9.4187	47.301
Troop (Ref: PT)	-0.798	12.33	-0.06	0.949	-25.781	24.184
Vigilance	621.106	262.7	2.36	0.023	88.824	1153.389
Foraging	-245.331	118.344	-2.07	0.045	-485.119	-5.542
Intercept	244.509	36.702	6.66	0.0001	170.143	318.875
b. Distance from front						
Sex (Ref: Female)	0.046	0.02	2.32	0.026	0.005	0.087
Troop (Ref: PT)	-0.026	0.017	-1.48	0.146	-0.062	0.009
Vigilance	-0.382	0.379	-1.01	0.321	-1.151	0.386
Foraging	0.023	0.171	0.13	0.894	-0.323	0.369
Intercept	0.488	0.053	9.19	0.0001	0.381	0.595

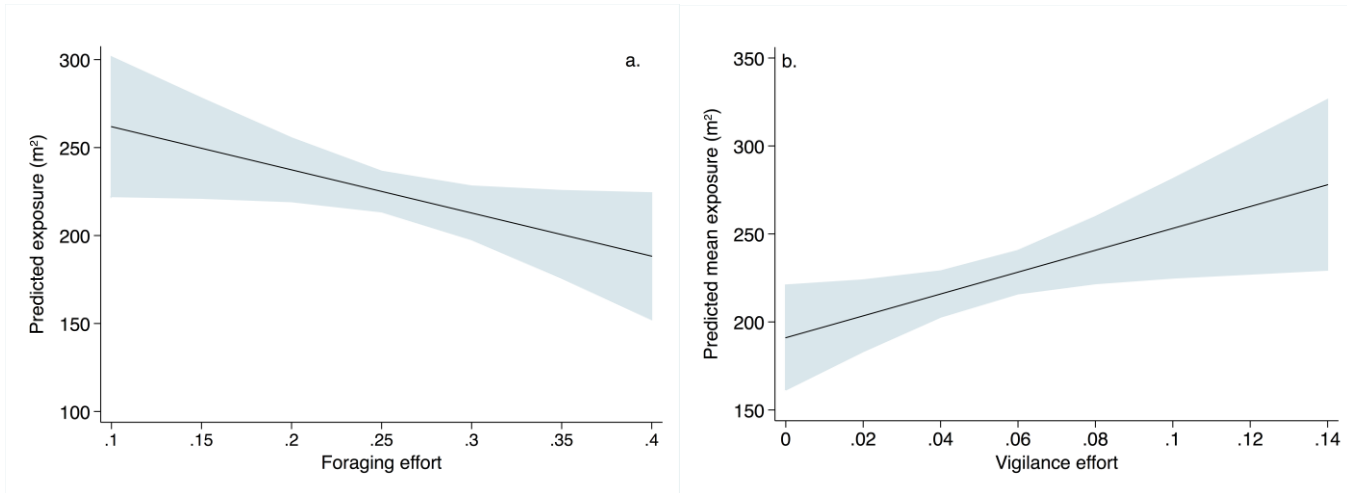


Figure 4.10 Predictive margins with 95% CIs for the relationship between mean exposure to risk and (a) foraging effort and (b) vigilance for adult vervet monkeys.

4.3.4 The effect of mean distance from the front on foraging and vigilance

The results of the regression are reported in Table 4.3b. The main-effects model was not significant ($F_{4,37} = 1.67$, $P = 0.177$. Adj. $R^2 = 0.06$). Parameter estimates confirm the difference between the sexes but reveal no significant effects for either vigilance ($f^2 = 0.151$) or foraging effort ($f^2 = 0.002$).

4.4 Discussion

The results support the prediction that increased social integration carries a beneficial reduction in exposure to risk in adult vervet monkeys. More particularly, animals that are sociable - i.e. invest in grooming a wide array of partners, or who are extensively groomed by others - have smaller domains of danger and, at least in the aggregate, spend less time vigilant and more time foraging. These twin benefits indicate that there has been no simple trade-off between safety and dominance-controlled access to resources for lower-ranking

animals (Krause, 1994). This may well stem from the fact that the spread of large groups in a mosaic habitat makes it easier, on the whole, to avoid agonistic contact (Hemelrijk, 2000; Henzi & Barrett, 2007). There is support for this in the earlier finding that, while the rate of food-related aggression in the large groups does not differ from that recorded in smaller groups, the overall rate of aggression is much lower (Henzi et al. 2013). That is, while animals may clash at concentrated food sources, they are less likely to do so under other circumstances. In the absence of the structuring influence of dominance rank, therefore, lower exposure to predation risk appears to be an unalloyed good for those that can engineer it.

Our relatively large, dispersed groups may also explain why higher ranking animals were not more likely to be found at the front of their groups. In these diffuse groups, as our results indicate, the 'front' may be an inadequate index of foraging potential and predation risk. That is, animals do not forage in a way (i.e., in some form of 'file' formation) that would result in there being a leading edge of animals that encounters new foraging patches ahead of all other animals, and would present a foraging advantage. Rather, in the case of such diffuse groups, a measure such as access to unimpeded foraging swathes, as suggested by Altmann (S. A. Altmann, 1974), is probably more appropriate, i.e., where animals attempt merely to forage along a trajectory that reduces the likelihood that they will encounter other animals in their path. The domains of danger I used in this study are likely to be a better index of risk from the animal's perspective.

Methodologically, my results point to the utility of using spatially explicit information in the analysis of social dynamics (Henzi and Barrett 2007). Until recently, for example, the use of qualitative or abstracted estimates of position to identify individuals at the 'edges'

and 'centres' of groups, has necessarily reflected procedural constraints that then impose a human-centred analytical framework that may only incidentally capture what is relevant to the animal itself (see (Isbell et al. 1998)). As things stand, it is unclear whether my results differ from those observed elsewhere (Teichroeb et al. 2015) or other species (Heesen et al. 2014) because of differences in approach or whether they reflect the structuring effects of local environments and group size. Regardless of the outcome, converging on a common, realisable methodology will make it possible to interrogate such questions in productive and interesting ways.

Admittedly, the effect sizes in my study are small. This no doubt reflects the fact that my analysis is rather coarse-grained and I have not fully characterised the environment in terms of variation in risk. That is, there are areas where actual predator densities are higher, and areas where risk of predation is higher due to the specifics of habitat structure. It may also be the case that movements near territory boundaries and the increased likelihood of inter-group encounters have an effect on spatial positioning within the troop that differs from the response to predation risk. All of these factors are likely to account for some of the unexplained variance. At the same time, my positional data are relatively coarse-grained, which results in somewhat noisy analyses (although this is demonstrably and powerfully remediable (Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015), even if not always practical). My aim here, however, has been to demonstrate the overall utility of such an approach to studies of spatial structure, and it is clear that more fine-grained analyses will only help improve our understanding of how this emerges in real-time.

The absence of rank-dominated social structure also reveals three things of relevance to the current concern with social influences on fitness outcomes (Berghänel, Ostner,

Schröder, & Schülke, 2011; Silk et al., 2003). First, it provides evidence that the short-term benefits of smaller domains of danger are not the passive consequence of patterns of spatial segregation mediated by rank or kinship (Henzi and Barrett 2007), but are actively pursued by group members, with the effects persisting beyond the interaction itself. Here, given that an animal's popularity is necessarily determined by the extent to which others groom it, its advantages are a by-product of others' social effort, and consequently less effective. On the whole, then, it appears better for vervets to give than to receive.

Second, regardless of grooming direction, the benefits of spatial position accrue to those in both sexes with broad, rather than narrow, social ties. While much attention has been directed at the advantages of strong ties to a few associates (Silk, 2009), our results, both here and elsewhere (McFarland et al. 2015. See also Murphy et al. in prep., for baboons), suggest that there are good reasons for social animals also to sustain wider affiliations. Second, while most studies have emphasised the long-term fitness benefits of sociability (Archie, Tung, Clark, Altmann, & Alberts, 2014; Silk, 2009), our results, both here and elsewhere (McFarland et al. 2015), are beginning to identify the more immediate mechanisms by which patterns of social interaction come to generate fitness outcomes. Third and finally, assessing whether the tension between strong, ultimately competitive (Cheney et al. 2012) and weak, integrative ties is constant and inherent, or whether the relative value of each differs across time and/or populations and taxa, represent fruitful lines of enquiry, not only in terms of individual strategies but also with respect to the stability of groups. With respect to the latter, the dominant argument has been that group fission follows inevitably from the increased within-group competition associated with increasing troop size, with cleavage following time constraints on the ability of individuals to

sustain strategic alliances (see, for example, Dunbar 1997). My observation of the attenuation of rank effects, alongside evidence of the benefits of broad social integration suggests that the dynamics of group fission may be more interestingly nuanced than generally presented, at least in these larger vervet groups.

CHAPTER SIX: GENERAL DISCUSSION

6.1 Key Findings

In Chapter 3 I tested whether change in cohort size predict changes in grooming patterns that reflect differences between vervets observed at Amboseli and those observed at Samara in 2009. I found that, in general, the patterns did match Amboseli more in the smaller troops and less in the large troops. The large troops were more similar to the patterns found at Samara in 2009. In particular as female cohort sizes increase, dominance no longer has an effect on the distribution of grooming and dominance hierarchies are not at despotic. I hypothesized that as cohort sizes increase, the benefit received from dominance decreases so females devote less energy towards maintaining well defined positions in the hierarchy.

From this I predicted that dominance may not have an effect on intra-troop spatial position of females but that social integration as measured by high rates of grooming given or received would. Dominance had no effect in either of the troops, both popularity and social effort predicted predation exposure but not optimal forage placement. I also showed that individuals with less exposure on the aggregate tended to spend less time vigilant and more time foraging suggesting additional benefits from lower domains of danger beyond decreased predation risk.

6.2 Limitations and Suggestions for Further Research

One major puzzle resulting from the analysis is how popularity is determined. If popularity was found to have no effect on spatial position a valid hypothesis would be that popularity differences are due to be random variability among troop members. But, since it has predictive value, it raises the question, is popularity more readily achieved by some

individuals than others? In contrast to popularity, females who display high social effort may simply be doing so in order to trade for other resources. But though females do solicit grooming from other females, at least at Amboseli successful solicitation in vervets has been found only to be affected by recent parturition, and not dominance (Seyfarth, 1980), so success at soliciting grooming is not likely to determine popularity. Even if it were, it would raise the question: what makes those females more successful at soliciting grooming? In small troops dominance is a predictor of popularity, but since it is not in larger troops, dominance status cannot fully explain popularity. Furthermore, since social effort is uncorrelated with popularity, it cannot be that grooming is simply traded for grooming, or, in other words, females cannot just work themselves into popularity.

A major limitation of this study is that kinship between females in our population is unknown. Kin based altruism (Hamilton, 1964a, 1964b) may explain grooming patterns even better than Seyfarth's model which depends primarily on dominance. In a study of grooming among immature vervets, Lee (1987) found increased rates of grooming between sisters, and between mothers and their daughters. Grooming received may therefore simply be a product of a large family size. If this is the case, it would help explain popularity. If kin are more attractive, or tolerated by more individuals in the troop, large family size would also explain why popular females are able to maintain positions of decreased exposure and higher foraging potential.

This study only examined female social structure excluding female-male and male-male interactions. The reason for this is that, because they do not transfer troops, females comprise the stable core of the troop (Seyfarth, 1980). Males and females do often interact by fighting, grooming or copulating with each other, so it is reasonable to suspect that those

interactions will have a significant effect on the structure of female-female interactions. Probably due to difficulty of integrating several complex systems—male and female dominance hierarchies, male and female grooming interactions— and needs—reproduction and survival—into one model, this has not yet been accomplished. If a model to explain patterns of interactions is created, it should have testable predictions on how the structure affects individuals' ability to survive and reproduce. Those predictions can then be tested with methods similar to those used in this thesis, as well as a variety of other methods.

An important aspect missing in my analysis is antagonism rates. If dominance is really less important in large troops, there should be lower rates of general antagonism. Also, if in small troops subordinates trade grooming for tolerance, dominants should show lower rates of aggression towards those who groom them more. Without an analysis of grooming rates, the validity of applying biological markets explanations to grooming patterns is at best a probable conjecture.

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