SOME ASPECTS OF MALE VERVET MONKEY BEHAVIOUR

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ABSTRACT

The permanent coresidence of males within a troop is unusual but occurs in vervet monkeys. Several hypotheses have been projected to explain the coexistence of male vervets (predation risk, breeding season length) but these hypotheses fall short in explaining the multimale nature of vervet monkeys. In order to determine the explanation for coresiding males, I collected male behavioural data from two troops over the course of nine months. My dataset was divided into two categories, male-male interactions and female-male interactions. The male-male data indicate that breeding season is the most active time for migration, aggressions and wounds. Coalitions were described for the first time, and affiliative interactions between males highlighted coping tactics of males in regards to their coexistence. The female-male data indicate there was little indication for distinct male or female choice for mating. Specifically, olfactory information appears to lower successful copulations of males, and female resistance also decreased successful copulations. Grooming was not a commodity traded for mating access. Male dominance was not correlated with mating success, and females seem to express their preference for sexual partners. The large cohort of males of my troops appears to alter behaviours observed at other sites. The maintenance of male-female associations after breeding season suggests that males may be preparing for next breeding season, and males may co-reside for breeding purposes.

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Charles Darwin, *The descent of man, and selection in relation to sex*, 1871

CHAPTER ONE: INTRODUCTION

1.1 Coexistence of male vervets

The permanent coresidence of males within a troop is unusual but occurs in numerous primate species (Isbell et al., 2002). The coexistence of male vervets throughout the entire year is uncommon (Henzi & Lucas, 1980), because each additional male in a troop increases competition for resources and mating opportunities. I am interested in highlighting the unusual nature of year-round residence of male vervets, and the consequences of this multimale existence. An emphasis will be placed on different tactics employed by the males as they negotiate living with other males and females whom with they will breed with. One may ask why males would live in multimale groups, inherently increasing their chances of aggression. This question has been asked by several researchers (Isbell et al., 2002; Henzi & Lucas, 1980; Baldellou, 1991). Group living has thought to be driven by predation risk (van Schaik, 1983), as increased group size characteristically increases the ability to detect predator through a gross increase of vigilance of the troop. The threat of predation for a lone male in the environment is high; therefore males may tolerate co-residing males to decrease predation (Baldellou & Henzi, 1992). While males were not found to be better at detecting predators than females (Baldellou & Henzi, 1992), males may minimize their own predation risk by predator dilution effects (Wrona & Dixon, 1991). Male residence patterns may be determined by female defensibility in regards to the spatial distribution of the females (Wrangham, 1980) and also the length of the breeding season. Unfortunately, these hypotheses and others do not fully explain the coexistence of male vervets (see Isbell et al., 2002 for

overview). This being said, there must be an explanation for the multimale nature of vervet monkeys.

1.2 Sexual selection

Since 1859 when Charles Darwin published his book *On the Origin of Species*, the theory of sexual selection has been under debate with researchers. The struggle to reproduce affects both males and females, through male-male competition and female mate choice (Darwin, 1859). The coexistence of male vervets throughout the year has several consequences for group living and reproductive success. One resident male allows for a monopolization of fertilizations, therefore the multimale system presents paternal conflict for vervets. Males may avoid this conflict by high ranking males having priority of access (Altmann, 1962), with status delegating copulatory access to receptive females. Alternatively, males may forgo rank privileges by addressing the paternal conflict directly: coercing the females into copulation.

1.3 Male dominance and hierarchy

Richards (1974) suggests that a dominance hierarchy is the arrangement of a social group of individuals. This arrangement occurs when competition for priority to resources leads to aggression. Physical confrontation between males establishes the hierarchy, but more subtle interactions such as supplants and displacements are more common for vervets (Struhsaker, 1967a). These physical fights that help establish the dominance hierarchy increases the chance of wounding, a consequence that may ultimately lead to death of the individual. Males may prevent physical conflicts with

other males by avoiding dominant males, or behaving submissively to avert aggression from the dominant individual (McGuire et al., 1983). With the formation of a dominance hierarchy, males of differing ranks have different priority of access to resources, with respect to their rank. This accessibility of resources can play a major role in the overall fitness of the animal, both reproductively and physically (Trivers, 1972). Vervet male associations are questionable as to how they develop and how the males associate together. As for evidence of cooperation between males, Baldellou (1991) reports friendly behavior is not common among adult male vervets. This being said, defense tactics such as coalitions may cause relationships to develop between males.

1.4 Access to sexually receptive females

How do males compete for mating with females? Which sexually selected behaviors are most important in shaping the mating system of vervet monkeys? One hypothesis has been suggested by Smuts (1985) with regards to baboons, suggesting that 'friendships' can form between males and females. This friendship could potentially increase the male's reproductive success in the following breeding season, and could explain why males stay within the troop year round. These findings suggest that males may allocate energy into maintain relationships with females throughout the year, which may influence their reproductive access in the following breeding season. I am interested in what strategies males employ to gain access to females and what the relative profitability's of these strategies are. Male rank in the hierarchy may also influence mating success (Altmann, 1962). As mentioned previously, a male's access to resources

may influence their reproductive fitness (Trivers, 1972) suggesting that males could potentially increase their reproductive success if they are high ranking.

1.5 Research aims

My general research has been directed towards all aspects of male vervet behaviour, including both intra-sex and inter-sex interactions and the consequences of these events. While I originally set out to observe the male reproductive behaviour and male-female interactions throughout the year, my interest was sparked by male-male interactions. Male-male relationships have received less attention than female social relationships in primate species (Richter et al., 2009), which is strange since the coexistence of unrelated males in matrifocal group raises a number of interesting issues. There must be an explanation for the multimale nature of vervet monkeys. With regards to female mate choice, an affiliative relationship between a male and female could potentially cause preferential mating access of that female for the male (Baldellou, 1991). Male rank in the hierarchy may also influence mating success (Altmann, 1962).

Regardless of the drivers for male coexistence, the nature of male-male interactions create, in turn, the context in which males interact with females, by establishing the dominance hierarchy, eliminating competing males by physical encounters resulting in injuries, and the potential for intrasex friendships. To understand male-female interactions, we must first understand all the components of a male vervet's life; therefore my research has two separate but congruent objectives. My first objective is to provide an overview of intrasex male vervet interactions throughout the year. By creating this background of information on male behaviour, I can in turn supplement my

second objective of intersex interactions of the vervets throughout the year, with special interest in the breeding season, which is when we might expect to see the reproductive consequences of male social behaviour.

1.6 Vervet cohort sizes

Most of the studies on vervets have been restricted to populations of vervets residing in Kenya, where the average troop size is small (N=23; Cheney & Seyfarth, 1983; Isbell et al., 2002; Struhsaker 1967a,b,c). My South African study troops are large (N=48+) and therefore comprise large male and female cohorts (see Chapter 2). Large male cohorts offer the prospect of being able to assess variability on male behaviour in some depth, while large female cohorts make it possible to obtain the sample sizes necessary for an accurate evaluation of reproductive strategies. It is reasonable to assume that the males in my two study troops residing in Samara Game Reserve, South Africa may display different behaviours than those previously recorded, since Kenyan troops have smaller cohort sizes.

1.7 Broad research goals

My broad aims are divided into two categories, each focussing on specific data sets:

a) Male-male social interactions
    a. Male migration
    b. Aggression and dominance
    c. Wounds
    d. Affiliative behaviour

b) Female-male social interactions

    a. Spatial associations before, during, and after the breeding season

    b. Breeding season dynamics (whose initiating, evidence of female choice)

    c. Grooming between males and females

    d. Seasonal differences in interactions between the two sexes

These aims will be described in the chapters three and four. Chapter two summarizes the study site, and materials & methods.

CHAPTER TWO: STUDY SPECIES, SITE, AND METHODS

2.1 Study species

Evolution and taxonomic affinities

Vervet monkeys *(Chlorocebus aethiops pygerythrus)* are one of the most widespread monkeys in Africa (Struhsaker, 1967a). Vervet monkeys are distributed through Ethiopia to the most southern tip of South Africa (Struhsaker, 1967b). Figure 2 shows the dispersal of the species throughout the continent of Africa. This species was previously classified as *Cercopithecus aethiops* (Butynski, 2002), which placed the vervet within the genus of guenons. Unfortunately this classification is incorrect, as guenons are typically forest-dwellers while vervets live a semi-terrestrial, semi-arboreal life (Fedigan & Fedigan, 1988). There are at least six species of vervets recognized, leading to the confusion of taxonomic classification. While vervet monkeys are now classified as the genus *Chlorocebus,* literature often misidentifies the six species and eight subspecies as a lump taxon of *Cholorcebus aethiops.* The taxonomic status is still unclear but the newly established classification for my study species is *Chlorocebus aethiops pygerythrus.* This species name may be revised in the future, as more subspecies are being identified and there is still confusion in regards to proper classification because of the widespread nature of this monkey (Groves, 2001).

Physical description and reproduction

Morphological features of vervets include cheek pouches which aid in storage of food (Rowe, 1996), and elongated nasal bones. The vervet monkey has a black face with

a band of white fur that encircles the forehead and cheeks. Their fur is mottled grey, and males have a red penis and blue scrotum (Struhsaker, 1967b). Vervets are mildly sexually dimorphic in size and weight (Turner et al, 1997; Figure 1), but the males' genitals are the distinguishing characteristic between the two sexes. Vervets are bimaturic, with females reaching puberty at 36 months and males at 48 months (Turner et al., 1997). Female vervets have cryptic ovulation (Andelman, 1987) and breeding seasonally in the months of April-July in South Africa. Gestation is approximately 163 days (Andelman et al.,1985), and the birthing season is September-December with the female producing a single offspring. Vervets do not exhibit infanticide, as female vervet monkeys cannot be reproductively coerced by males (Seyfarth, 1980). Males do not provide paternal care for infants (Cheney et al, 1981).

Figure 1. Visual representation of physical size difference between males (farthest right vervet) and females (farthest left vervet).

Figure 2. IUCN (International Union for Conservation of Nature) distribution of *Chlorocebus pygerythrus* as of 2008. (Kingdon et al., 2008).

Ecology

Vervet monkeys are most abundant near riparian vegetation of the savannah, but can utilize riverine forest, karoo semi-desert and even urban areas (Struhsaker, 1967b; Henzi, 1979). This eclectic habitat use may solely be restricted by water and sleeping site

availability (Wrangham, 1980). Vervets are opportunistic omnivores, but usually feed upon plants and insects. Bird eggs and chicks can supplement the diet (Struhsaker, 1967b). Home ranges of vervets vary between 0.06 to 1.78 square kilometers (Struhsaker, 1967a; Willems & Hill, 2009) with seasonal availability of food and water causing the fluctuation in home range. The average troop size is 25 monkeys (Fedigan & Fedigan, 1988), although mean troop sizes fluctuate throughout the literature (18: Willems & Hill, 2009; 12-27: Cheney & Seyfarth, 1983).

Social Organization

Vervet monkeys live in multimale-multifemale troops, in which the females are closely related due to philopatry (Wrangham, 1980). Natal males emigrate upon reaching puberty, resulting in adult males in the troop being immigrants from neighbouring troops (Henzi & Lucas, 1980). Males usually emigrate twice, once from their natal group and once again as adults (Cheney & Seyfarth, 1983). Male transfer usually occurs over several days (Cheney & Seyfarth, 1983), and migrations occur significantly more frequently during the breeding season (Henzi, 1982). Adult dominance hierarchies are linear. Female rank is stable and underpinned by maternal rank (Cheney & Seyfarth, 1989). Male rank is more volatile and depends primarily on fighting ability (Cheney & Seyfarth, 1989).

1.7 Materials and Methods

1.7.1 Study site

This study was conducted in Samara Private Game Reserve, Graaff Reinet, Eastern Cape, South Africa (32° 22'S, 24°52'E). Samara is situated 35 kilometers east of

Graaff Reinet and approximately 260 kilometers north of Port Elizabeth (see Figure 4). Samara is an area of semi-arid karoo, with a riverine population of *Acacia karoo* trees (Figure 5a). The Melk river runs through Samara and the vervet populations are centered on the acacia woodland bordering the riverbed. The riverbed is dry during the austral winter and can flood during the austral summer.

Samara is home to 63 species of mammal, with only a few being large. Some of the species mammals include giraffe (*Giraffra camelopardalis),* eland (*Taurotragus oryx)* and white rhinoceros (*Ceratotherium simum*). A number of carnivores are found on the reserve, these include the black-backed jackal (*Canis mesomelas*), cheetah (*Acinonyx jubatus*) and caracal (*Caracal caracal).* Moderately sized mammals include the aardvark (*Orycteropus afer*), African porcupine (*Hystrix cristata)* and bushpig (*Potamochoerus larvatus*) (Haltenorth & Diller, 1980).

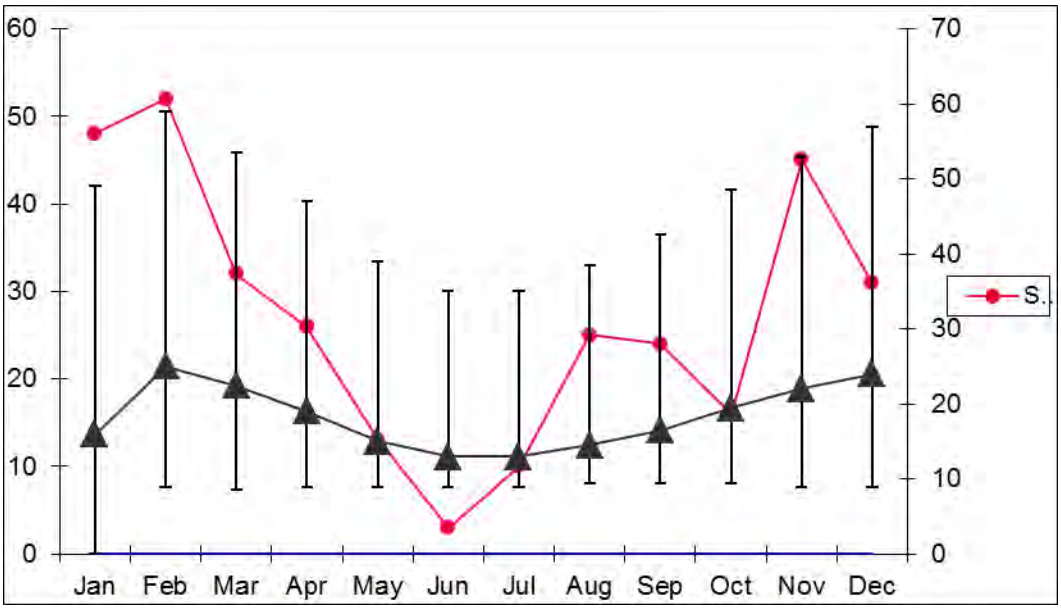

Figure 3. Total precipitation levels (mm) and temperature (°C) data for Graaff Reinet over 2010. Red line represents the total precipitation levels (mm) per month. The gray line represents the mean Celsius temperature per month with errors bars denote the mean high and low temperature recordings.

The mean annual rainfall is 330mm, and the average annual temperature is 18.6°C (Courtesy of South African Weather Service) (see Figure 3). The photoperiod peaks in December at 14.1 hours and is reduced to 9.6 hours in June. Samara Game Reserve was originally grazing farmland prior to becoming a game reserve in 1997.

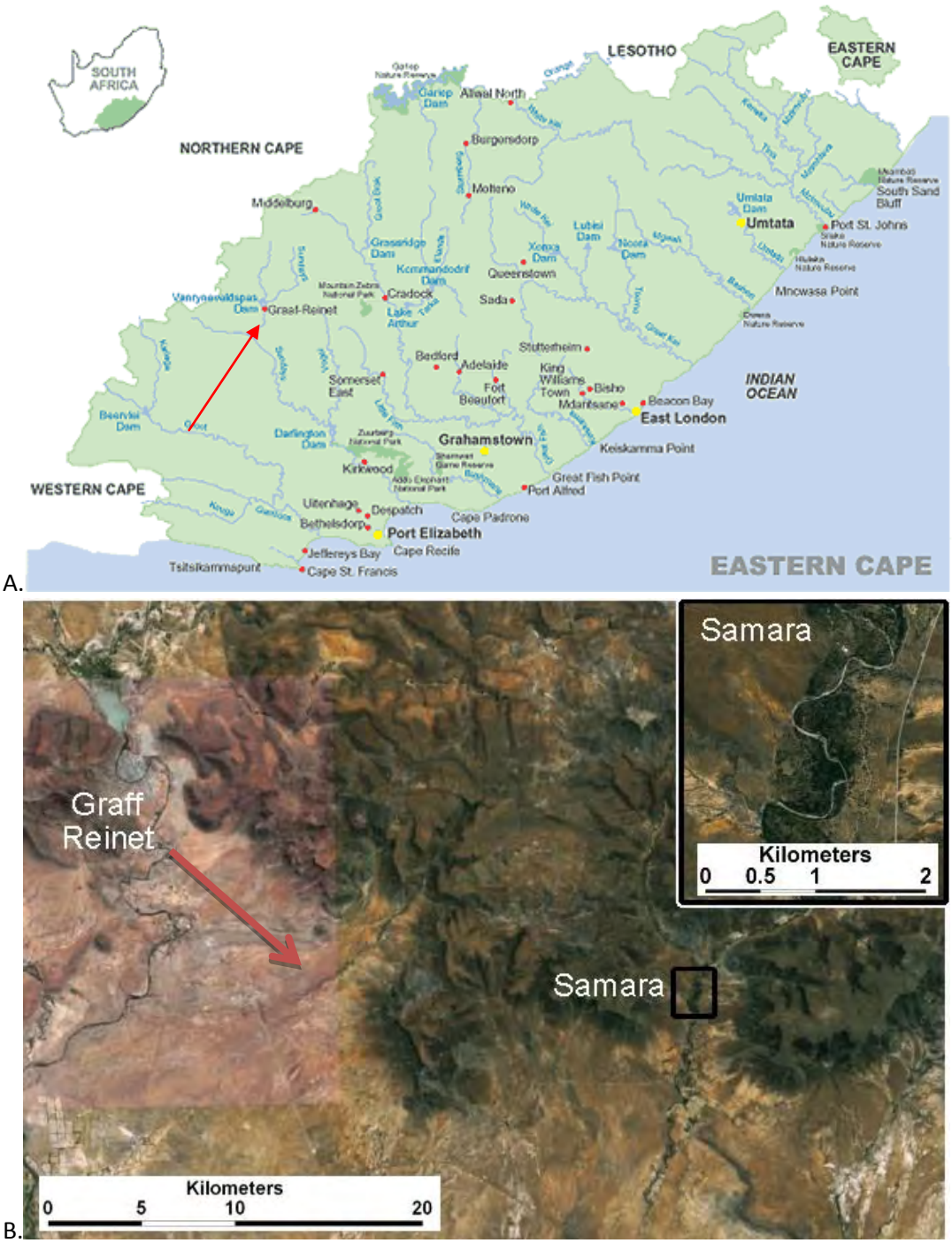

Figure 4. A. Map of Eastern Cape, South Africa. The location of Graaff Reinet is indicated with an arrow. B. Samara Game Reserve in relation to Graff Reinet (Samara located in inset)

A

B

Figure 5. The Samara study area. *A*. Study group in acacia woodland along river, vervets resting in the primary food source *Acacia karoo*. *B*. Study group at an ephemeral water source in an otherwise dry river bed.

1.7.2 Study Population

Data presented in this thesis was collected from two troops over a nine month period (02/10-11/10). Both troops have been under constant observation since September 2008, resulting in the troop members being fully habituated prior to data collection starting. Males immigrated into both RiverSide Troop (RST) and RiverBend Mob (RBM), and this necessitated a period of habituation before reliable data could be collected from them. The home ranges of the two troops are adjacent, and intertroop encounters were frequent, each troop encountering up to five troops during the course of the study period. Operational sex ratio in Table 1 was defined as the ratio of females who conceived to the number of adult males in the troop. Adult males were defined as males with descended testes and sexual interest in females. The two troops differed in absolute size and home-range territories.

Table 1. Adult composition of RST and RBM troops

	RST	RBM
Male number	12-14	4-9
Female number	23-26	18
Oestrous	18	11
Anoestrous	7	7
Absolute sex ratio	1.92-1.86	4.5-2
Operational sex ratio	1.5-1.29	2.75-1.22
Group size	72	49

The study subjects were recognized though the natural variation in physical characteristics. After spending the first month in close quarters with the habituated monkeys, individual characteristics were distinguishable for each adult vervet. Scars, ear rips, white coloration under eyes, tail abnormalities and nipple color were some of the markers used for identification.

1.7.3 Data collection protocol

Males were the focus of this research, but females were included in instantaneous scan sampling for comparisons of nearest neighbour identities. Troops were followed for 10 hours per day, and the photoperiod was integrated into the decision of when the data collection would begin and end. In summer, data collection would begin at either at dawn and continue for 10 hours, or begin 10 hours prior to dusk. This allowed the collection of an equal of 'early start' and 'late start' days over a two-week period. Focal animal samples were allocated to four evenly divided diurnal timeblocks and a goal of three focal sample/timeblock/month was set at the beginning of the study period.

Individuals were followed at a distance of 3-10 meters depending on the signs of comfort shown by the individual. If any signs of discomfort were shown, the observer distance was increased until the individual resumed his earlier behaviour. Data from each troop were collected on alternate days, although there was a slight bias towards RST to account for the difference in absolute male number. Data were collected on a Trimble Juno handheld data logger using data collection protocols produced in Pendragon Forms Manager 5.1. Three main sampling techniques were used: 1) Focal Animal Samples 2) Instantaneous Scan Samples and 3) Ad libitum Samples (Altmann, 1974).

Focal Animal Samples

The focal animal sampling technique was the most important sampling technique used for this study. For each focal sample, the starting time, identity of individual and timeblock were specified prior to data collection. An effort was made to collect data systematically within the confines of the 20 minute focal period (Altmann, 1974). Focal

individuals could move out-of-sight of the observer, and this time was subtracted from the total focal period. If the focal duration was less than ten minutes, the focal was discarded. All focal samples under ten minutes were not included in Table 4, but recorded as ad libitum observation minutes. A total of 69 focal samples were removed from the dataset of 2133 focal samples. Individuals were not focal-sampled within three hours of their previous focal sample, and no individual was focal-sampled more than three times a day.

Activity states

The basis of the focal sample was to record the five main activity states of the individual 1)Foraging; 2)Resting; 3)Moving; 4)Vigilant; 5)Social. See Table 2 for definitions of activity states. Activity states were recorded every two minutes (named intervals) starting at zero minutes of the focal sample. If the male was out of sight for more than five seconds, 'out of sight' was recorded until the male was spotted. The focal sample was abandoned if the male out of sight for more than five minutes.

Table 2. Activity states and their associated definitions recorded during focal animal samples

Activity	Definition
Foraging	Eating from food sources that may be clumped or dispersed
Resting	Sit, stand, lay, or sleep; neither feeding nor socializing Autogroom: grooming self
Moving	Locomoting on ground or trees via walking or running
Vigilant	Alert state for more than three seconds, ceasing all other activities
Social	Playing with other individuals Grooming (ID of partner)

Focal sample events

Copulations, aggressions (Figure 6), sniffs, coalitions, changes in proximities and vocalizations were treated as 'events' and recorded instantaneously in the focal sample (see Table 3). The rate of these behaviours could then be calculated from the 20 minute samples. Approach and withdrawal interactions involving adult females or males were defined as a movement within or out of proximity of two meters of the focal subject. An additional three intervals (six minutes) were recorded after copulations, agonistic encounters, or grooming bouts were recorded during a focal sample. These three intervals allowed me to monitor the change in behavioural state after the focal sample event. Focal samples of an individual did not begin if a focal sample event was witnessed just prior to the focal sample.

Table 3. Behavioural events and their associated definitions recorded during focal sample and ad libitum observations

Event	Definitions
Copulation	
1. Initiator	Individual approached within two meters of another individual
2. Female present	Female turned hindquarters directly towards the face of the male
3. Location	Ground, open ground, shrub or tree was noted
4. Grab	Male used both hands to grab pelvis of female
5. Mount	Grab pelvis and elevate forequarters onto pelvis of female, resting feet on female's ankles. Weight is fully supported by female, but no pelvic thrusting
6. Copulate	Mounting with pelvis thrusts, culminating in assumed full ejaculation
7. Sniff	Olfactory inspection of female's perineum, sometimes with touching
8. Female resist	Female resisting grab or mount by physical aggression or changes in proximity
9. Harasser	Individual that auditorily or physically attacked the copulating pair
10. Nearest male	Up to two male IDs were recorded in proximity of 25 meters from the copulating pair
Aggression	
1. Displace	One individual's proximity causing a distancing of proximity by another individual
2. Supplant	Removal of space, food or grooming partner from one individual by another (Struhsaker, 1967a)

3.	**Vocal threat**	Low grunt directed at an individual
4.	**Eyelid threat**	Raising of eyelids. Often paired with gaping jaw to reveal canines (Figure 6)
5.	**Grab**	Rapid jerking of paw towards an individual, intent for physical contact
6.	**Chase**	Charging run towards individual over a period of distance
7.	**Bite**	May or may not result in wounds
8.	**Lunge**	Leaping or jumping towards an individual
9.	**Hand swipe**	Rapid jerking of paw towards individual, no intent for contact
10.	**Submissive vocalise**	Continuous tonal exhalation that occurs with a grimace performed by subordinate (Struhsaker, 1967c)
11.	**Cower**	Rapid flexing of spine, resulting in shoulder shrug or crouch position
12.	**Leave proximity**	Walk or run away from individual, often with startle jerk
13.	**Redirection**	Redirection of aggression onto subordinate individuals in proximity
14.	**Lipsmack**	Repetitive open and closing of lips, resulting in 'popping' noise
15.	**Facial threat**	Eyethreat or gaping of jaws (Fig 6)
16.	**Physical aggression**	Retaliation of individual against initial aggressor or physical fight started by initial aggressor

Figure 6. Behaviours of aggression in vervet monkeys. Adult female (Smudge), raised eyelid threat, extended neck, with open mouth face

Nearest neighbours

The spatial location of the male was recorded each interval (Ground, Open, Shrub, Tree). Up to six nearest neighbours and their respective distances were recorded each interval, as was the number of juveniles within five meters. This provided data on affiliative interaction of the focal individual with other troop members. For each 20 minute focal sample, a total of eleven 'nearest neighbour' events were recorded.

Hour beginning	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Total
5:00	0	0	0	0	0	0	0	0	100	177	276
6:00	20	192	101	61	0	0	0	79	323	217	993
7:00	37	322	382	452	335	291	383	342	377	203	3124
8:00	61	408	502	579	547	589	668	364	494	273	4486
9:00	101	326	450	443	462	541	473	309	383	344	3832
10:00	156	534	384	533	512	633	492	304	525	405	4477
11:00	185	479	322	209	457	476	463	288	511	464	3854
12:00	202	480	528	492	469	605	497	330	480	358	4440
13:00	153	415	433	418	403	611	475	280	448	318	3955
14:00	78	372	239	381	612	485	439	240	373	225	3444
15:00	94	531	506	517	495	585	613	339	487	267	4434
16:00	76	311	293	373	396	431	347	100	361	287	2975
17:00	81	74	99	20	0	0	20	78	225	240	838
18:00	0	0	0	0	0	0	0	0	0	27	27
Focal sample time	1243	4442	4238	4480	4688	5247	4870	3054	5087	3804	41154
Ad libitum											
Focal sample time	44.0	123.0	70.8	95.7	35.9	13.7	14.7	39.5	11.9	4.3	453
Total	1287	4565	4308	4576	4724	5261	4885	3093	5099	3808	41607
Total, h	21	76	72	76	79	88	81	52	85	63	693

Table 4. Distribution of focal sample time and *ad libitum* focal sample time, in minutes

Instantaneous Scan Sampling

An instantaneous scan sample is a snapshot of an individual's activity state, along with the nearest female and male with their respective distances in meters. These scan samples provided additional data on activity and spatial associations. Instantaneous scan sampling occurred every thirty minutes for a period of five minutes, resulting in 21 scan sampling periods throughout the study day. Adult males and females were scan sampled, and an effort was made to record a minimum of five scan samples per five minute scan period. Over 11,000 scan samples were recorded during the duration of the study, and were combined with other researchers' scan samples for a total of more than 68,000 data points. Inter-observer reliability tests were conducted prior to the study period beginning,

scan samples were simultaneously collected on the same vervet individuals for the entire day by all researchers, and accuracy of data was found to be acceptable.

Ad libitum Sampling

Ad libitum samples of behaviour allowed all observed copulations, aggressions, sniffs, and mate-following to be recorded (Altmann, 1974). Ad libitum data were also collected while focal sampling if behaviours were observed that did not involve the focal animal. The principal use of these data were to increase the sample size of dominance interactions for the creation of dominance hierarchies, to record any sexual behaviour as well as all incidences of wounding. Wounds were recorded ad libitum for all adult individuals, wound type and location will provide information on the bodily harm intent of aggressions. It was not assumed that the ad libitum samples yielded random samples of behaviour of all troop individuals, but it was assumed that the random sampling of dyadic agonistic interactions was comparable to all samples of the dyad. The ad libitum observations were biased to conspicuous behaviour, while the focal sampling was not biased against subtle, inconspicuous behaviour. A daily census of all adult females and males was made.

1.7.4 Statistical analysis

The mixed model on factors affecting copulations was conducted by Dr. Parry M. Clarke using the R statistical software (R Foundation for Statistical Computing, 2011). All remaining tests were conducted with the JMP 9 statistical package (SAS Institute,

2007), with alpha set at 0.05 or IBM SPSS Statistics Version 19 statistical package with alpha set at 0.05.

CHAPTER THREE: MALE-MALE ASSOCIATIONS

3.1 Objectives

My aims in this chapter are to examine the male migration patterns and attempt to determine the seasonality and direction of the migrations, and possibly the mechanism driving the movements. The dominance hierarchies of both troops will be created, and the different levels of aggression characterised. Male wounding locations and types are categorized, and compared against female wounding patterns. Male-male coalitions are reported for the first time in vervets, and several aspects of coalition formation are examined to understand the mechanism behind partner choice.

3.2 Male migration

Multi-male multi-female social groups are commonly found in many Old World monkey taxa, such as macaques, several subspecies of baboons as well as vervet monkeys (Melnick, 1987). Seventeen of 44 cercopithecine species live in permanent multi-male groups (Smuts et al., 1987). Vervet monkey groups contain several immigrant adult males who can co-reside for two or more years, which is unusual for guenons (Henzi & Lucas, 1980). Vervet females remain in the home ranges in which they were born, while males emigrate to neighbouring troops at sexual maturity (Struhsaker, 1967a). By leaving their natal group before reaching sexual maturity, males avoid endogamous (Melnick, 1987). Males change social groups several times throughout their lifetime, with a timing that suggests that this reduces the risk of mating with their sexually mature daughters (Henzi & Lucas, 1980). This is supported by Melnick`s (1987) observation that wild cercopithecine populations appear to have evenly distributed

genetic variation within multi-male social groups, suggesting that male transfer rates are sufficient in preventing the possibility of inbreeding.

In seasonal breeders like vervets, male generally transfer to neighbouring troops during the breeding season. Henzi (1982) reported that male migrations occurred significantly more frequently during the breeding season, as did Cheney & Seyfarth (1983). Although the migrations occurred predominantly during the breeding season, the number of sexually receptive females did not affect the direction of migration (Henzi, 1982). However it has been argued that males may transfer to troops from which they receive little aggression (Cheney & Seyfarth, 1982). Additionally, natal male vervets have been reported migrating together (Cheney & Seyfarth, 1983), although the second emigration is performed singly, without a partner or relative. Finally, subordinate males transfer troops more frequently than dominant males (Henzi & Lucas, 1980; Cheney & Seyfarth, 1983). These male movements may be made possible during inter-troop encounters which give a migrant male the opportunity to interact with neighbouring troops (Henzi, 1982).

3.3.1 Dominance

A dominance hierarchy is the arrangement of a social group of individuals that occurs when competition for priority to resources leads to aggression (Richards, 1974). Struhsaker (1967a) suggests that the functional significance of a social dominance hierarchy is to reduce physical aggression, thereby reducing energy costs. Male dominance rank may best predict direct access to a resource, providing this competition for a resource is not immediately exhaustible (Gerald, 2002). In addition to resources,

high ranking individuals have primary access to thermoregulatory beneficial locations such as shade within the environment (Gerald, 2002). Behaviours associated with social dominance include: spatial displacement of subordinate males, highest percentage of wins in adult male agonistic encounters, and erect posture and body language (McGuire et al., 1983). Silk (1999) agrees that top ranking males could potentially be distinguished from their posture, behaviour or condition, but vervets exhibit dominance hierarchy by physical fighting and displacement interactions (Isbell, 1995). As a result of these agonistic encounters, priority to food, spatial positions and grooming relationships can be established from the hierarchy (Struhsaker, 1967a). Male adult vervets direct most of their aggression towards other males (Baldellou, 1991), and self-initiated displays of subordination by subordinate males to high ranking males is common (Henzi, 1982). These self-initiated displays, or 'homage', may decrease potential aggression from higher ranking males, as the display is a submissive sign to the top ranking males.

3.3.2 Aggression

Multi-male groups are subject to greater male-male intra-specific competition than uni-male groups, as measured though injuries caused by aggressive encounters (Plavcan & van Schaik, 1997). Henzi (1982) reports an increase in quantity and intensity of agonistic encounters during the breeding season, and also an increase of frequency of wounds for male vervet monkeys when compared to females. Adult male vervets received more wounds than females in Baldellou's (1991) study, but males did not receive more head or face wounds than females. Stump-tailed male macaques (*Macaca arctoides)* show a higher rate of wounds when compared to females, lower-ranking males are wounded more frequently, and males are more frequently wounded on forequarters

(Whitten & Smith, 1984). These findings are echoed in the Chapman & Legge (2009) study of Cercopithecoid monkeys, reporting males having higher frequencies of fractures on forequarters and the cranium. They postulate that chases and physical aggression may contribute to the amount of bone trauma.

3.4 Male-male associations

Schnell et al. (1985) reported social proximity between females is less than the distance maintained between males. Female vervets are more involved in grooming as a consequence of being philopatric (Struhsaker 1967a). Male vervets in St. Kitts engage in individual behaviours 86-94% of the time (McGuire et al., 1983), and engage in dominance-related behaviours no more than 3% of the time. This large time allocation to individual behaviours suggests that male vervets are predominantly solitary in nature. Affiliative time with other troop members ranged between 2-8% of the time, but interactions was not divided between age classes or sex (McGuire et al., 1983). Baldellou (1991) reports friendly behaviour such as body contact is not common in adult male vervets and play typically occurred only between younger males on rare occasions. Both Baldellou's (1991) and McGuire et al. (1983) observations suggest that male affiliative behaviour is rare, but present. Grooming between males was directed up the dominance hierarchy, with the top ranking male receiving more grooming than he gave (Baldellou, 1991). Baldellou (1991) also suggests that male-male grooming was most prominent between males close in rank, and has the same proximate reasons (hygiene) as female-female grooming .

3.5 Coalitions

It is impossible to know if the common goal of a coalition was independently or communally decided upon before the event happened (Chalmeau & Gallo, 1995). For cooperation to occur, both individuals need to understand the situation and act accordingly with the help of their partner. Barrett & Henzi (2002) suggest that all or most of primate's behavioral decisions are based on short-term causal relations between social events. Noë (1986) define coalitions as two or more individuals acting in a coordinated way against one or more target individuals. This group of individuals may be the result of one individual coming to the aid of the other, or both directing aggression simultaneously. Alternatively, de Waal & Harcourt (1992) define coalitions as coordinated attacks by at least two individuals against a common target of at least one individual. Under this definition one male coming to the air of another male is not necessarily cooperation, since it is impossible to know if the aider is helping the actor or directing aggression towards the target independently. Partner preferences may be the individuals in proximity at that moment.

Olson & Blumstein (2009) suggest that ovulatory duration, group size and an establishment of a dominance hierarchy are all highly correlated with male coalition complexity. For example, a confined breeding season or a long ovulatory cycle prevents males from monopolizing the females. A dominance hierarchy is the third prerequisite for coalition complexity, with males relying on coalitionary support from other males to disrupt the dominance hierarchy.

By definition, male coalitions among male group members require the social structure of the group to be multimale, with at least 3 males residing in the troop.

Coalitions are common among primates but not all species exhibit them. Several of the Cercopithecinae subfamily exhibit male coalitions (e.g., savannah baboons, *Papio hamadyas*: Noë, 1986; Bercovitch, 1988; Packer, 1977; Hausfater, 1975; bonnet macaques, *Macaca radiata*: Simonds, 1974; Barbary macaques, *Macaca sylvanus*: Kuester & Paul, 1992) along with other multimale primate species (e.g., chimpanzees, *Pan troglodytees*: de Waal, 1982; white-faced capuchins, *Cebus capucinus*: Perry, 1998). Most Old World monkeys exhibit female philopatry (Smuts et al., 1987), leading to close genetic relatedness among group infants each year. Therefore, males dispersing from their natal troop can give rise to kin immigrating into the same troop. Access to kin increases the likelihood that coalitions occur, as kin are more likely to act as allies against conspecifics (Pusey & Packer, 1987; Meikle & Vessey, 1981). However, it should be noted that male coalitions can be formed with non-kin individuals, Packer (1977) reports non-kin male baboons repeatedly forming coalitions. Additionally, coalitions may form based on the male residency time in the troop (Collins, 1981). This hypothesis has been built-upon by Smuts (1985) who suggests that males with affinitive relationships, measured though those males that, on average, have lower individual distances, are more likely to form coalitions. This type of relationship may be made possible by a long period of shared residence rather than the relatedness of the individual males.

Coalitions may relate to reproductive benefits, with males forming coalitions for access to sexually receptive females being guarded by another male (Bercovitch, 1988). The energetic costs of a coalition is argued not to influence the male's overall fitness, while reproductive fitness could increase if a consorting male is chased away from the receptive female (Bercovitch, 1988). Coalitions may be formed on reciprocity, males

should support those who supported them in the past, and refuse to support males who ignored their solicitation (Packer, 1977). Coalitions frequency may relate to cohort size, as Barrett & Henzi (2002) suggest that smaller cohorts within a group would have lower number of coalitions, since each individual would have a smaller number of potential partners.

Male coalitions may exist because of acquisition and maintenance of dominance rank (Chapais, 1992). Male may improve their rank by mounting a coalitionary threat against a higher ranking male (Smuts et al., 1987). A high ranking male does not need to form coalitions, as his rank allows him to achieve his goal without assistance (Noë & Sluijter, 1990). A successful coalition is expected to occur if the combined fighting ability of the coalition members- measured by their rank- is higher than the target's rank. (Noë, 1994). This asymmetry in strength predicts that any two males can form a successful coalition as long as their combined fighting power is higher than the opponent. Coalition formation can be described into three types: all down, bridging, and all up coalitions. All down coalitions require both coalition partners having a higher rank than the target. Bridging coalitions have one coalition partner ranking higher and one partner ranking lower than the target. Finally, all up coalitions are characterised by both coalition partners ranking lower than their target. Figure 7 gives a visual interpretation of the three types of coalitions.

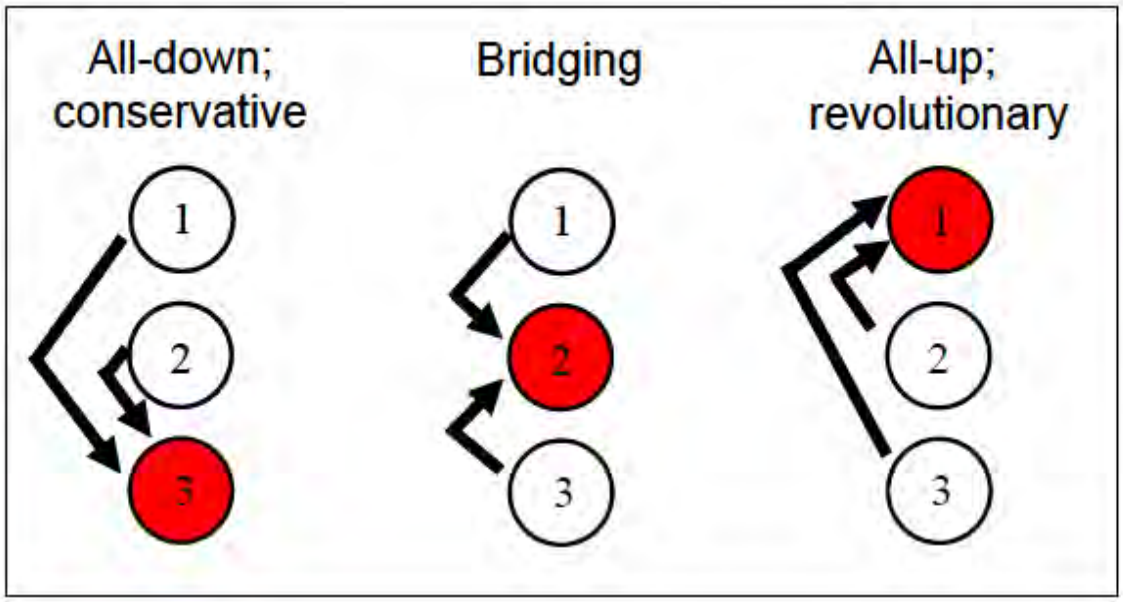

Figure 7. Schematic representation of the basic formations of coalitions (Bissonnette, 2009). Highest ranking male represents number 1. The target is shown in grey, partners shown in white, and the direction of the attack indicated by the arrows.

Despite relatively detailed data on coalitions in other cercopithecine species, there are few data on male coalitions in vervets. Although Baldellou (1991) report observations of male-male coalitions, she was able to do no more than provide a brief account of the structure of these coalitions. Coalitions were mostly low ranking males targeting the alpha male, and male-male coalitions were rare.

3.6 Predictions

a) *Social structure:* The frequency of male migrations will increase during breeding season, both for emigrating natal males and immigrating adult males. Natal males should transfer to neighbouring troops, and may possibly transfer together with males from their natal troop. As the river system creates neighbouring troops

either up or down river, I predict the majority of migrations to occur within a one-troop distance from the original troop.

b) *Dominance and aggression:* As the male hierarchy is volatile but linear, I predict that fluctuations in dominance rank will occur, possibly in connection with breeding season or severe wounding of opponents. Immigrant males should receive higher frequencies of aggression during their move-in period, as the social stability of male association would be perturbed by their arrival. Additionally, it is expected that a higher frequency of agonistic encounters will occur during the breeding season, as the limiting resource for the time period is sexually receptive females. Higher ranking males should produce higher frequencies of displacements/supplants, as these reinforce the hierarchy without requiring physical aggression. Nevertheless, more severe aggression should occur during the breeding season and as a result an increase in frequency of male wounds should be observed at this time (see Henzi, 1982).

c) *Positive associations:* I predict that male-male grooming will be at a lower frequency than female-male grooming, and that grooming should be directed up the dominance hierarchy. Commodities such as tolerance of proximity may be traded for grooming (Barrett et al., 1999), therefore an inequality in grooming time would be observed, in that higher ranking males should receive more grooming than their time spent grooming other individuals. Furthermore, I expect to see more 'friendships' between males of similar in rank, measured through inter-individual distance, and that these males of similar rank groom each other than other males.

d) *Coalitions:* Coalition members should be of similar residency time, rank and experience levels (Collins, 1981). Coalition members should be associates, with increased frequencies of proximity than other non-coalition members and a measurable social bond such as grooming (Smuts, 1985). The majority of coalitions were predicted to be all-up coalitions, as high ranking males gain nothing from a partner during an aggression on a lower ranking individual. Coalitions should increase during the mating season in response to priority of access to sexually receptive females (Bercovitch, 1988).

3.7 Materials and Methods

Study site and animals

I collected the data reported here at Samara Private Game Reserve near Graff Reinet, South Africa. The vervet monkeys in this study consisted of two separate troops, with data collected over a nine month period (02/10-11/10). Both troops were under constant observation since 2008, resulting in the troop members being fully habituated prior to data collection starting. Adult male numbers fluctuated throughout the year in each troop, RST had 12-14 males, and RBM had 4-9 males. Emigration and immigration of adult males occurred throughout the year, deaths also varying the male count in each troop. Resident males were defined as males present from the beginning of the study, immigrant males were defined as males who entered either troop after January 2010. Focal Animal Samples (Altmann, 1974) were collected on the males throughout the study period, and ad hoc observations of dominance displays and coalitions were recorded by all observers (N=4). A total of 686 focal sample hours was collected during the course of the study period.

Assessment of male rank

Dominance was calculated on the basis of summed interactions and supplants/displacements of one individual by another. Observed agonistic behaviour between males was recorded in focal animal samples and ad libitum samples. The dominance ranks within the male cohorts for both troops were determined using dyadic interactions and identifying winners and losers. Dominance ranks were assigned from decided agonistic interactions, and a total of 740 interactions were used to build the hierarchy. David Scores were originally developed as a standard ranking method, as David Scores are the most suitable measure of the steepness of the hierarchy and individual dominance ranks. David Scores calculate dominance ranks of individuals in a group based on dyadic agonistic interactions, (de Vries et al, 2006). Each month, a dominance matrix was assembled to assess monthly rank changes (see Figures 12 and 13), and all monthly dominance matrixes were compiled to create the complete male interaction dataset (de Vries et al., 2006). (see Table 5 and 6).

Table 5. Total RST outcomes of agonistic bouts between males. The frequency of winning is indicated in the row and the frequency of losing is indicated in the columns

Winner		**Loser**												
	Aj	Or	Ju	Go	Bu	Sp	Bo	Tw	Ko	Oz	To	Dg	Mu	Pa
Aj	*	15	4	7	16	2	1	1	4		5	7	2	7
Or	19	*	4	10	13	13	4	0	7	7	18	13	3	8
Ju	0	4	*	3	1	3	6	1	4	4	10	4	2	3
Go	0	1	5	*	14	4	4	0	4	2	1	1	2	5
Bu	0	0	8	5	*	6	1	2	12	7	4	8	3	0
Sp	0	2	1	0	8	*	2	0	9	8	6	1	1	3
Bo	0	1	0	0	0	2	*	0	3	0	1	0	1	2
Tw	0	0	0	0	0	0	0	*	0	0	0	0	0	0

Ko	0	0	0	0	0	0	1	0	*	1	3	4	2	6
Oz	0	0	0	0	1	0	2	0	1	*	3	1	1	9
To	0	1	0	0	0	0	0	0	0	3	*	2	0	2
Dg	0	0	0	0	0	0	0	0	0	4	1	*	1	3
Mu	0	0	0	0	0	0	0	0	0	0	0	1	*	0
Pa	0	0	0	0	0	0	0	0	0	0	0	0	1	*

Table 6. Total RBM outcomes of agonistic bouts between males. The frequency of winning is indicated in the row and the frequency of losing is indicated in the columns

Winner	**Loser**								
	Vi	Ca	Dn	St	Wh	Kp	Ha	Eg	Ta
Vi	*	16	24	8	0	10	4	3	2
Ca	0	*	13	6	2	19	15	22	9
Dn	0	18	*	7	0	8	6	3	1
St	0	1	0	*	0	2	6	10	2
Wh	1	0	0	0	*	0	0	0	0
Kp	0	0	0	3	0	*	8	5	10
Ha	0	0	1	0	0	1	*	6	5
Eg	0	0	1	1	0	1	4	*	3
Ta	0	0	0	0	0	0	0	1	*

Data collection

Each troop was followed for a minimum of 10 days per month, 10 hours per day. Data were collected on a Trimble Juno handheld using data collection protocols written in Pendragon Forms Manager 5.1. Focal animal samples, instantaneous scan samples and ad libitum samples were conducted throughout the day (Altmann, 1974), with ad libitum samples primarily being used to increase the sample size of agonistic encounters. Grooming bouts within the 20 minute focal animal sample were recorded within 5 seconds of a partner beginning or ending, and the focal sample was extended for six minutes after the cessation of a grooming bout. Focal samples were also extended six

minutes after an agonistic encounter in order to record any behavioural changes caused by the aggression.

Associations

A number of males entered and subsequently left the troop during the course of the study, but remained peripheral. These males were impossible to rank and were excluded from the dataset. Proximity association indices (PAI) were calculated for each dyad on the basis of the frequency with which males were nearest neighbours during scan samples. Proximity association indices were calculated using the equation PAI: PAB/(PAB+PA+PB). The frequency of times a dyad (Male A and Male B) were in proximity of each other is labelled PAB, the total nearest neighbour frequency for Male A minus the dyad proximity frequency is labelled PA, and the total nearest neighbour frequency for Male B minus the dyad proximity frequency is labelled PB. They ranged between zero (males were never observed together) and one (males were always observed together (Bejger et al., 1998). Grooming association indices were calculated using the equation GAI: GAB/(GAB+GA+GB). The amount of time a dyad (Male A and Male B) groomed each other is labelled GAB, the total grooming time for Male A minus the dyad grooming time is labelled GA, and the total grooming time for Male B minus the dyad grooming time is labelled GB. The index ranged between zero (no grooming) and one (the dyad solely groomed each other and no other individuals). Male-male grooming is exhibited in Figure 8.

Grooming duration reciprocity indices were calculated using Mitani's (2009) version of grooming reciprocity, labelled dGRI: dGRI=1−|gAB/(gAB+gBA)−gBA/(gAB+gBA|. The amount of grooming that individual

A gave to individual B is labelled gAB, the amount of grooming given by individual B to individual A is labelled gBA, and the total amount of grooming between the two individuals is labelled gAB + gBA. The index ranged between zero (no reciprocal grooming) and one (grooming duration was always fully reciprocated).

Conceptions

Conception dates were calculated by backdating the birth date 163 gestational days (Andelman, 1987).

Figure 8. An example of male-male grooming

Wounds

Severe wounds were recorded on an ad hoc for males and females throughout the study period. The location of the wound was allocated by dividing the body into five sections: head, front limbs, torso, hind limbs, and tail. Head and front limbs were subsequently combined into 'forequarters', and hind limbs and tail were combined into 'hindquarters'. Type of wound was indicated when possible (slash, bite wound, puncture, abrasion). Example of wound types are visible in Figure 9a and 9b.

Figure 9a. Foot wound inflicted on a male during the breeding season. The foot was extremely swollen until the male chewed the upper portion of the foot, enabling the infection to be expelled.

Figure 9b. Puncture wound on a male that may have contributed to his disappearance several days later. Note the absence of fur around the wound, he picked this area bald over the course of several days.

Coalition formation

Coalitions were defined as simultaneous attacks by at least two individuals against a common target of at least one individual (Pandit & van Schaik, 2003; de Waal & Harcourt, 1992). For each coalition, the aggressor, target and supporter were identified. Coalitions were identified as being either interference coalitions, where a male includes himself in an ongoing conflict and sides with one opponent, or parallel coalitions where two males attack at least one opponent in coordination (Bissonnette et al, 2009).

3.8 Results

Migration

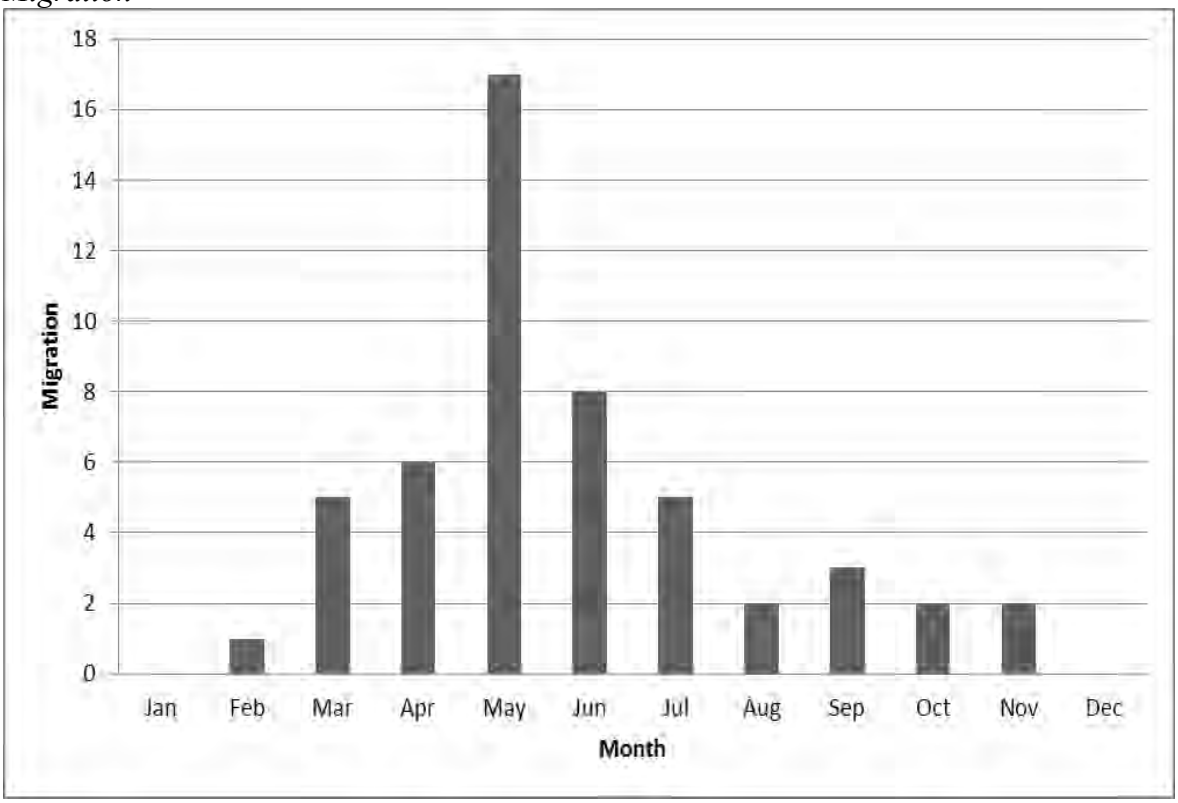

Figure 10. The frequency with which males migrated into troops per month for 27 months

From the beginning of the field project, 51 male migrations occurred over a 27 month period (September 2008-December 2010). Eleven males immigrated and subsequently emigrated from the troop, and 29 males performed only one immigration or emigration. The average residency time for males in RST (Mean number of males=14) was 12.1 ± 9.6 months, while RBM's average residency time was 12.4 ± 8.5 months (Mean number of males=10). The shortest residency time was 0.5 months during the breeding season of 2010, and there were eight males who remained in the same troop for the entire 27 months. Eight males migrated during the 2010 breeding season (May-July). RST had 19 males emigrate or immigrate during the two breeding seasons; while only

eleven males migrated into and out of RBM over the same period. One male`s death is suspected due to a large wound (seen in Figure 9b). The monthly frequencies of migration and conception dates for 2010 were significantly correlated (r=0.975, N=12, *P*<0.001), with the peak of migration occurring in May (Figure 10), which is associated with the peak of conceptions.

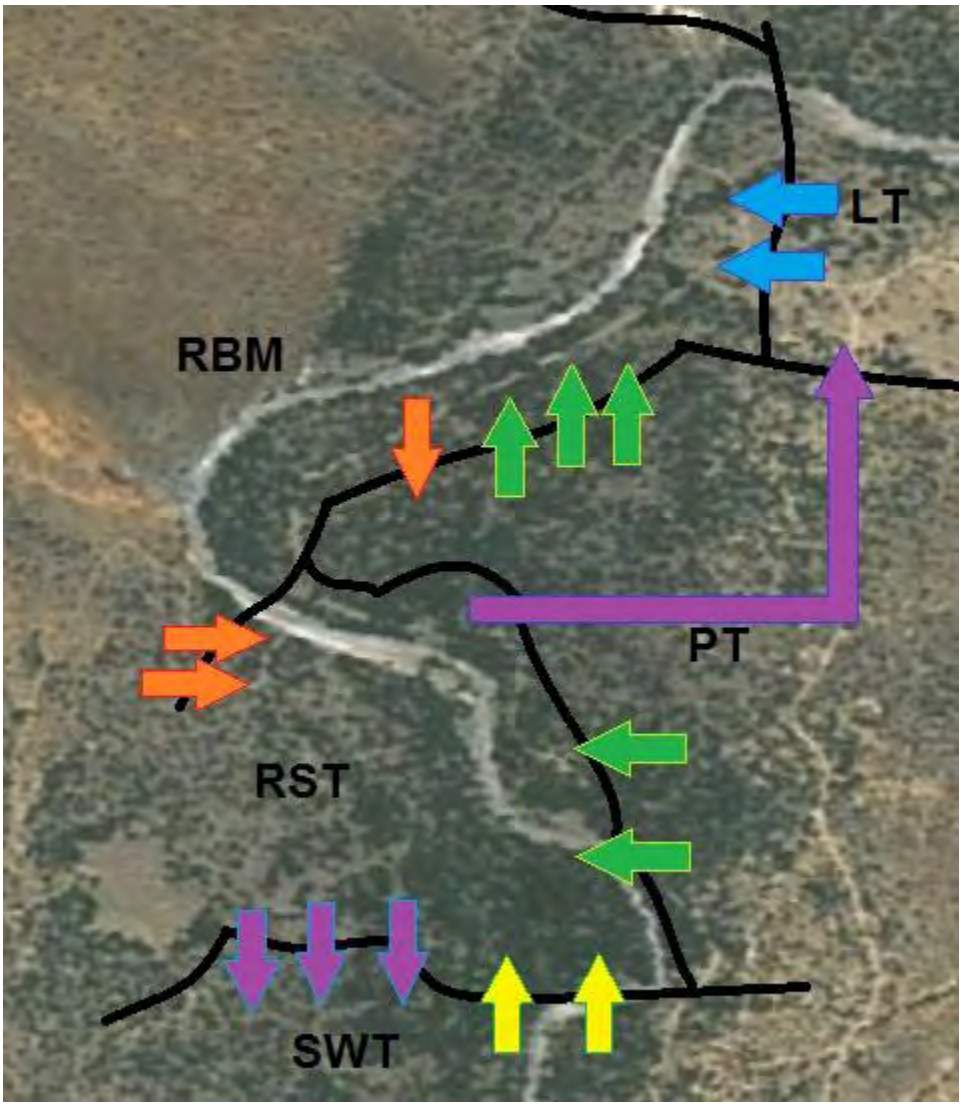

Figure 11. 2010 migration paths of males for both study troops (RBM and RST), and three neighbouring troops. Each arrow indicates one male transfer.

Of 24 males that transferred into or out of the two study troops for 2010, prior or subsequent location of the migrants is known for 14. Two males from PT spent a month

in RST troop during the breeding season before emigrating to their subsequent troop (counted as two migrations per male in Figure 11). 13/14 known location males (93%) transferred one troop either up or down the river system. One male from PT (as described above) used RST as a transfer group, ultimately residing in LT, a troop two territories upstream. Each study troop had two natal males a year apart in age (as estimated from their size).

Aggression and Dominance

David Scores

David Scores calculate dominance ranks of individuals in a group based on dyadic agonistic interactions. Normalised David Scores were calculated as suggested by de Vries et al., (2006). The male's calculated NDS and rank was used for all results regarding dominance.

Table 7. Normalised David Scores and rank for each male for both troops.

Troop	Male	Normalised David Score	Rank
RBM	Vi	7.969348894	1
RBM	Ca	7.649934539	2
RBM	Dn	6.937124118	3
RBM	St	5.362629269	4
RBM	Wh	5.132665945	5
RBM	Kp	5.049603175	6
RBM	Wy	4.745174964	7
RBM	Ha	4.2379329	8
RBM	Eg	4.073030102	9
RBM	Bl	3.554094516	10
RBM	Ta	2.470777581	11
RST	**Aj**	**19.46438808**	**1**
RST	**Or**	**14.19353946**	**2**
RST	**Ju**	**13.0202762**	**3**
RST	**Go**	**12.95862161**	**4**

RST	**Bu**	**12.50565322**	**5**
RST	**Sp**	**12.01970863**	**6**
RST	**Bo**	**10.48225469**	**7**
RST	**Tw**	**10.3051175**	**8**
RST	**Ko**	**10.09695075**	**9**
RST	**Oz**	**9.941213259**	**10**
RST	**Dy**	**9.4430577835**	**11**
RST	**To**	**8.944902308**	**12**
RST	**Dg**	**8.901733856**	**13**
RST	**Mu**	**8.556473322**	**14**
RST	**Pa**	**8.149908578**	**15**
RST	**Tr**	**2.470777581**	**16**

A total of 1321 male-male agonistic encounters were recorded throughout the study period. 707 of these interactions were observed within a focal sample of a male, giving approximately 1.02 aggressions per focal hour. The context was recorded for 203/1321 interactions, and are described in Table 9. Behaviours observed during the aggressions are described in Table 8. Using the dominance matrix created for calculating David Scores (N=740), the top five ranking males in RST were involved in 551supplant/displacement interactions while the lowest ranking five males were involved in 241dominance encounters (supplants or displacements). Similarly, the top four ranking males in RBM were involved in 333 supplants/displacements, while the lowest four ranking males were involved in 181dominance encounters.

Table 8. Frequencies of known-cause aggressions (N=203)

Aggression context	**Frequency of event**	
Food	141	(69.4%)
Proximity to a female	42	(20.7%)
Grooming partner	9	(4.4%)
Space (sun/shade)	11	(5.4%)

Table 9. Descriptive behaviours of both aggressor and recipients in an agonistic encounter, and the resulting frequencies of each action. (N=1321)

Individual	Behaviour	Frequency (%)	
Aggressor	Physical aggression	17	(1.3%)
	Displacement	434	(32.9%)
	Supplantation	190	(14.4%)
	Facial threat	214	(16.2%)
	Chasing	66	(5.0%)
	Headbob/Bi-pedal headbob	53	(4.9%)
	Vocal threat	67	(5.1%)
Recipient	Submissive vocalization	682	(51.6%)
	Counter aggression	40	(3.0%)
	Redirection of aggression	24	(2.0%)

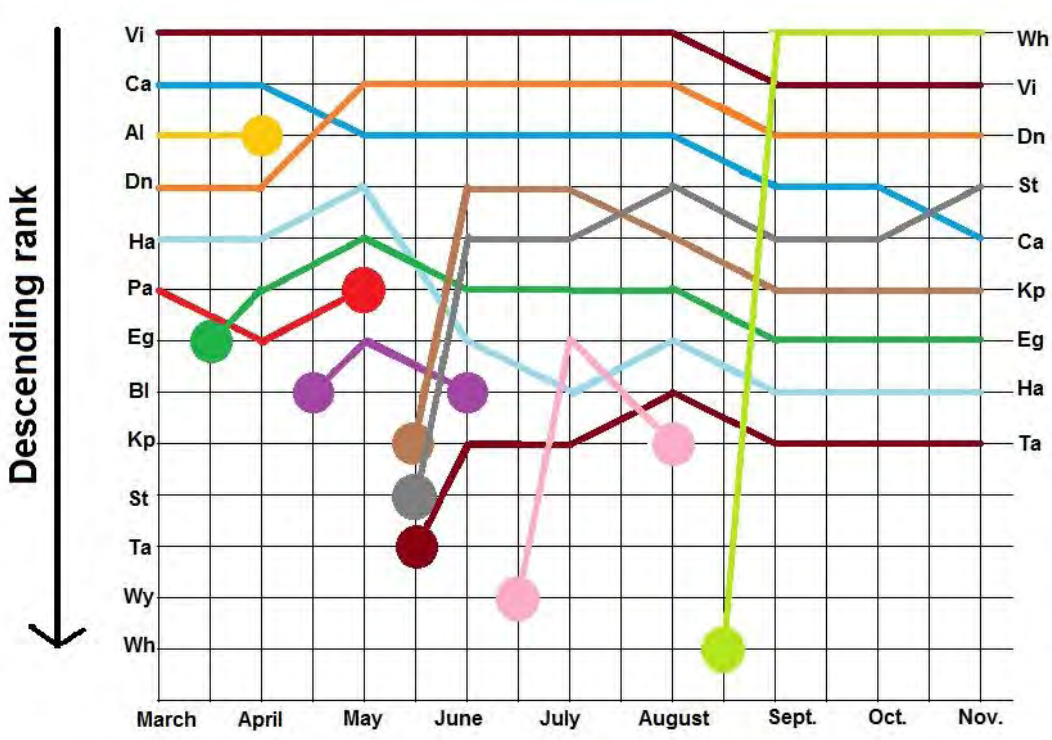

Figure 12. Consistency of RBM adult male dominance relationships over the period of nine months. Monthly hierarchy was calculated from total wins/losses of each dyad

Male ranks fluctuated with emigrations and immigrations of other males, and the volatile nature of the hierarchy is evident via at least one rank change observed every

month (Figure 12). The top ranking male (Vi) lost alpha to an immigrant male (Wh), whom had no observed agonistic encounters with any other male of the troop.

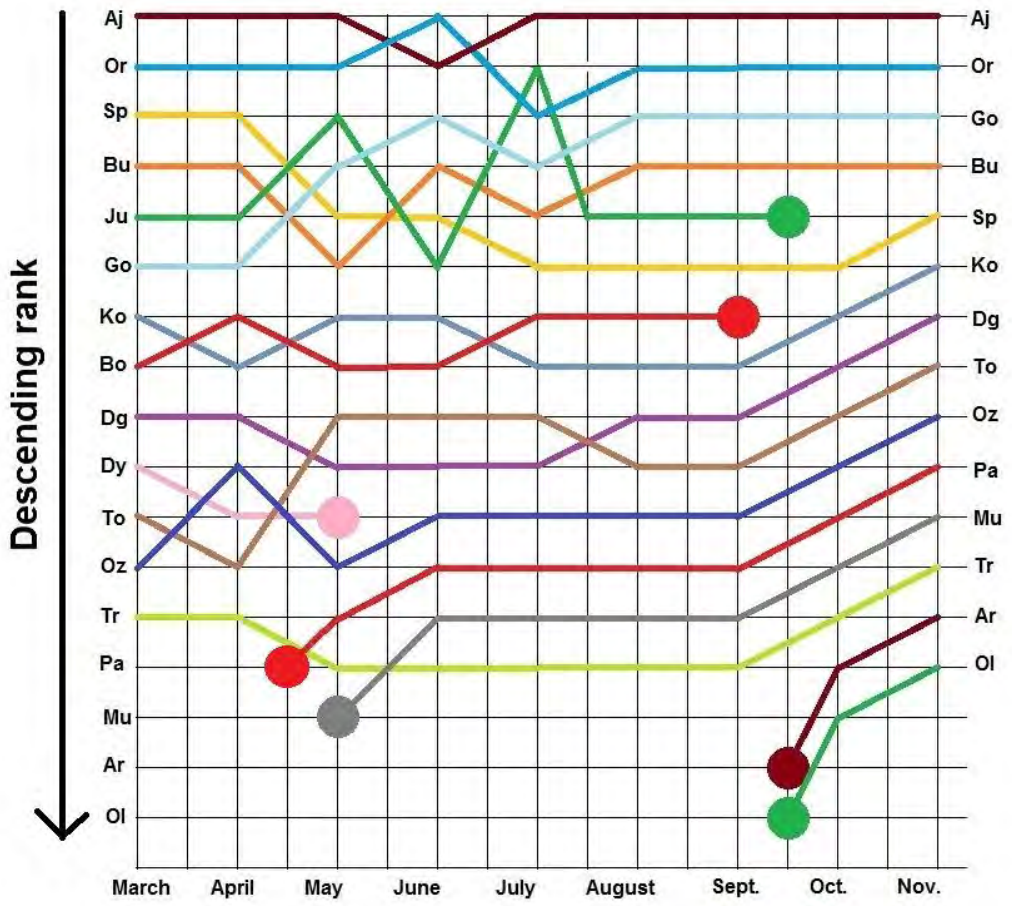

Figure 13. Consistency of RST adult male dominance relationships over the period of nine months. Monthly hierarchy was calculated from total wins/losses of each dyad.

Male ranks began fluctuating in April, and the majority of rank changes occurred within the breeding season of May-July (Figure 13). The male hierarchy can be grouped visually into clusters, with the obvious high ranking and low ranking groups. This grouping effect is also visible in Table 7 of the Normalised David Scores. Emigration of three males created a general rise in rank for individuals ranking lower than the emigrant.

A rank reversal was observed twice in one troop during the period of the study, both occurrences involving the highest and second highest ranking males (see Figure 13). The top ranking male (Aj) received a severe bite wound on the abdomen May 27, 2010 from an unobserved agonistic encounter. The second ranking male (Or) effectively removed Aj from the highest ranking position by May 31,2010 with two days of no observations in the span of the rank reversal. Or maintained the highest ranking position until receiving a severe wound on his right rear foot on July 6, 2010 by an unobserved aggression (seen in Figure 9a). Two days after Or's injury, Aj resumed the top ranking position of the troop, and maintained the position until leaving April 2011.

Wounds

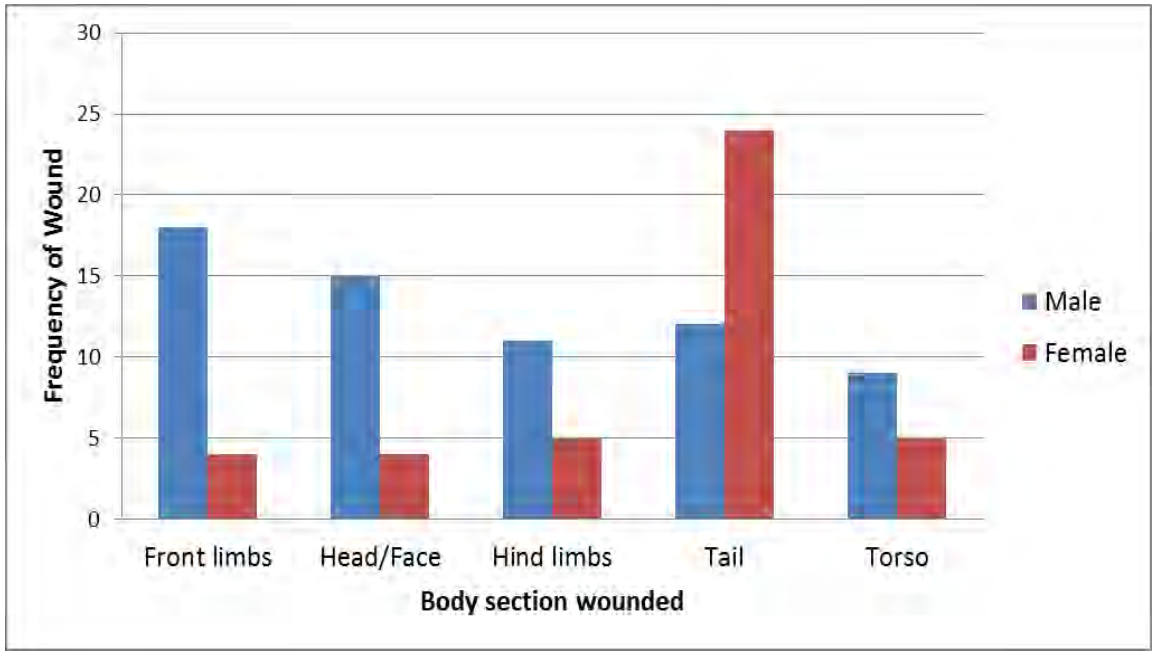

Figure 14. Sex differences in frequency of wounds and location (N_F=18, N_M=28)

27 adult and one sub-adult male were wounded out of a total of 35 males, and 18 out of 36 adult females were wounded throughout the study period (Figure 14). Of the 18 females, four head/face wounds were recorded out of a total of 47 wounds (8.5%). Of the 28 males, 15 head/face wounds were recorded out of a total of 66 wounds, equalling 23% of all wounds. Out of 15 males who migrated *into* one of the two study troops during the course of my study, nine males received a wound while in the new troop. Seven males (47%) received a wound within the first 22 days of immigration, with a mean of 12 ± 7.9 days of wounding from the initial immigration date.

Male wound frequency significantly increased during the breeding season, when compared to pre- and post-breeding months (Chi^2= 20.0, 2 df, P<0.001). There was no correlation between male rank and frequency of wounding (Spearman's Rank Correlation: r_s=0.280, N=26, P=0.307). Female received wounds significantly more on their hindquarters than their torso or forequarters (Chi^2= 16.3, 2 df, P<0.001), while male forequarter injuries were the predominant location of wounds before and during the breeding season, (66.6% and 50%, respectively).

Grooming and associations

A high GAI was not indicative of a high PAI, as seen in Tables 11 and 12. No PAI was zero for any dyad, suggesting that males do not exclusively avoid any particular male, but prefer to maintain proximity with certain individuals (as seen with higher PAI's). However, both Tables 10 and 11 have GAI's of zero, suggesting that males have particular males whom they have forged an affiliative relationship, while not engaging with other males.

Table 10. Grooming association indices(GAI), proximity association indices (PAI) and grooming reciprocity indices (dGRI) for each RBM dyad

Male A	Male B	GAI	PAI	dGRI
Ca	Dn	0.017735	0.207347	0
Ca	Ha	0.156117	0.272073	0.7562
Ca	Vi	0.649254	0.275585	0
Ca	Eg	0	0.169992	0
Ca	Kp	0.167273	0.083579	0.354037267
Ca	St	0	0.041304	0
Ca	Ta	0.205651	0.073423	0.3246
Ca	Wh	0	0.003802	0
Dn	Eg	0	0.229446	0
Dn	Ha	0.293607	0.267327	0.774193548
Dn	Kp	0.314658	0.097143	0.953
Dn	St	0	0.033167	0
Dn	Ta	0	0.092308	0
Dn	Vi	0.168239	0.237691	0
Dn	Wh	0	0.010593	0
Eg	Kp	0.186495	0.086538	0.988505747
Eg	Ta	0.12982	0.076696	0.8812
Eg	Ha	0.421352	0.169355	0.9176
Eg	St	0	0.080824089	0
Eg	Vi	0	0.149254	0
Eg	Wh	0	0.01	0
Ha	Kp	0	0.091633	0
Ha	Ta	0.341280972	0.075472	0.7324
Ha	St	0	0.049614	0
Ha	Vi	0.062703	0.225371	0
Ha	Wh	0	0.009021	0
Kp	Ta	0	0.090498	0
Kp	Vi	0.200326	0.090722	0
Kp	St	0	0.108860759	0
Kp	Wh	0	0.018939394	0
St	Ta	0	0.115942	0
St	Vi	0	0.042383	0
St	Wh	0	0.023952	0
Ta	Vi	0.03642	0.058696	0
Ta	Wh	0	0.004673	0

Table 11. Grooming association indices(GAI), proximity association indices (PAI) and grooming reciprocity indices (dGRI) for each RST dyad

Male A	Male B	GAI	PAI	dGRI
Aj	Bu	0.169056	0.102515	0.887983707
Aj	Or	0.074677	0.069282	0
Aj	Sp	0.138558	0.105657	0
Aj	To	0.068391	0.117987	0
Aj	Dg	0	0.089041	0
Aj	Go	0	0.085174	0
Aj	Ju	0	0.11264	0
Aj	Ko	0.20665	0.063123	0.5594
Aj	Oz	0	0.071707	0
Aj	Mu	0.363101	0.049628	0.608027327
Aj	Pa	0	0.039735	0
Aj	Tr	0	0.069795	0
Aj	Bo	0.07497	0.086364	0
Bo	Bu	0.444015	0.103191	0
Bo	Go	0	0.07818	0
Bo	Ju	0	0.073901	0
Bo	Dg	0	0.081148	0
Bo	Ko	0	0.07027	0
Bo	Or	0	0.095109	0
Bo	Oz	0.116145	0.08831	0.6667
Bo	Mu	0	0.026685	0
Bo	Pa	0	0.03177	0
Bo	Sp	0	0.07852	0
Bo	To	0	0.083184	0
Bo	Tr	0	0.067843	0
Bu	Or	0.237892	0.055877	0.836363636
Bu	Oz	0.076726	0.076581	0.9111
Bu	Sp	0	0.065259	0
Bu	Tr	0	0.054054	0
Bu	Dg	0	0.055459	0
Bu	Go	0	0.053097	0
Bu	Ju	0	0.077767	0
Bu	Ko	0	0.073755	0
Bu	Mu	0	0.049536	0
Bu	Pa	0	0.042017	0
Bu	To	0	0.058935	0
Dg	Oz	0.111255	0.125445	0.662790698
Dg	Ju	0	0.090413	0
Dg	To	0.620009	0.157658	0.6272
Dg	Go	0	0.071895	0

Dg	Ko	0	0.093656	0
Dg	Mu	0	0.033477	0
Dg	Or	0	0.10091	0
Dg	Pa	0	0.046857	0
Dg	Sp	0	0.109682	0
Dg	Tr	0.047348	0.067298	0
Go	Tr	0.196629213	0.040247678	0.01386
Go	Ju	0	0.072826	0
Go	Ko	0	0.066597	0
Go	Mu	0.379462	0.05151	0.695560254
Go	Or	0	0.053403	0
Go	Oz	0.338983	0.069231	0.9256
Go	Pa	0.245852	0.042969	0.838445808
Go	Sp	0	0.062565	0
Go	To	0	0.05102	0
Ju	Ko	0	0.088662	0
Ju	Mu	0	0.029677	0
Ju	Or	0	0.108826	0
Ju	Oz	0	0.123802	0
Ju	Pa	0	0.03453	0
Ju	Sp	0	0.078565	0
Ju	To	0	0.099243	0
Ju	Tr	0	0.05	0
Ko	Or	0	0.096854	0
Ko	Oz	0	0.132251	0
Ko	Pa	0	0.036601	0
Ko	Sp	0	0.116337	0
Ko	To	0.061387	0.081015	0
Ko	Tr	0	0.054697	0
Ko	Mu	0	0.042892157	0
Mu	Or	0.046537	0.035802	0.5476
Mu	Oz	0	0.020112	0
Mu	Pa	0.587413	0.239782	0.6288
Mu	Sp	0	0.034398	0
Mu	To	0	0.026699	0
Mu	Tr	0.115411	0.038375	0
Or	Oz	0.101043	0.073038	0
Or	Sp	0.43804	0.1534	0.217821782
Or	Tr	0	0.057485	0
Or	Pa	0	0.064559	0
Or	To	0.201178	0.081414	0.6195
Oz	Sp	0	0.100697134	0
Oz	Pa	0	0.03436	0

Oz	To	0.065696	0.123751	0
Oz	Tr	0.084644	0.06413	0
Pa	Sp	0	0.034076	0
Pa	To	0	0.02228	0
Pa	Tr	0	0.019405	0
Sp	To	0	0.080327869	0
Sp	Tr	0	0.05125149	0
To	Tr	0.066236811	0.048292108	0

There were 110 male-male grooming interactions throughout the study period, totalling 290 minutes of grooming time. Of a total of 693 focal hours, males spent 4.83 hours grooming other males, representing 0.69% of total time engaging in intra-sex grooming. With 15614 instantaneous male scan samples, 110 scans recorded male-male grooming (0.70% of all scans).

Table 12. Total grooming duration time (s) between RST dyads. The rows are male grooming effort, and the columns are male grooming received.

	Aj	**Bo**	**Bu**	**Dg**	**Go**	**Ju**	**Ko**	**Mu**	**Or**	**Oz**	**Pa**	**Sp**	**To**	**Tr**
Aj	*	124	273	0	0	0	113	815	0	88	0	221	0	0
Bo	0	*	0	0	0	0	0	0	0	47	0	0	0	0
Bu	218	115	*	0	0	0	0	0	96	41	0	0	0	0
Dg	0	0	0	*	0	0	0	0	0	115	0	0	414	0
Go	0	0	0	0	*	0	0	617	0	361	284	0	0	22
Ju	0	0	0	0	0	*	0	0	0	0	0	0	0	0
Ko	291	0	0	0	329	0	*	0	0	0	0	0	100	0
Mu	356	0	0	0	0	0	0	*	23	0	581	0	0	170
Or	133	0	69	0	0	0	0	61	*	0	0	360	127	0
Oz	0	94	49	57	419	0	0	0	126	*	0	0	158	113
Pa	0	0	0	0	205	0	0	1267	0	0	*	0	0	0
Sp	0	0	0	0	0	0	0	0	44	0	0	*0	0	0
To	201	0	0	906	0	0	0	0	283	0	0	0	*	113
Tr	0	0	0	25	293	0	0	0	0	0	0	0	0	*

Table 13. Total grooming duration time (s) between RBM dyads. The rows are male grooming effort, and the columns are male grooming received.

	Ca	Dn	Eg	Ha	Kp	St	Ta	Vi	Wh
Ca	*	31	0	152	265	0	87	966	0
Dn	0	*	0	228	264	0	0	107	0
Eg	0	0	*	306	88	0	89	0	0
Ha	250	144	361	*	0	0	171	58	0
Kp	57	290	86	0	*	0	0	0	0
St	0	0	0	0	0	*	0	0	0
Ta	449	0	113	296	0	0	*	0	0
Vi	0	0	0	0	123	0	81	*	0
Wh	0	0	0	0	0	0	0	0	*

RST males groomed between zero and seven of the potential fourteen grooming partners, while RBM males groomed between zero and five of the potential eight grooming partners. One male in each troop neither groomed nor received grooming from other males.

Of the 110 bouts, 74 (67%) were strictly unidirectional (seen in Tables 12 and 13), and 43% of these unidirectional bouts (32/74) consisted of grooming up the hierarchy (lower ranking male grooms higher ranking male, grooming is not reciprocated). In the remaining bouts (N=36), 17 (47%) were reciprocated once (Male A grooms B, Male B grooms A, both individuals stop) and 19 (53%) were grooming bouts that were reciprocated several times (A groom B, B grooms A, A grooms B again…) . 32% of grooming bouts were between males side-by-side in rank.

There was a significant positive correlation between grooming association index (GAI) and proximity association index (PAI) for each male dyad (r_s=0.447, N=126 dyads, P<0.01). There was no correlation between dGRI and the number of grooming

bouts (Pearson's Correlation: r_s= -0.056, N=55, *P*=0.685). There was an absolute mean distance of 4.26 ranks per dyad.

A mixed model was run to determine the relationship between male rank and PAI (if any) as high ranking males were expected to have higher levels of associations due to their status (Table 14).

Table 14.The fixed effects and random effects from the second ranked model (Timing +RankMaleA +RankMaleB)

	Estimate	Std. Error	t value
(Intercept)	0.015881	0.024540	0.647
Male.A.SDS	0.062093	0.021417	2.899
Male.B.SDS	0.052224	0.034190	0.034190
TimingB	-0.034569	0.005525	-6.256
TimingD	-0.008923	0.005525	-1.615
Groups	**Name**	**Variance**	**Std.Dev.**
Male B	(Intercept)	0.00081229	0.028501
Male A	(Intercept)	0.00021509	0.014666
Residual		0.00193057	0.043938

Note: Male.A.SDS: Standardized David Score of Male A; Male.B.SDS: Standardized David Score of Male B; TimingB: Scan samples before breeding season; TimingD: Scan samples during breeding season.

No relationship was found between male rank and PAI, although higher ranking males had higher association levels than lower ranking males (Figure 15).

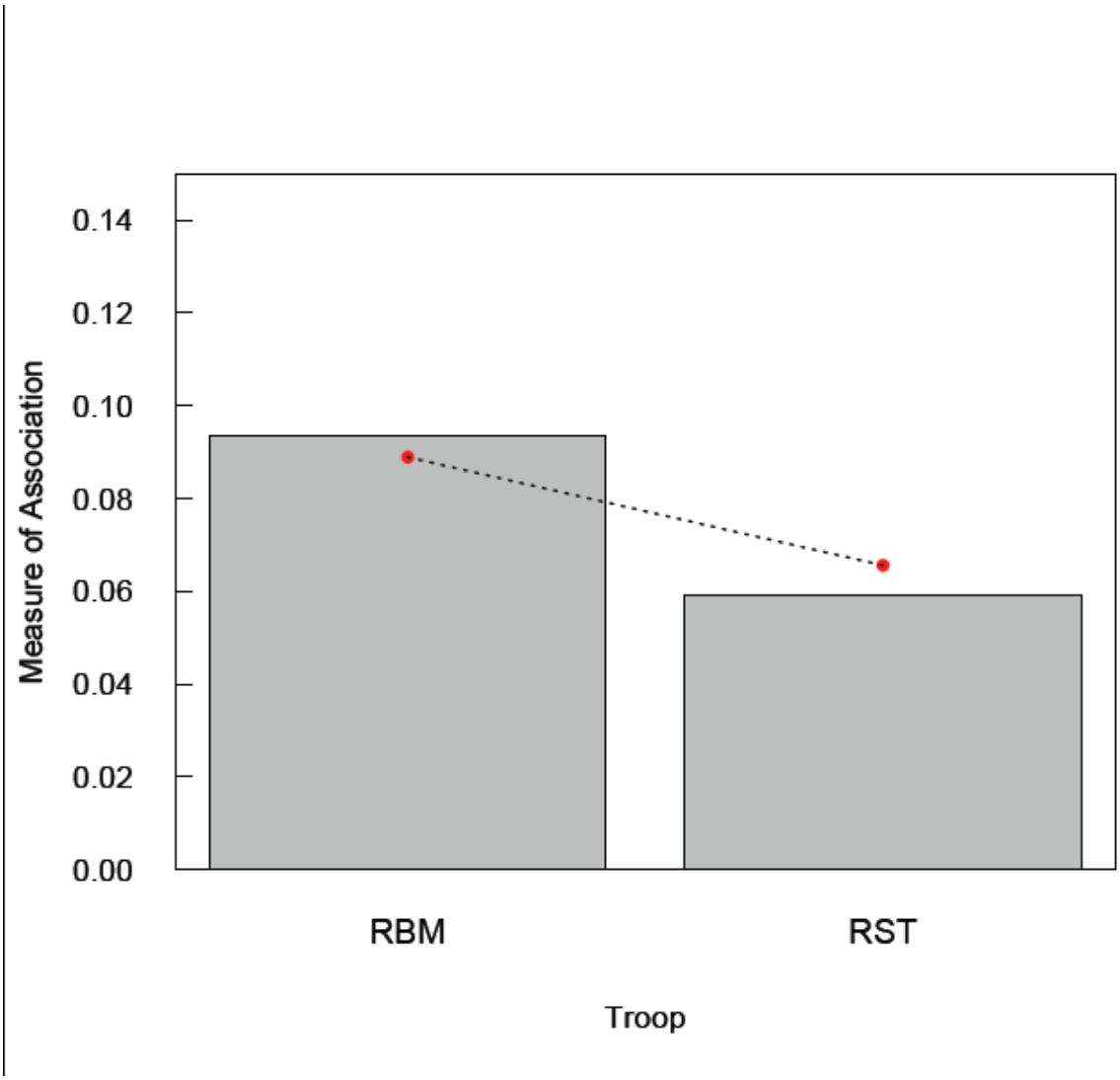

Figure 15. Relationship between proximity association index and male rank, where black points and line indicate data and effect for Male A, and red points and line indicate data and effect for Male B.

Coalitions

16a.

Males 4, 9 and 20 are foraging as male 18 arrives (numbers indicate ordinal rank). The footage was taken in 2009, before the current study began and when the male cohort was larger.

16b.

18 turns and threatens 20, as then does 4. The context of the threat was not identifiable.

16c.

20 moves back with defensive bared teeth expression. 9 then threatens 20 as do 4 and 18.

16d.

18 stands bipedally and headbobs at 20 while 4 observes and 9 vocalises.

16e.

18 goes to 9 and grooms him; 4 moves towards 20 threatening as 1, the alpha male arrives and walks in front of 20 en route to 18 and 9 .

16f.

As 1 sits by 18, 9 runs towards 20 who moves off. 4 stops threatening. 18 then joins 9 in chasing after 20 (not shown).

Figure 15. Video footage of male coalition formation.

General description of coalitions

A total of 62 coalitions was observed during my study period. These constituted 3.6% of all male-male agonistic encounters, with a focal participating at a rate of 0.04 coalitions/ hour. Both troops were observed to have coalitions, with RST totalling 41 coalitions (N=12-14 males) and RBM totalling 21 coalitions (N=4-9 males). 85.5% (N=53) of the coalitions were triadic, while14.6% (N=9) of the coalitions were polyadic (11.3% three against one, and 3.3% two against two). Several times (N=11), coalition support was solicited by repeated glancing of the initial aggressor between the target and partner. Seven attempted coalitions were observed, with the initial aggressor failing to solicit support from another male in proximity. Forty coalitions were observed from their onset. 32.2% (N=20) of coalitions involved the partner vocally threating the target, and 50% (N=31) of coalitions involved one or both partners chasing the target from the immediate vicinity.

Dynamic of coalitions

All male ranks participated in forming partnerships in coalitions, and/or were targeted by a coalition dyad (Figure 17).

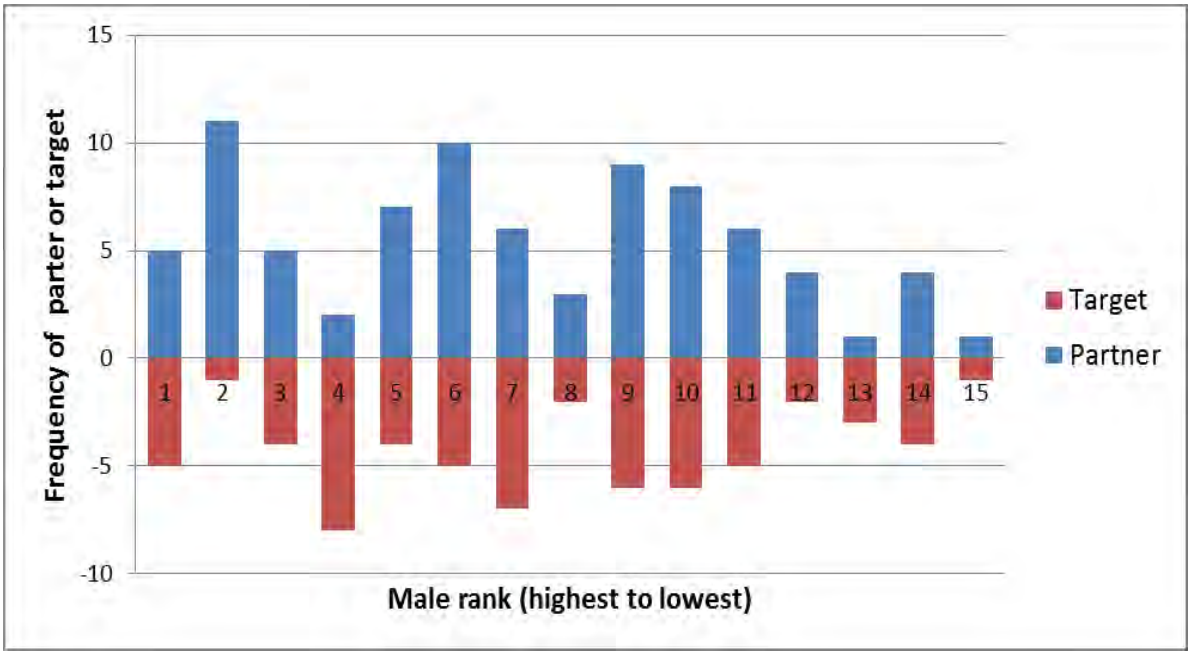

Figure 17. Frequency of coalition partner or target depending on male rank

The relationship between a male's rank and the frequency with which he was a partner in a coalition was not statistically significant (r_s= -0.444, N=15, *P*=0.097). There was no relationship between male rank and the frequency with which he was a target of the coalition (r_s= -0.252, N=15, *P*=0.364). 9.67% (N=6) of coalitions were formed by two immigrant males, 12.9% (N=8) of coalitions were formed by one immigrant and one resident male, and the remaining 77.4% (N=48) of coalitions were formed by two resident males. Immigrant males were the targets of 33.9% of all coalitions, which is significantly different than expected (Chi^2=6.229, 1df, P<0.05). Expected values assumed that immigrant males would receive the same frequency of targeting that resident males received. The reciprocity between coalition partners was not statistically significant (r_s= 0.289, N=39, *P*=0.075). If Male A joined Male B, and subsequently Male B joined Male A in a coalition, this was labelled as reciprocation. Reciprocity was calculated as the

frequency of reciprocated coalitions out of the total number of coalitions the dyad were involved in. Targets only retaliated on 13/62 occasions (21%) and were not more likely to do so if they were higher ranking than the initiator (Chi^2=0.136, 1df, *P*=0.71, Yates correction applied). Only three (23%) targets retaliated during an all-down coalition while the remaining ten targets retaliated during an all-up or bridging coalition (five retaliations per coalition configuration, respectively). No observed coalitions resulted in visible wounding of the target.

Classification of coalition type

Classification of coalitions was assessed by Pandit and van Schaik's (2003) model of coalitions (see Figure 18). All-down coalitions comprised of 20.97% of all coalitions with a frequency of 13 occurrences. Bridging coalitions had a frequency of 21 occurrences (33.87%), and all-up coalitions occurred most frequently at 45.16% (N=28) of all coalitions. Asymmetry of strength, as measured using Normalised David Scores, between coalition partners and target did not indicate successful coalitions (Chi^2=0.0016, 1df, P=0.096). A successful coalition was defined as the target not retaliating against the aggressors.

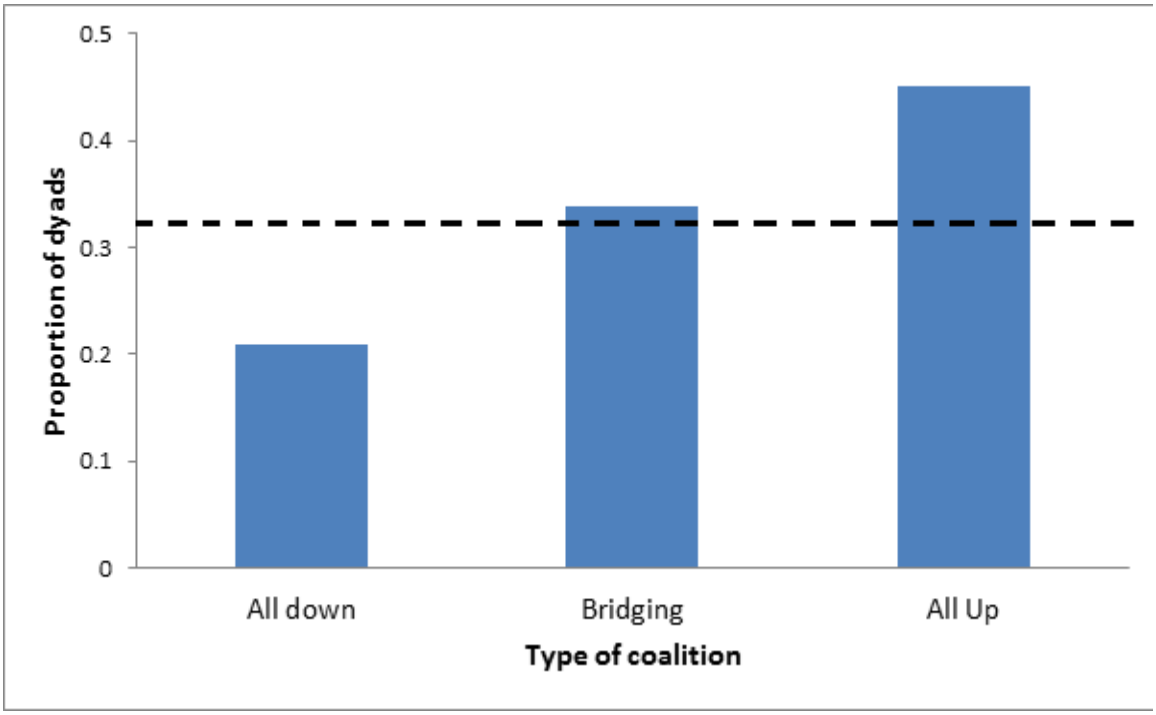

Figure 18. The rank-related configuration of coalitions. The dashed line indicates the expected distribution, on the assumption that the three configurations are equally likely.

Context of coalitions

The initial context of the coalitions was known for 20/62 (32.58%) of all observed coalitions (see Figure 19). 40% of known cause coalitions were over the target's proximity to a sexually receptive females. Coalition members chased the target individual away from the female 5/8 times, and vocally threatened the target in all cases. Neither coalition partner ever copulated with the consorting female subsequently.

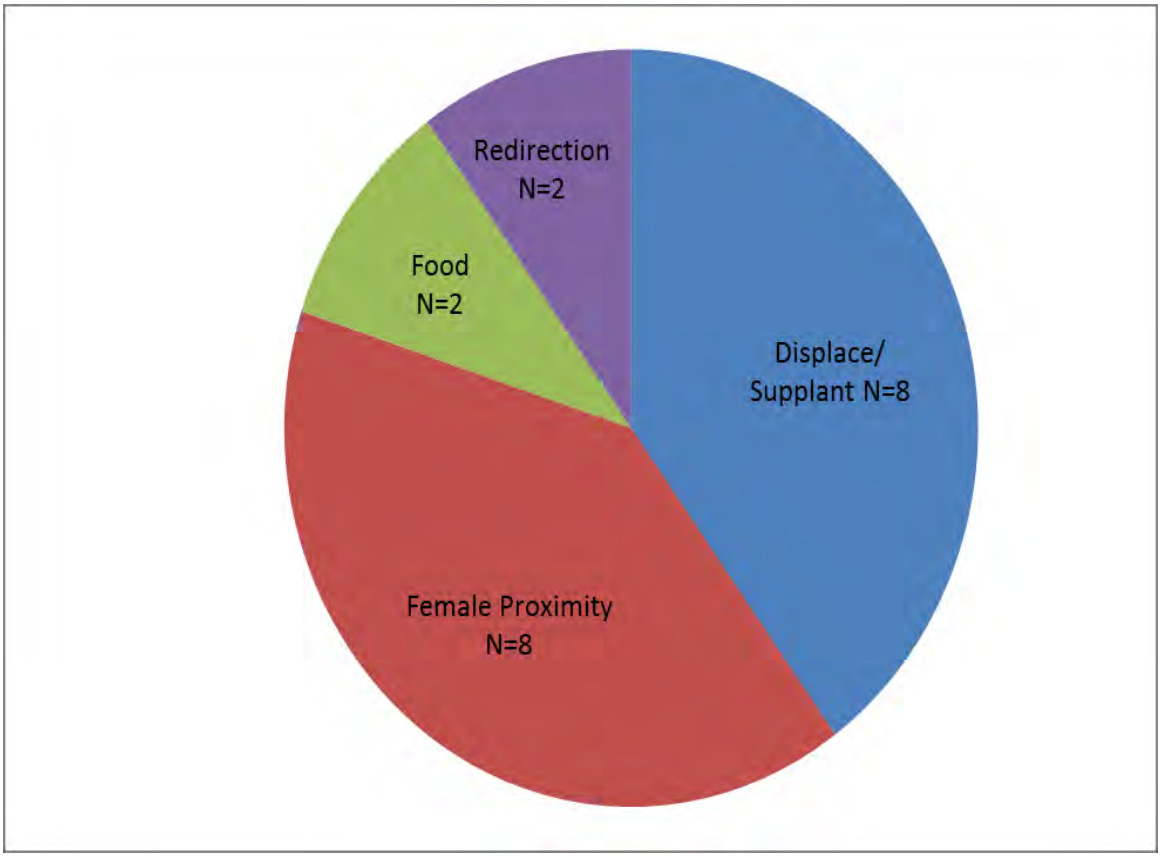

Figure 19. Context of known cause coalitions (N=20)

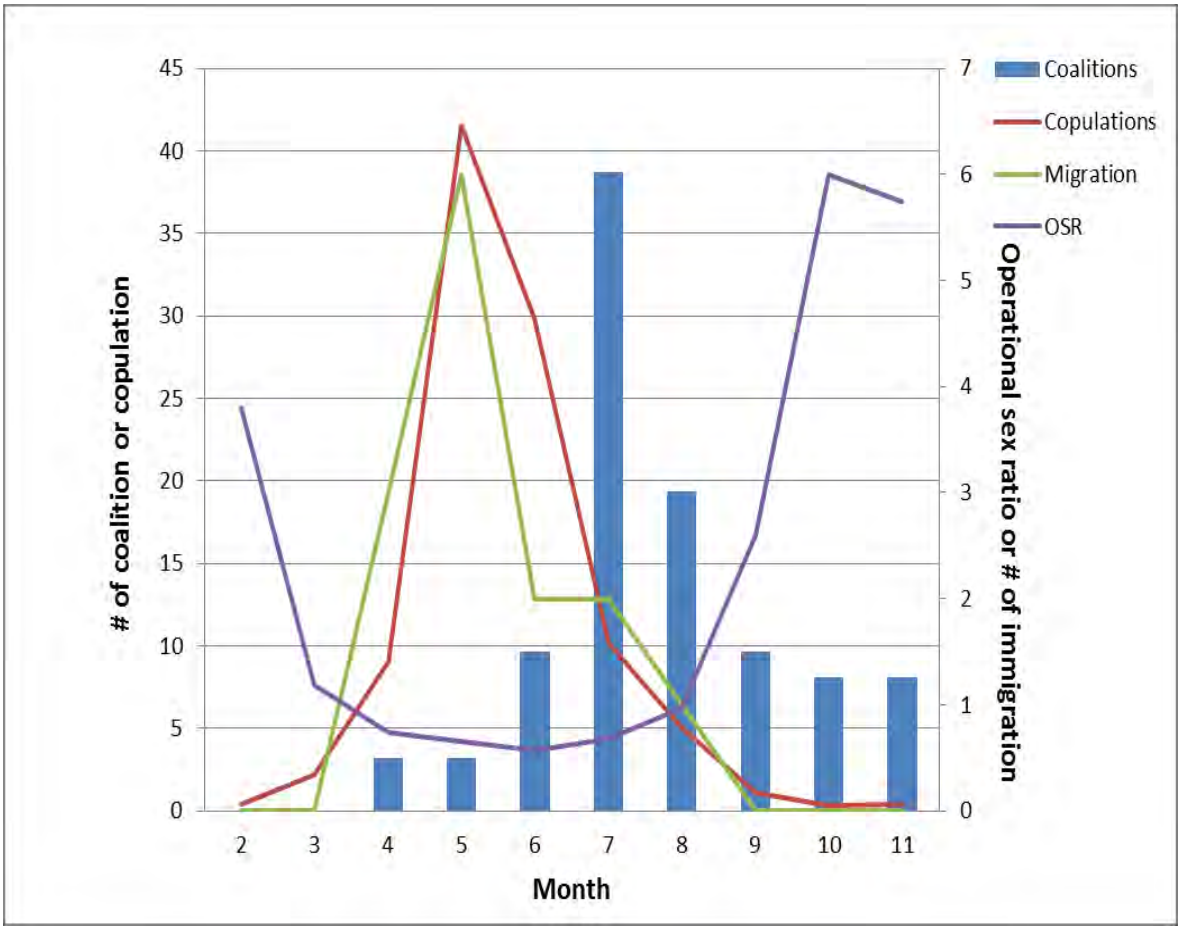

Figure 20. The temporal relationship between mating activity and male coalitions (left axis), and observed monthly frequency of male migration (right axis). The operational sex ratio (OSR: males/receptive females) is also indicated.

While there was a significant relationship between monthly migration and copulation frequency across months (Figure 20), mating activity peaked two months before coalition formation and their monthly frequencies not correlated (rs=-0.02, N=10, *P*=0.94). There was also no correlation between coalition frequency and OSR (r=-0.24, N=10, *P*=0.5).

Familiarity of coalition members

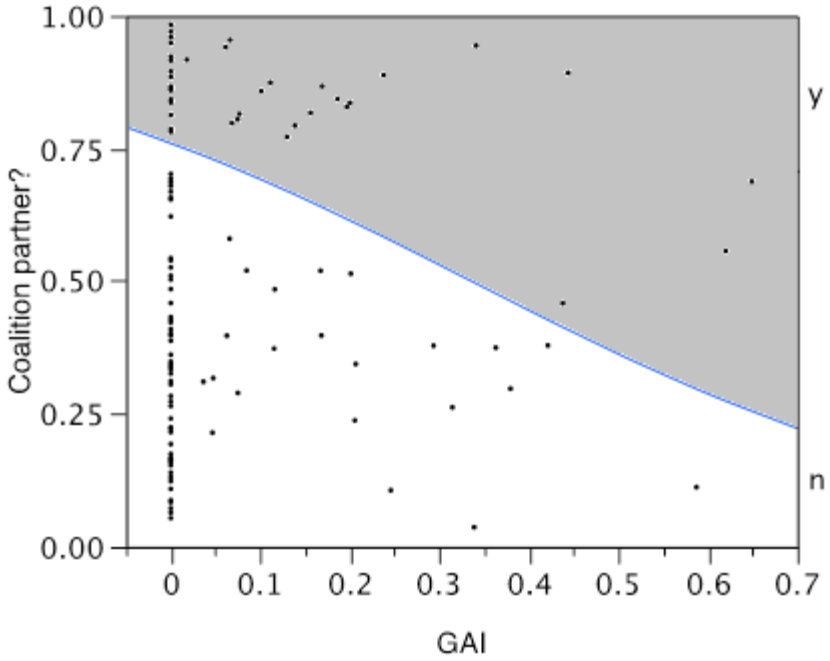

Figure 21. Probability of two males being coalitions partners in relation to their grooming association index

A logistic regression (Figure 21) indicates that male dyads who groomed frequently were significantly more likely to be coalition partners (Chi^2= 6.32, 1 df, P<0.05). The same relationship held for proximity associations based on nearest neighbours (Figure 22), suggesting that males who has a high PAI were significantly more likely to be coalition partners (Chi^2= .

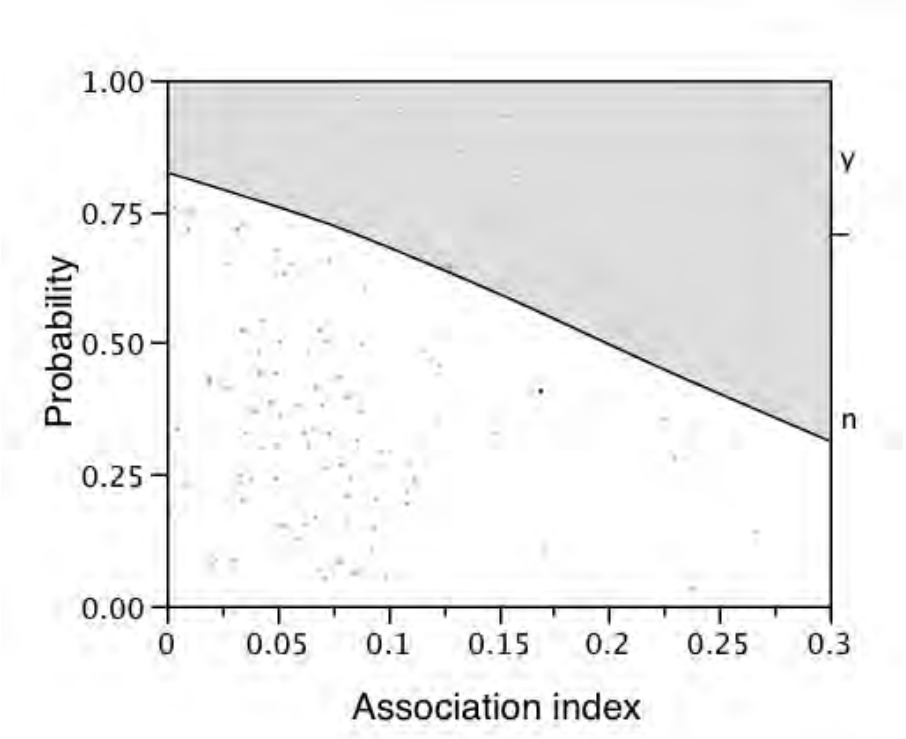

Figure 22. Probability of two being coalition partners in relation to their proximity association index.

3.9 Discussion

Migration

Cheney & Seyfarth (1983) report male vervets migrating from their natal troop with genetically related peers (both maternal or paternal half-brothers), and also report males are more likely to migrate to a particular troop over others. However, these non-random dispersals do not decrease the genetic differences between groups because non-natal males migrate in less predictable fashions and also migrate to more distant troops. Cheney & Seyfarth (1983) support this hypothesis of non-natal males migrating to more distant troops with reports of some males always migrating to non-adjacent troops. van Noordwijk & van Schaik (1985) confirm both of these hypotheses for natal and non-natal male long-tailed macaques (*Macaca fascicularis)*. While I observed two pair of natal

male dyads migrated together (within a week's lapse) into the neighbouring troop, with only four migrations out of the 24 total males who migrated during 2010, my data does not support the Cheney & Seyfarth (1983) hypothesis. The frequency of known-location migrants was low for non-adjacent troop migrations, but I did have one male migrate two troops upriver in the breeding season. The remaining 8/24 males whose starting or ending migration location was not known could possibly have moved up or down river to troops that my two study troops did not interact frequently with. It has been suggested that natal males migrate with peers into neighbouring troops for ease of access to allies (Cheney & Seyfarth, 1983). While this hypothesis may be supported with evidence of coalitions, it is difficult to determine if the familiar presence of a known natal male decreases the stress level of the immigrant (since their interactions are previously known) therefore increasing the likelihood of coalition formation. The simple presence of a 'known face' in the sea of unknown individuals may be sufficient for dual migration with peers, without even considering the chance of supporting each other during aggressive encounters.

Male residency seems to fluctuate in the literature. Henzi & Lucas (1980) reports an average residency length of 34.4 months, while my study observed an average of 12.3 months per male (mean of both troop's residency times). The large cohort size of my troops may cause the observed residency time. Subordinate males transfer troops more frequency than dominant males (Henzi & Lucas, 1980), and the large cohort size inherently creates more low ranking positions as the cohort increases in size. This may explain why RST (the larger troop) has a slightly smaller residency time than RBM (12.1 months to 12.4 months, respectively), although the difference is almost negligible.

For long-tailed macaques, the operational sex ratio of the troop did not seem to influence the immigration rate of males (van Noordwijk & van Schaik, 1985). My data supports this hypothesis, with RBM receiving less immigrants than RST (RBM had 11 males, RST had19 males over two breeding seasons) even though RBM's OSR was higher than RST's (Table 1). I report a significant correlation in migration and copulation frequencies, and reported macaque data is highly supportive of this trend: long-tailed macaques (van Noordwijk & van Schaik, 1985), barbary macaques (Kuester & Paul, 1999), and rhesus macaque males (Boelkins & Wilson, 1972) report higher dispersal rates during the mating season. Henzi (1982) and Henzi & Lucas (1980) also report a correlation between breeding season and high frequency of migrations for vervets. The possibility of conception seems to be the driving factor for migration, although the operational sex ratio did not seem to affect the number of immigrants into a troop. The number of sexually mature females did not affect the direction of male movement in Henzi & Lucas' (1980) study either.

Henzi (1982) reports newly immigrated males receiving 67% of all wounds, and received more harassment from established males than previously received in their prior troop. While only 47% of all immigrating males received a wound within the first 22 days of migration, the total wounds received by immigrating males observed equalled 15% for all wounds throughout the study period. When only male wounds are examined, immigrant males received 14/65 (21.5%) of all male wounds, suggesting that migrants are not being targeted for physical aggression. Regardless of the percentage of immigrant male wounding, these observations suggest that immigration can incur a cost of serious aggression from resident males. The significant correlation between migrations and

conception may override the chance of serious wounds, considering aggression was shown to increase during the breeding season.

Dominance and aggression

Drews (1996) reports a one-step drop in dominance associated with injury in two male baboons, where ranks were reversed after the wounding. A rank reversal was observed twice during the course of my study, involving the same individuals during the breeding season, as described in the Results section. The male hierarchy was linear but unstable (Cheney & Seyfarth, 1989) therefore dominance displays were a daily occurrence of all males (evident from the large sample size of 1321 aggressions during the study period). This being said, the wounding of a male may allow another male to rise in rank above the injured male as a result of his compromised condition. In each situation, the inability to assert dominance by the top ranking male allowed the second highest male at the time to assume the highest rank within four days of the injury. It is not assumed that the second ranking male was the individual to injure the highest-ranking male for either case, but this male *was* the individual rise in rank accordingly. Physical aggression during agonistic bouts was rare, (1.3%) suggesting that physical combat was usually avoided with the consequence that injuries were avoided. Fighting is energetically expensive and increases the chance of wounding, therefore this behaviour would have been selected for only if the benefits outweighed the costs (Baldellou, 1991). Overt aggression is unnecessary if a supplant or displacement is sufficient to reassert the priority relationship between two males. Just under half of all interactions, (47%) involved a displacement or a supplant between males. This suggests that this behaviour typically is sufficient to reassert the dominance relationship. Male aggressors employ

other low-energy tactics during agonistic encounters such as facial or vocal threatening. Chasing was only seen in 5% of agonistic bouts, a behaviour that is more energetically expensive than facial threatening (which was usually performed while standing still, pers. obs). Henzi (1982) coined the term 'homage' to refer to self-initiated displays of subordination: and such behaviour was the predominant response of the recipient (as seen in Table 9, labelled 'submissive vocalisation'). Homage may function to demonstrate the subordinate's submissiveness thereby appeasing the dominant male (Baldellou, 1991). This appeasement may prevent the interaction from escalating because the recipient is demonstrating subordination immediately. The low rate of counter aggression against the aggressor (3.0%) and physical combat by the aggressor (1.3%) highlights the effective nature of dominance displays, supporting Struhsaker's (1967a) hypothesis.

Of the 82 changes in the adult male composition of both study troops seen in Figures 12 and 13, 25 resulted from 13 males immigrating or emigrating from the troop. Emigration can positively affect the males ranking lower than the emigrant, by causing a rise in rank for all lower-ranking individuals. Alternatively, immigration negatively affects all males ranking lower than the immigrant, by causing a decrease in rank for all lower-ranking individuals. With over 30% of rank changes associated with migration, this highlights the linear but unpredictable nature of the male dominance hierarchy described by Cheney & Seyfarth (1989). Agonistic aggressions between males resulted in the remaining 70% of rank fluctuations, suggesting that males were contesting status although the exact explanation for male rank is undecided. High ranking male rhesus macaques supplanted, displaced, approached and attacked other males more often than low ranking males (Silk, 1994), and my data support the idea that high ranking male

vervets perform all of these aggressive behaviours more often than low ranking males (with top ranking males involved in 47.7% more aggressions [884 encounters vs. 422 encounters] than low ranking males).

The nature of a supplant (agonist gaining space, food or grooming partner) and my reported frequency of supplants (191/1321, 14.4%) suggest that higher ranking males can gain resources that lower ranking males otherwise would not be able to access. The immediate gain of food or grooming partner can increase the overall fitness of the individual through nutrition, hygiene and stress reduction.

Wounds as indicators of severe aggression

The consequences of injury can lower mating opportunities due to the reduction or competitive ability, or the physical incapability of grasping and mounting the female (Drews, 1996). One male (Aj) in my study injured his right hand during the breeding season, and many attempted copulations were unsuccessful due to the inability to properly mount the female with the injured hand. My results support Chapman & Legge's (2009) report of Cercopithecoid males having higher frequencies of forequarter wounding. My males were observed to have higher frequencies of wounding during the breeding season, reporting the same finding as Henzi (1982) regarding increased agonistic encounters during the breeding season. However, the similarities of wounding pattern between males and females do not show the same results as Baldellou's (1991) or Henzi's (1982) study, as my study observed male head/face wounding is over twice as likely as female head/face wounding. This discontinuity was continued with differing reports of Whitten & Smith's (1984) observations of stump-tailed macaques. These

researchers report that male forequarter injuries are the highest of all injuries only in the breeding season, while my study reports the pre-breeding and breeding season months having high frequencies of forequarter injuries. High ranking males were found to have a significantly higher likelihood of wounding, which is directly opposite than the stump-tailed macaques findings. This discrepancy in rank and likelihood of wounding is unusual as low ranking males are at the bottom of the hierarchy and are the recipients of aggression from high ranking males. Whitten & Smith (1984) suggest that older males may be more skilful in avoiding injury, but unfortunately the age class of my males cannot be deciphered because of the short time period since the study site began. Male baboon fights can result in either the winner or loser sustaining an injury (Drews, 1996), therefore being the high ranking male in a fight has no guarantee against injury. Drews (1996) reports the alpha male sustaining the highest number of wounds per damaging fight, a statistic congruent with the alpha males in this study. Injured olive baboons will avoid interacting with other males (Harding, 1980), and other troop males may directly seek out and aggress against the wounded male (Drews, 1996). This phenomena was observed in my study, Or (ranked #1 at the time) sustained a severe foot wound and was observed paying homage (subordinately chuttering) to any male that approached him.

Grooming and Association

Social bonds between males are thought to be based on kin selection, and are rare between unrelated individuals because of competition for the same resources (van Hooff & van Schaik, 1994). These social bonds are formed through repeated affiliative interactions such as grooming (Berghänel et al., 2011). Male social interactions can range

between more agonistic or affiliative between species. Male bonnet macaques are generally affiliative, while male lion-tailed macaques (*Macaca silenus)* are more agonistic in their interactions (Singh et al., 2010). Males may use grooming to lower the amount of agonistic interactions they receive (Watts, 2002). Avoiding aggression by appeasing other males may lower stress and increase access to resources. This being said, allogrooming of males serves multiple purposes (hygiene, release of endorphins) therefore males may not be exchanging grooming for anything other than the act itself (Henzi & Barrett, 1999). Male savannah baboons (Noë, 1990) do not groom each other yet form alliances, supporting Henzi & Barrett's (1999) hypothesis that social interactions are not solely mediated by grooming. Top ranking males may demand grooming from low ranking males without reciprocating the behaviour (Watts, 2002) and this was observed multiple times throughout my study period. Silk (1994) suggests that grooming up the hierarchy may be maintenance by lower ranking individuals because higher ranking individuals are more valuable in coalitions and support is usually given to males who groom the most.

Baldellou (1991) suggests that vervet male-male grooming differs from female-female grooming in its long-term implications for social bonds. Comparatively, male Barbary macaques rarely groom one other, and when they do so, use an infant as a buffer to facilitate the interaction (Paul et al, 1996). Vervet males do not use infants as affiliative buffers, but male-male grooming was a rare behaviour, which is the same for Barbary macaques. While McGuire et al. (1983) report 2-8% of all male vervet time spent engaging in affiliative behaviour between both sexes, Henzi's (1982) study reports 48.5% of all *social* interactions of males are grooming. Henzi's data broken down into

sexes gives 11% of grooming time was male-male grooming, and 53% of grooming time was directed towards females and males. When my total grooming times are broken down, I report 19.9% of grooming total time was spent male-male grooming, and 56.9% grooming total time was spent grooming females. Comparing my data to McGuire et al.'s data set, my males spent 4.23% of their time engaging in affiliative behaviour between sexes. This discrepancy may be caused by captive (provisioned) versus wild males and differing cohort sizes. Total focal hours also differed between the three studies: Henzi=279 hours, McGuire et al.= not reported, Freeman=693 hours.

Vervet males have been reported to follow a trend of grooming up the hierarchy (although in my study, only 43% of unidirectional grooming was directed to the higher ranking male), with the top ranking male receiving the most grooming (Baldellou, 1991). This trend is seen also between male bonnet macaques (Adiseshan et al., 2011), males focused their grooming up the hierarchy and males tended to interact with their own age category the most (Silk, 1994). Top ranking male Tibetan macaques (*Macaca thibetana)* were not highly affiliative with other high ranking males (Berman et al., 2007). My data suggests that vervet males do not have a reciprocal grooming system even over ten months of observation (RBM: 9 dGRI's calculable from 15 GAI's (60%); RST: 16 dGRI's calculable from 28 GAI's (57%)). While the male vervet mating system appears to not adhere strictly to reciprocal grooming, increasing the length of my study may help trends become more visible. Bonnet macaques may have grooming altruism over a period of months (Adiseshan et al., 2011) therefore this trend may be seen with male vervets with an extended dataset. Grooming can help dyads increase familiarity and trust, which in turn can increase the willingness of the partner to return sociopositive interactions or

social relationships (Watts, 2002). As seen in bonnet macaques (Silk, 1994), males tended to maintain proximity and interact with individuals close in age. Two separate male vervet dyads immigrated together during the course of the study, and these males maintained close proximity and were often observed huddling and grooming (Table 11: Mu/Pa: GAI=0.587413, PAI=0.239782). Baldellou (1991) reports males who spent more time in proximity with each other did not groom each other at higher rates than males who avoided each other. These observations are in direct opposition of the correlation between grooming and proximity associations found in my study (r_s=0.447, n=126 dyads, $p<0.01$). This discrepancy may be caused by captivity of one of Baldellou's troops, as a general closer proximity from the cage may interfere with the preferred proximities that my study males had. A forced closer proximity may artificially increase the PAI therefore the correlations between GAI may be overshadowed as grooming may not increase due to close proximity.

Closely ranking male vervets establish proximity associations preferably over males more distant in rank (Baldellou, 1991). In my study, the ranks of the males involved have only a marginally positive effect on the measure of PAI, suggesting that there is no significant correlation between male rank and PAI.

Coalitions

General descriptions of coalitions

Baldellou (1991), who first recorded coalition formation in male vervets, referred only to it being uncommon and my results confirm this: polyadic aggression was rare, constituting only 3.6% of all male-male agonism at Samara. Richter et al. (2009),

similarly, reports that male stump tailed macaque coalitions were rare, accounting for only 4% of all conflicts. The rare nature of male-male coalitions is expected on theoretical grounds, as kin selection cannot mediate encounters between unrelated competitors, and suggests too that successful engagement is dependent on many factors such as partner choice, reciprocity, rank and other aspects that will be discussed further in this chapter.

Dynamic of coalitions

Males should support those who supported them in the past, and refuse to support males who ignored their solicitation (Packer, 1977). While Packer (1977) reported reciprocal altruism in regards to coalitions among male olive baboons, Bercovitch (1988) contradicts this statement with his field study of male olive baboons that refused a solicitation and were still solicited by the same male at other times. Recording reciprocity in coalitions is difficult, as it is impossible to count the number of cases in which a male does not perform the reciprocation (Noë, 1990). There are too many factors to record regarding the would-be coalition partner (e.g., proximity, behavioural state, attention towards aggression) to assess if he chose not to engage in the aggression or simply was not attentive to the event. Therefore, the only records of reciprocation are the visible joining of the ongoing aggression, but no data can be recorded if there is no action from the would-be joiner to observe. This being said, I did report repeated glancing between individuals on 11 occasions, seven of these resulting in unsuccessful coalition attempts. Packer (1977) labels this behaviour as `head-flagging`, and interpreted this as a solicitation of aid for the ongoing aggression. Head flagging has also been recorded for male bonnet macaques (Silk, 1999), and barbary macaques (Bissonnette, 2009). While

headflagging may be viewed as coordinating the attack, this visual signal must not be the predominant form of coordination, as it was not observed for the majority of coalitions. Males refusing to participate in a coalition could highlight the cost-benefit balance of joining a coalition when solicited. Noë (1990) reports solicitation refusals for male yellow baboons, and a surprisingly low number of male bonnet macaque solicitations (24%) were successful in receiving support (Silk, 1999). The unwillingness of a male to join a coalition may be caused by particular `friendships` (Smuts, 1985) that form between individuals, the target of the aggressor could have been a male that the solicitee associated with. This phenomenon has been reported by Silk (1992), who observed some males consistently supporting particular males during agonistic encounters, and rarely intervened or joined a coalition against them.

Familiarity of coalitions

The length of time a male has been resident in a troop may affect coalition formation, as a minimal period of time may be a prerequisite for relationships to form with other males. This hypothesis has been labelled the 'familiarity hypothesis' (Collins, 1981) and several studies have supported this hypothesis for coalition formation (Noë, 1992). Alternatively, Noë & Sluijter (1995) along with Bercovitch (1988) suggest that a long-lasting relationship between resident males is not a requirement for coalition formation. My results also support that familiarity is not necessary for coalition formation, with over 22% of observed coalitions involving at least one immigrant male. While the immigrant males themselves could be familiar with one another if they originally came from the same troop, the observed coalition partners involving one immigrant and one resident male (N=8) still suggests that familiarity is not a prerequisite.

These data would be unexpected if resident males were avoiding forming coalitions with immigrants due to their unfamiliarity. Smuts (1985) took the familiarity hypothesis and advanced the criteria one step further suggesting the 'friendship' hypothesis. Males with an affiliative relationship (close proximity, grooming, low aggression) are likely to form coalitions because of tolerance and attachment. Bonnet macaque males seem to create cooperative relationships with other males by grooming them (Silk, 1994).In contrast, Noë and Sluijter (1995) found that the majority of male baboon coalitions do not support the friendship hypothesis. Coalition dyads were not often in proximity, but they did report two pairs of males that were often close in proximity and formed coalitions together. This observation suggests that while the majority of coalition dyads do not associate with each other, there is marginal support for this hypothesis from those specific male dyads.

Bercovitch (1988) reports that preferred male baboon allies did not systematically associate with each other (maintain proximity) when a female was not also in proximity. Correlations were found between coalition members and residency time, and social proximity for male rhesus macaques (Higham & Maestripieri, 2010). While I reported a significant correlation between grooming and probability of forming a coalition, and proximity and probably of forming a coalition, these 'friendship' characteristics have a significant correlation between themselves (PAI and GAI). The literature on the friendship hypothesis is a spectrum with support for both sides of the argument. Male baboons may not support the friendship hypothesis because of their lack of male-male grooming (Noë, 1990), therefore removing an entire prerequisite for the hypothesis. Male rhesus macaques and male vervets have more similar life history traits (e.g. philopatry,

seasonal breeding, migration, male-male-grooming) therefore the correlation between proximity, grooming and coalition partnership probability for both species is expected. This being said, Noë and Sluijter (1995) suggest that one needs to be careful on deciding what came first in the dyad relationship: the alliance or the proximal association? Offensive use of coalitions forces the dyad to maintain proximity for much longer than the actual coalition itself. I observed two males following a male in consort for much of the day, and witnessed repeated attacks on this male throughout several hours. This trailing of the consort pair artificially increased the two males' association index for the day, as both males were waiting for the 'right time' to attack the consort male. Secondly, Noë and Sluijter (1995) suggest that coalition dyads that are formed defensively create the need for the dyad to maintain proximity to prepare for the future aggressions from an individual. They suggest that the friendship hypothesis should be relabelled the 'opportunistic hypothesis', as the coalition dyad creates a positive feedback for itself regarding proximity for either defensive or offensive aggressions. Noë (1994) modeled male baboon coalitions using fighting ability as the crucial factor, and suggested coalitions are formed when a suitable partner is within immediate proximity. While Bercovitch (1988) published his findings several years before Noë & Sluijter (1995), this researcher agrees that coalitions can be explained by the males acting in their own self-interest, rather than in a mutualistic or altruistic manner. I agree with these researchers and partially reject the Smuts (1985) friendship hypothesis, because although certain male dyads have a higher grooming and proximity association index, this affiliation was not consistent for all coalitions observed. Vervet males do not use other affiliative gestures to establish relationships, such as male baboon greetings (Whitman &

Maestripieri, 2003). I agree that coalitions are opportunistic and the right individual may at the time become the coalition partner.

Male rhesus macaques who participated in coalitions were more similar in rank (Higham & Maestripieri, 2010), and targeted males were of high rank (ranks ranging from one to thirteen out of a total 35). All ranks of males participated in coalitions in my study, and there was no correlation between rank and frequency of partner or rank and frequency of target. In sum, I did not observe the targeting of higher ranking males that has been reported in other literature (Higham & Maestripieri, 2010; Noë, 1990; Pandit & van Schaik, 2003). A study on chimpanzees reported the top six ranking male were the most involved in the observed coalitions (Watts, 2002). While all-up coalitions were the predominant coalition type for my study, over 20% of coalitions were all-down, defined as both partners being higher ranking than the target. High ranking males do not require coalition partners because their rank alone is sufficient to win an aggression (Pandit & van Schaik, 2003; Noë, 1994). Mid to low ranking males formed the all-up coalitions, but I never witnessed revolutionary coalitions (Chapais, 1995) that altered the hierarchy by dominating the target. The combined power of the subordinates has been argued to determine the coalition's success, where the combined fighting ability is higher than the target's ability (Bercovitch, 1988). Noë & Sluijter (1990) estimated that an individual's fighting ability is comparable to agonistic rank, therefore the combined fighting ability of the coalition dyad is the sum of their ranks. This asymmetry of strength between the partners and target (Noë, 1994) can predict the coalition success, and this hypothesis has been supported for Barbary macaques (Bissonnette et al, 2009). Asymmetry in strength

was a significant predictor for coalition success, explaining up to 78.6% of the successful coalitions for Bissonnette et al. (2009). My results do not replicate this asymmetry in strength hypothesis, I found no correlation between success and relative strengths of the target and partners (Chi^2=0.0016, 1df, P=0.096). All-up coalitions are thought to have a greater risk since both partners are below the opponent's rank (Noë & Sluijter, 1995). The risks included injury for either partner if the aggression is not coordinated, and/or a higher risk of injury for the solicitor if the partner refuses to join them (Berghänel et al., 2010). I observed a failed attempt for solicitation where the solicitee redirected on the initial aggressor when the target approached. Bissonnette et al. (2009) reports male targets counterattacking the coalition partners if the asymmetry of strength was too small. With 21% of targets retaliating against the coalition partners in my study, I suggest that the motivation of the target may affect the outcome of the coalition, especially when coalition context is known (e.g., female consort).

Coalition Context

Isolation of competitors by coalitions has been reported for Barbary macaques (Paul et al., 1993), who interpreted these coalitions as an alternative male reproductive strategy by lowering the mating success of the target males. With half of the observed coalitions involving chasing of the target male away from the vicinity, this could be support the hypothesis of alternative breeding strategies of vervet males. However, my results indicate that the removal of the target male from a female's proximity did not directly influence the coalition partner's mating success with the said female. No mating attempts were performed by either of the coalition partners when the context of the

coalition was known. Priority of access to females is not as skewed in vervets as it is in other species (e.g. savannah baboons; Bercovitch 1988), which may explain why isolation of competitors did not immediately allow access to the sexually receptive female. Male baboons form coalitions to gain access to a sexually receptive female currently being consorted by a male (Bercovitch 1988). As the baboon mating system displays hierarchical promiscuity, a sexually receptive female can potentially be consorted by a single male for the duration of her fertile period. Packer (1979) reports males avoiding a consort male without regards to his dominance rank, as the consort male is more likely to fight to protect his access to the sexually receptive female. This being said, Packer also reports male dyads harassing the consort male as potentially a tactic to gain access the sexually receptive female. The formation of a coalition may reduce injury costs to both males, as the threat is distributed between both members instead of one. Hausfater (1975) reports the most serious wounds inflicted on male yellow baboons occurred during the mating season. Although I reported no coalition-caused wounding of the target, male vervet wounds in this study doubled in frequency during the breeding season when compared to pre and post-breeding season months. Female vervet monkeys exercise mate choice (Keddy, 1986), therefore the removal of a consorting male does not immediately allow access for another male to copulate. The seasonal breeding and promiscuous nature of vervet monkeys also prevents monopolization of sexually receptive females by one male. This being said, the removal of a consorting male still could directly influence the reproductive success of a male, as vervets display concealed ovulation (Andelman, 1987). If coalitions could potentially increase reproductive success for either of the members, we would expect a peak in coalitions during the breeding

season. Our results do not support this hypothesis, as seen in Figure 20. Mating season peaked two months before the highest frequency of coalitions. The lack of correlations with copulations or operational sex ratio suggests that priority of access to females is not the ultimate mechanism for male coalitions in vervets. Male bonnet macaques who participated in coalitions did not increase their dominance rank or gain access to sexually receptive females (Silk, 1994). Male Tibetan macaques rarely use coalitions to defeat the consorting male, thereby apparently rank is the sole mechanism for competition of mates (Zhao, 1993). Coalition frequency increased significantly for male Barbary macaques during the breeding season (Berghänel et al., 2010),

Mechanisms for coalitions

My results support the Barrett & Henzi (2002) hypothesis that smaller cohort sizes will limit coalition formation. RST males had twice the frequency of coalitions than RBM, which could possibly be explained by a higher number of potential coalition partners within the troop. Berghänel et al. (2011) report higher frequencies of coalitions in Barbary macaque groups with higher male numbers. van Schaik et al. (2006) agree with Barrett & Henzi's (2002) hypothesis and predict that a larger male group size will also increase the coalition sizes. In my study, while several some coalitions contained four individuals, the majority of the coalitions were the classic two against one. Males can use coalitions to drive out extra group males (Smuts et al., 1987). While over a third of coalitions were targeting immigrant males, no immigrant or extra group males were repelled from either troop by coalitions.

CHAPTER FOUR: FEMALE-MALE ASSOCIATIONS

4.1 Female choice

While infanticide is a common male reproductive strategy in primates (van Schaik, 2003), there are some species, including vervets, that are distinguished by the absence of any evidence for its occurrence. In line with this, female vervets provide no visual clues to ovulation, which has consequently been considered to be concealed from males (Andelman, 1987). As selection for the broadcast signaling of ovulation is generally assumed to be one of a suite of responses to the ability of males to sequester females, thereby limiting their reproductive access to preferred partners and increasing their vulnerability to infanticide (Clarke et al., 2010), there is the prospect that the regulation of reproduction is under female vervet control, allowing her to exercise mate choice in ways that are not available in species with male-controlled consortships. By the same token, vervet social organisation is multimale, suggesting both that no single male can defend a group of females (another form of sequestration) and that females have available to them a range of males from which to choose.

To the extent that the supposition of female control is correct, it will have a direct bearing on the mating strategies of males (Arlet et al., 2007). Given female choice as well as the local presence of competitors, we would expect males to employ a range of tactics to increase reproductive access to females (Smuts, 1985). In broad relief, these will be tactics that either increase the probability of access to a proceptive female, such as affiliative grooming by males, or that are directed at reducing the options of females and the mating opportunities of rival males, such as mate guarding and harassment. Given a clear dominance hierarchy in vervets, reinforced during the breeding season (Ch 3), we

might also expect that tactics are associated with male rank – the options open to a high ranking male may well be less circumscribed than those available to low-ranking males. Finally, these tactics may well co-vary with those of females'. Here, for example, we might expect an expressed female preference for a male to be reciprocated, as is the case in 'friendships' (Smuts, 1985). Here a male might forego some prospect of mating with many females in favour of securing mating opportunities with one or a few.

4.2 Male breeding tactics

One of the consequences of concealed ovulation is that males are faced with the problem of its detection. There is little evidence that the concealment is perfect, only that it makes the task more difficult and requires female cooperation. Ovulation may be pheromonally cued or detectable from changes in vaginal odour and there is ample evidence from different species that males use these close-range cues to increase the probability of a conceptive mating (Mugatha et al,. 2006; Clarke et al., 2009). To do so, however, males need to be sufficiently familiar with a female's odour (Weingrill et al. 2003) and be able to get sufficiently close to smell the ano-genital region. Detection therefore requires that females tolerate male proximity, in both the short and longer-term. We therefore expect male tactics, such as the provision of a service, such as allogrooming (Stopka& MacDonald, 1999; Gumert, 2007), that make female cooperation more likely.

4.3 Objectives

My primary objectives in this chapter are two-fold. The first is to investigate some possible male tactics in relation to mating activity. Here I examine attempts to obtain olfactory information about female reproductive condition in relation to grooming of females by males (Figure 23), as well as patterns of male-female association in relation to

the mating season and male rank. The second is to determine what factors predict successful copulation and to do so in terms of who it is that controls mating. Given the possible interrelationships among a number of relevant variables, such as those considered above, I specify no discrete predictions but take a model selection approach after identifying a number of candidate models.

4.4 Materials and Methods

Data for the analyses come from focal samples of all adult males as well as ad hoc observation of copulation attempts and were recorded by myself and four other researchers during the 2010 breeding season. When a copulation attempt was observed, the following data were also recorded in as much detail as possible (Table 15).

Table 15. Information collected during a copulation attempt

Category	Definition
Location	Ground, Open, Tree, Shrub
Male ID	Identity of male
Female ID	Identity of female
Initiator	Sex of monkey who initiates proximity
Female sexually present?	Female present genitals to male
Copulation Act	
Grab	Male grabs females hips
Sniff only	Male sniffs female's genitals and leaves
Mount	Male mounts female's backs of knees, no thrusting
Copulate	Male mounts and begins thrusting
Other	Uncharacterised behaviour, fill in comments section
Success?	
Female resist	Female runs/aggresses against male/sits/prevents action from taking place
Interrupted	Harasser interrupts behaviour of male via approaching, vocalising, or attacking
Success	At least one thrust completed
Female resist activity?	

Before	Female resists initial act
After with aggression	Female shows aggression after copulation
After with proximity	Female runs from male's proximity after copulation
None	Female did not resist copulation
Grooming?	Male grooms female after OR Male grooms female before OR Female grooms male before OR No grooming
Male vigilant?	Vigilant or on periphery of troop?
ID harasser	Identity of individual
Sniff Genitals?	
Yes	Male sniffs female's genitals before or after activity
No	No sniff
Unknown	Did not see complete copulation activity
Nearest Neighbour1 ID	Identity of nearest male
Nearest Neighbour1 distance	3,5,10,15 or 20 meters distance
Nearest Neighbour2 ID	Identity of nearest male2
Nearest Neighbour2 distance	3,5,10,15 or 20 meters distance
Notes	Comments of copulation

All data were recorded onto handheld data loggers, using custom forms designed with Pendragon Forms software. Male rank was determined from ad hoc observations of agonism (see Ch 3). Overt placement of a male's muzzle against a female's anogenital region was scored as anogenital inspection (Figure 24).

Figure 23. Adult female grooming adult male

Figure 24. Example of anogenital grooming performed by a male to a receptive female during the breeding season. Note the lack of sexual swelling on the female.

Conception dates were calculated from the subsequent birth data of each female's infant, by subtracting the average vervet gestation period (163 days, Andelman, 1987). Copulations, which were relatively infrequent, were recorded on an ad hoc throughout the day, as well as within focal animal samples (Figure 25). Definitions of copulatory behaviour are given in Table 3 in Chapter 2.

Figure 25. Copulation posture. Note the hips are grasped and the full weight of the male is supported by the female's hindquarters.

Statistical Analysis

The statistical analysis was conducted on my behalf by Dr. Parry Clarke (University of Sheffield, UK), using a mixed model approach. Male and female identities were included as random effects in all analyses. Analyses were conducted in the open-access R (2.7.1) statistical software [R Development Core Team, 2004], with the ''lme4'' package add-on [Bates & Sarkar, 2005]. Aikake Information Criterion (AIC) values were used to determine the fit of the models.

4.5 Results

(i) The Occurrence of Copulation

Males were observed copulating in 6.0 % (175/2934) of all focal samples. In 97.1 % of these males mated only once, while in the remaining 2.9 %, they were seen mating twice. The vast majority of copulations, 87.4 % (153/175), occurred during the breeding season as defined by dates of conception. Within the breeding season, however,

copulations often occurred well outside the window for conception, with only a small percentage appearing likely to lead to fertilization (see Figure 26).

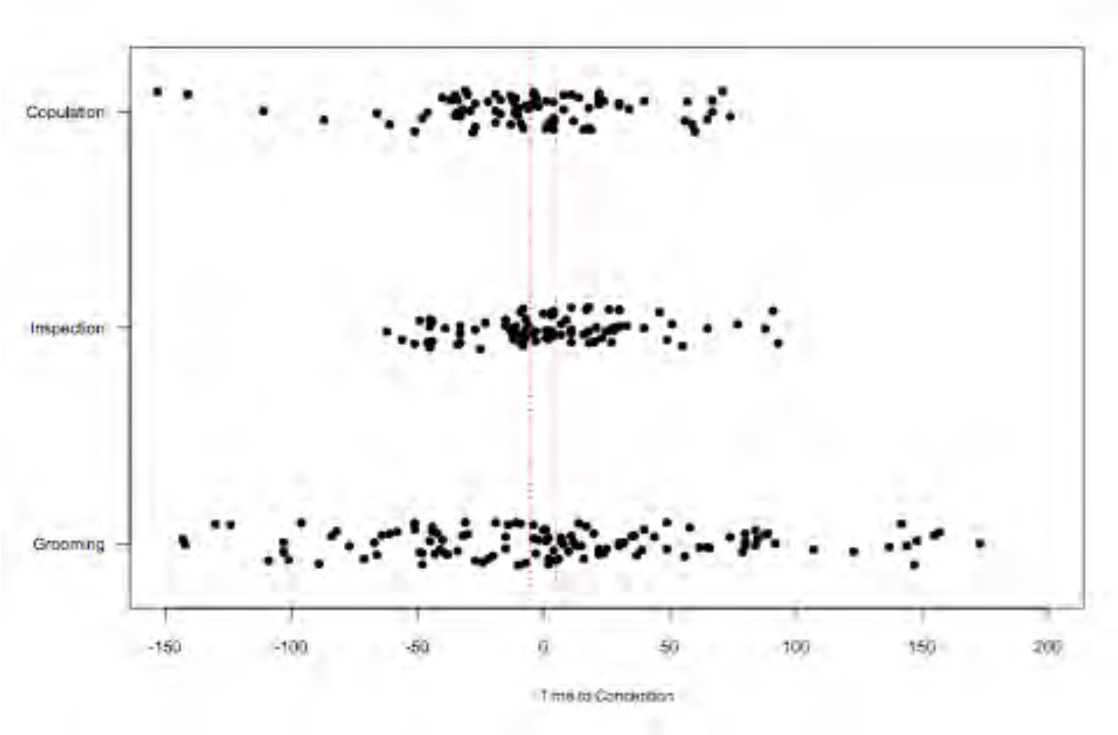

Figure 26: Relationship between the occurrence of copulation, inspection and grooming by males and the time until their female partners in these activities conceived. For all behaviors points indicate the binary occurrence within a focal both plots. These points are offset to illustrate the relative concentration of data. The vertical dashed red lines demarcate the probable window for conception, defined as the ten days around the estimated point of ovulation. Note that the range of copulation and inspection across time does not conform exactly with the frequencies presented in the text because not at all females could be identified at the point of collection.

Table 16 shows the top models of the binary occurrence of copulation between adult males and females. It can be seen that a model considering only the main effects of breeding season and the anogenital inspection of females by males was ranked top, carrying over 70 % of the available model weight. The high weight of this model

suggests that it was the most likely best-fit, within the context of the candidate model set. The second ranked model also carried a relatively high weight, however, and, thus, cannot be completely disregarded. Along with the same main effects included in the top ranked, it also included the interaction between breeding season and anogenital inspection.

Table 16: Parameter number (k), log-Likelihood (logLik), AIC and Akaike weights (wi) for top models of the binary occurrence of copulation between adult males and females.

Mode	*k*	logLik	AIC	*wi*
BS+MI	4	-541.864	1091.728	0.729
BS*MI	5	-541.851	1093.702	0.271

Parameter estimates from both the top and second-ranked model predic that copulations were more likely to occur inside rather than outside the breeding season (Table 17). Surprisingly, however, it can be seen that only a relatively weak effect was predicted. The same was true of the predicted relationship with the occurrence of anogenital inspection by males: while the occurrence of copulation was associated with the occurrence of inspection by males, both models suggest that it was only weakly so (Tables 17 and Figure 27). The second ranked model suggests that effect of male inspection seen in the top-ranked was mainly attributable to its effects on the probability of copulation during the breeding season. When the predicted effects of this interaction are plotted out it can be seen, however, that there was in fact little appreciable difference between seasons.

Table 17: Parameter estimates and standard errors from top models of the binary occurrence of copulation between adult males and females. Models ranked in descending order from left to right

	Model	
Variable	BS+MI	BS*MI
Intercept	-4.549 +/- 0.237	-4.541 +/- 0.241
BS	2.344 +/- 0.239	2.335 +/- 0.245
MI	4.809 +/- 0.378	1.471 +/- 1.064
BS:MI	NA	0.169 +/- 1.087

.

(ii) The Occurrence of Anogenital Inspection by Males

Males inspected females in 4.6 % of all focal samples (134/2934). When inspecting, males typically only inspected once per sample (83.6 % (112/134); although, higher frequencies were observed (N= 2: 11.9 % (16/134), *N* = 3: 2.0 % (3/134) and *N* = 4: 1.5 % (2/134)). As with the occurrence of copulation, the vast majority of inspections occurred within the breeding season (85.1 % (114/134)). Within the breeding season, inspections were relatively spread out and showed a remarkably similar distribution to the occurrence of copulations (Figure 26).

Table 18 shows the top models of the binary occurrence of when males inspected the anogenital region of females. The top-ranked carried only the main-effects of breeding season and the binary occurrence of male grooming. It carried over 70 % of the available model weight and, thus, can be considered the best-fit with reasonable confidence. As before, the second-ranked also carried a relatively high weight. This model also considered the main effects of breeding season and male grooming, as well as

their interaction.

Table 18: Parameter number (k), log-Likelihood (logLik), AIC and Akaike weights (wi) for top models of the binary occurrence of female anogenital inspection by males.

Model	***k***	**logLik**	**AIC**	***wi***
BS+MG	4	-466.941	941.881	0.731
BS*MG	5	-466.941	943.8812	0.269

Estimates from both the top- and second-ranked models suggest that breeding season had a weak positive effect on the probability of inspection by males (Table 19). That is, males were marginally more likely to inspect females during the breeding season rather than out of it. The apparent weakness of the effect is slightly misleading, however, given that the majority of inspections did, in fact, occur during the breeding season (see above). The weakness of the estimate simply reflects the fact that inspections were relatively rare in general, regardless of the season.

Table 19: Parameter estimates and standard errors from top models of the binary occurrence of female anogenital inspection by males. Models ranked in descending order from left to right.

	Model	
Variable	BS+MG	BS*MG
Intercept	-4.492 +/- 0.240	-4.492 +/- 0.240
BS	2.331 +/- 0.250	2.333 +/- 0.250
MS	-15.79 +/- 752.575	-14.131 +/- 1165.101

BS:MG	NA	-2.338 +/- 1603.252

In addition, both models suggest that the occurrence of inspection by males may be related to the timing of their grooming females (Table 18). Parameter estimates from these models (Table 19) predict that this relation will be negative, with inspection being more likely to be seen during samples when they were not also seen grooming. This finding, however, is undoubtedly a consequence of the fact that males were never seen grooming and inspecting in the same sample (Figure 27b); meaning that is was impossible to get a reliable parameter estimate, as indicated by the standard errors on the observed estimates (Table 19).

(iii) The Occurrence of Male Grooming

Males were observed grooming females in 5.6 % (115/2062) of all focal samples, 7.3 % (52/712) of these samples were collected during the breeding season and 4.7 % (63/1350) collected outside the breeding season. There was some suggestion in the data that males exhibited marginally more grooming effort around the time of probable conception (Figure 26). In 58.3 % (67/115) of all samples where males groomed females, they also received grooming from them. This pattern remained constant across seasons, with reciprocation observed in 57.7 % (30/52) of samples collected during the breeding season and 58.8 % (37/63) collected outside the breeding season. All models predict that male rank, both as a main effect and in interaction, was a weak predictor of male grooming (Table 20), with there being some suggestion that males of low rank tended to groom females more than high-ranking males (Fig 27a).

Table 20: Parameter number (k), log-Likelihood (logLik), AIC and Akaike weights (wi) for top models of the binary occurrence of male grooming.

Model	*k*	logLik	AIC	*wi*
BS*FG+MR	6	-414.598	841.195	0.451
BS*FG*MR	9	-412.245	842.490	0.236
BS*FG+BS*MR	7	-414.374	842.748	0.207
BS*FG+MR*FG+BS*MR	8	-414.193	844.386	0.091

All models agree, however, that the binary occurrence of grooming by females was a strong predictor, both as a main effect and when in interaction with breeding season (Table 21). They all predict that the probability of a male grooming a female will increase by over 50% if their female grooming partner was also observed grooming them. That is, male grooming was more likely to be observed if female grooming had also been observed (Figure 27b). All models further predict that the extent of the coincidence will depend on whether interaction is occurring during or outside the breeding season. Specifically, they predict that male and female grooming are more likely to coincide outside the breeding season (Figure 27c).

All models also predicted a strong effect of breeding season, both as a main effect and, more strongly, when in interaction with the occurrence of female grooming (Table 21). When these predictions are plotted out (Figure 27), it can be seen that breeding season had no discernible overall impact on the probability of male grooming, however. In fact, it appears that breeding season only had a discernible impact in samples where females were observed grooming males (Figure 27c). In this case, the models predict that

males were less likely to groom females during the breeding season than outside of it. This finding echoes the effects of the interaction between female grooming and breeding season evident when focusing on the relationship between male and female grooming (Figure 27b).

Table 21: Parameter estimates and standard errors from top models of the binary occurrence of male grooming. Models ranked in descending order from left to right. [a]All models included random intercepts by Male ID. Standard deviation in each model: (i) BS*FG+MR = 0.782, (ii) BS*FG*MR = 0.798, (iii) BS*FG+BS*MR= 0.783 and (iv) BS*FG+MR*FG+BS*MR = 0.783

	Models[a]			
Variable	BS*FG+MR	BS*FG*MR	BS*FG+BS*MR	BS*FG+MR*FG+BS*MR
Intercept	-5.372 +/- 0.553	-6.102 +/- 0.733	-5.562 +/- 0.629	-5.701 +/- 0.679
FG	4.855 +/- 0.316	6.315 +/- 0.857	4.867 +/- 0.319	5.194 +/- 0.632
BS	0.831 +/- 0.259	1.903 +/- 0.704	1.173 +/- 0.578	1.174 +/- 0.581
MR	0.096 +/- 0.050	0.160 +/- 0.064	0.113 +/- 0.056	0.126 +/- 0.060
BS:FG	-1.315 +/- 0.411	-3.390 +/- 1.113	-1.347 +/- 0.414	-1.360 +/- 0.414
BS:MR	NA	-0.132 +/- 0.071	-0.031 +/- 0.414	-0.031 +/- 0.046
FG:MR	NA	-0.095 +/- 0.057	NA	-0.031 +/- 0.051
BS:FG:MR	0.311 +/- 0.131	0.192 +/- 0.097	NA	NA

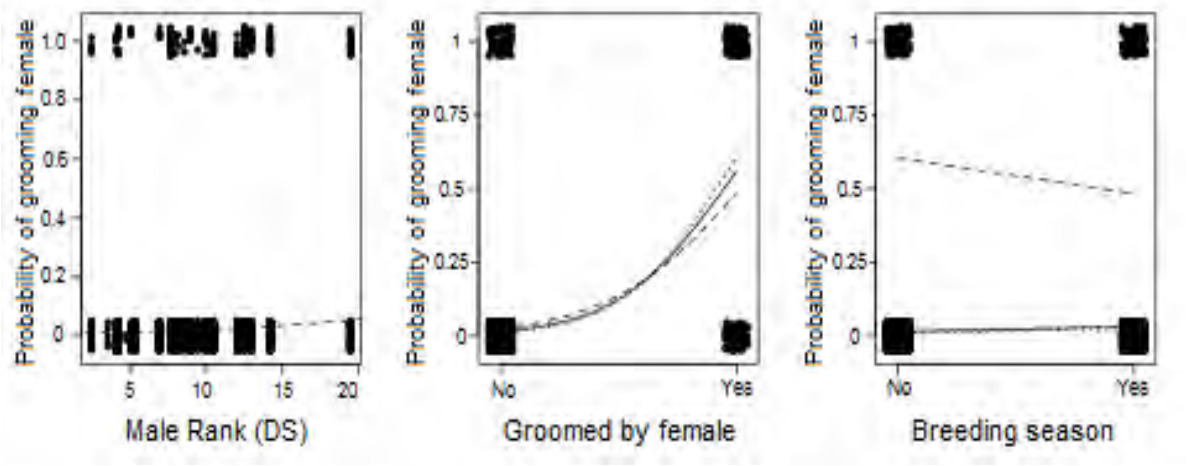

Figure 27: Relationship between the probability of a male grooming a female and (a) male rank, (b) the occurrence of female grooming and (b) the breeding season. In all plots lines indicate relationship predicted by the top-ranked model. In (a), the dashed line describes the main effect of male grooming. In (b), the solid, dashed and dotted indicate the effect of female grooming across seasons, inside and outside the breeding season, respectively. In (c), the solid, dotted and dashed lines describe the effect of breeding season across all samples and when males were and were not groomed by females, respectively. For all plots, points offset to illustrate the distribution of data

(iv) Male-female association

To determine whether males formed associations with females, I ran the following 11 models, where 'timing' is relative to the breeding season (Before, During, After) and SDS is the Standardised David's Score (SDS) of male rank:

m0: (AI~1+(1|Male)+(1|Female)

m1: (AI~Timing+(1|Male)+(1|Female)

m2: (AI~Female.SDS+Male.SDS+(1|Male)+(1|Female)

m3: (AI~Female.SDS+Male.SDS+Timing+(1|Male)+(1|Female)

m4: (AI~Male.SDS+Timing+(1|Male)+(1|Female)

m5: (AI~Male.SDS+(1|Male)+(1|Female)

m6: (AI~Troop+(1|Male)+(1|Female)

m7: (AI~Troop+Timing+(1|Male)+(1|Female)

m8: (AI~Troop+Female.SDS+Male.SDS+(1|Male)+(1|Female)

m9: (AI~Troop+Female.SDS+Male.SDS+Timing+(1|Male)+(1|Female)

m10: (AI~Troop+Male.SDS+Timing+(1|Male)+(1|Female)

m11: (AI~Troop+Male.SDS+(1|Male)+(1|Female)

Table 22. **Model identity, degrees of freedom, AIC and Akaike weights (wi) for models of male-female association index (AI).**

Model	AIC	DF	dAIC	*wi*
m4	-4370.1	7	0	0.44504
m5	-4369.7	5	0.4	0.36165
m1	-4365.9	6	4.3	0.05269
m0	-4365.5	4	4.7	0.0428
m10	-4364.7	8	5.4	0.02954
m11	-4364.3	6	5.8	0.02403
m3	-4363	8	7.2	0.0123
m7	-4362.8	7	7.4	0.01113
m2	-4362.5	6	7.6	0.01
m6	-4362.3	5	7.8	0.00906
m9	-4357.9	9	12.3	< 0.001
m8	-4357.5	7	12.7	< 0.001

Table 23. **Parameter estimates and standard errors of the top-performing model (m4).**

	Estimate	Std. Error	t value
(Intercept)	0.037885	0.0196748	1.926
SDS	0.0856796	0.0252198	3.397
Timing - Before	-0.0099588	0.002367	-4.207
Timing - During	0.0007307	0.002367	0.309

The best performing model was one that included male rank and timing (Table 22, Table 23), whereas the second-best model contained only male rank. This, together with the weights of these two models suggests that male rank is a robust predictor, while timing is only of marginal significance. Visual inspection of the data indicate that higher ranking males have higher association indexes although the absolute magnitude of AI is very low. Interestingly, AI values drop in the three months prior to the breeding season but sustain their breeding season levels subsequently (Figure 28).

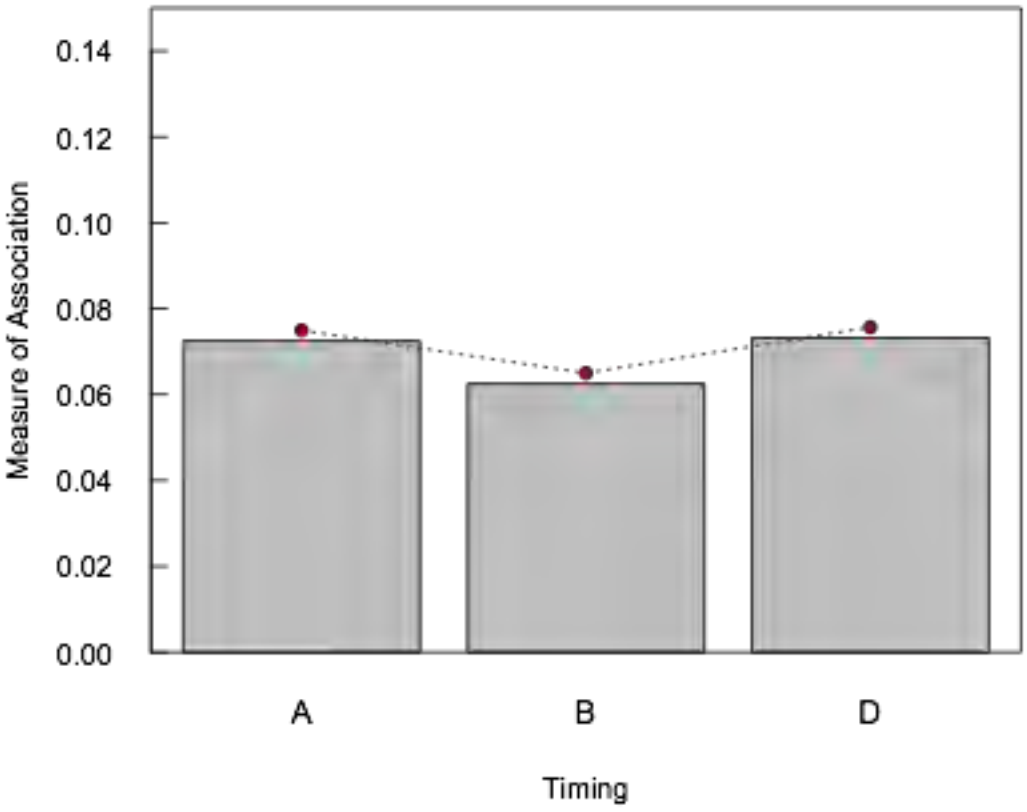

Figure 28. The relationship between male-female association and timing relative to the mating season. On the x axis, A indicates after breeding season; B indicates before breeding season; D indicates during breeding season

(v) Copulation success

A total of 1344 copulation attempts was observed. Of these 44.5% (598/1344) were successful. In 85.5% (1149/1344) of samples the initiator could be determined. Males initiated 91.9% (1056/1149) and were successful in 40.8% (431/1056) of their attempts, thereby being responsible for the initiation of 88.3% of all successful copulations. While females initiated only 8.1% (93/1149) of copulation attempts, these were successful in 61.3% (57/93) of cases.

Females copulated with males for 36 weeks out of the year, with copulations observed 18 weeks before and after the estimated date of conception. This trend of

extended range of mating behaviour was also observed for males, as seen by the unsuccessful copulations (female refused) ranging from 18 weeks pre-conception to 19 weeks post-conception. RBM female conception dates spanned 81 days during the breeding season, with an average of 8.1 days separation between each female's conception date (N=10). RST female conception dates bridged 98 days during the breeding season, and averaged 7 days between each female's conception date (N=14). Overall, the conceptive period for both troop's females was 89.5 days, averaging 7.5 days between each female.

(vi) Determinants of copulation success

Variance Components

There are three clear levels of sampling in the dataset: (i) Females, (ii) Males and (iii) Troops. A comparison of models using different random effect structures revealed the inclusion of Female ID and Male ID provided the best fit for all candidate models. Models with Troop ID always performed poorly, simply because sampling from different troops consistently had no effect on parameter estimates. All models considered therefore included only random intercepts for Female ID and Male ID.

Candidate Model Set

I distinguished between candidate models by the assumptions they make regarding who controls mating outcomes.

A. First, there are those that assume that males are primarily in control. Here, then, mating success should depend on the amount of information males have on the timing of

ovulation or conception and/or their relative competitive ability, summarized by the models:

(i) DC (Days to Conception)

(ii) DC + MI (MI = male inspection of the female anogenital region)

(iii) DC:MI

(iv) MR (MR = Male rank)

(v) DC + MR

(vi) DC + MI + MR

(vii) DC:MI + MR

I have no standard measures of the intensity of competition (e.g. OSR), simply because male number did not vary sufficiently during the breeding season and there was insufficient variance in female receptivity using the measures I have available (e.g. Conception Date). I can, however, use some proxies, such as 'Vigilant' (V: Yes vs. No) and 'Peripheral' (P: Yes or No). Vigilance or peripheral copulations may suggest that males employ 'sneaky' copulations if the mating competition is high. Therefore, I also considered:

(viii) DC + V + P

(ix) DC + MI + V + P

(x) DC:MI + V + P

(xi) MR + V + P

(xii) DC + MR + V + P

(xiii) DC + MI + MR + V + P

(xiv) DC:MI + MR + V + P

B. The second group of models can be classed as those that permit females some control over mating outcomes. Perhaps the most subtle and the one that comes closest to a 'classic' markets model (cf Gumert, 2007) is the one predicting that, in addition to competing for mating access, males must groom females in order to mate successfully. This perspective can be considered by simply including male grooming effort (MGE: Yes vs. No) in all the above models, yielding

(xv) DC + MGE

(xvi) DC + MI + MGE

(xvii) DC:MI + MGE

(xviii) MR + MGE

(xix) DC + MR + MGE

(xx) DC + MI + MR + MGE

(xxi) DC:MI + MR + MGE

(xxii) DC + V + P + MGE

(xxiii) DC + MI + V + P + MGE

(xxiv) DC:MI + V + P+ MGE

(xxv) MR + V + P+ MGE

(xxvi) DC + MR + V + P+ MGE

(xxvii) DC + MI + MR + V + P+ MGE

(xxviii) DC:MI + MR + V + P+ MGE

It seems feasible to suggest that females may actually have a high degree of control over mating outcomes, however. Given this, I also considered the effects of female efforts to regulate the frequency of mating success, either by refusing male attempts to mate (FR: Yes vs. No) and/or by encouraging males to mate, via solicitation (FS: Yes vs No). Models of this kind will then vary by the extent to which females respond to variance in male quality and efforts to win favour. Note that here, by 'win favour', I refer to grooming for mating access, not grooming for access to olfactory information. The possibility that females are in complete control of mating is captured by the model (xxix) FR+FS. If females have only partial control then I expect other factors to play a role. This possibility was accommodated by considering (xxix) in combination with models (i) to (xxviii). It is also possible that whether a copulation attempt is successful or not has less to do with the behaviour of the male and female involved and more to do with the behaviour of 3rd parties. I therefore also considered models incorporating the role of the harassment of mating pairs (H: Yes vs NO), which in its most extreme form assumes that it is only the harassment of mating pairs that determines mating outcomes: (xxx) H. I also considered this model in combination with all the previously defined models (i) to (xxix), to permit consideration of the possibility that harassment is only one of several pressures/behaviours mediating mating outcomes. Finally, I also considered the empty model, containing only the mean probability of success, as a benchmark for minimum acceptable performance. In total, I considered over a 100 possible models. This is a lot of models, but there is nothing inherently wrong with

that, especially considering all the models I looked at are of a fairly low dimension and I have plenty of data (approx. 1300 samples).

Model comparison revealed no clear best-fit (Table 24). 90% of the cumulative model weight came from 14 models, with the top four all carrying much the same weight and the remaining ten characterised by an only marginally lower ones. The poor and comparable performance of these models prevents me from ascertaining the relative utility of the hypotheses underlying them. I can, however, clearly identify variables that play a strong role in the occurrence of copulation success: all models contain the effects of DC (days to conception), MI (male inspection), FR (female resistance) and FP (female presentation), suggesting that (i) male knowledge of the probability of conception and (ii) female regulation of mating are important in determining mating success. Model-averaged parameter estimates suggest that the effects of days to conception (DC) were largely negligible, however (Figure 29).

Table 24: Parameter number, K, log-likelihood, log L, AICc and Akaike weights, wi, for those models of the binary occurrence of a successful copulation cumulatively carrying 90% of the available Akaike weight.

Model	K	LogL	AIC_c	w_i
DC + MI + FR + FP + H	**10**	**-359.05**	**738.41**	**0.17**
DC + MI + MR + FR + FP + H	**13**	**-356.00**	**738.54**	**0.16**
DC + MI + MGE + FR + FP + H	**11**	**-356.26**	**738.90**	**0.13**
DC + MI + MR + MGE + FR + FP + H	**14**	**-355.22**	**739.06**	**0.12**
DC + MI + V + P + FR + FP + H	**12**	**-358.02**	**740.50**	**0.06**
DC + MI + MR + V + P + FR + FP + H	**15**	**-355.12**	**74-/94**	**0.05**
DC + MI + V + P + MGE + FR + FP + H	**13**	**-357.27**	**741.07**	**0.04**
DC + MI + MR + V + P + MGE + FR + FP + H	**16**	**-354.36**	**741.51**	**0.04**
DC : MI + FR + FP + H	**13**	**-357.65**	**741.83**	**0.03**
DC : MI + MR + FR + FP + H	**16**	**-354.57**	**741.94**	**0.03**
DC : MI + FR + FP	**12**	**-358.98**	**742.41**	**0.02**

DC : MI + MR + MGE + FR + FP	**13**	**-358.01**	**742.55**	**0.02**
DC : MI + MGE + FR + FP + H	**14**	**-357.01**	**742.63**	**0.02**
DC : MI + MR + MGE + FR + FP + H	**17**	**-353.94**	**742.78**	**0.02**

Note: DC: Days to conception; MI: Occurrence of male inspection? MR: Male Rank; MGE: Occurrence of male grooming female before copulation attempt? FR: Occurrence of female resistance to mating? FP: Occurrence of anogenital presentation by females? V: was mating vigilant during attempt? P: Did mating occur on the periphery of the group? H: were the mating pair harassed?

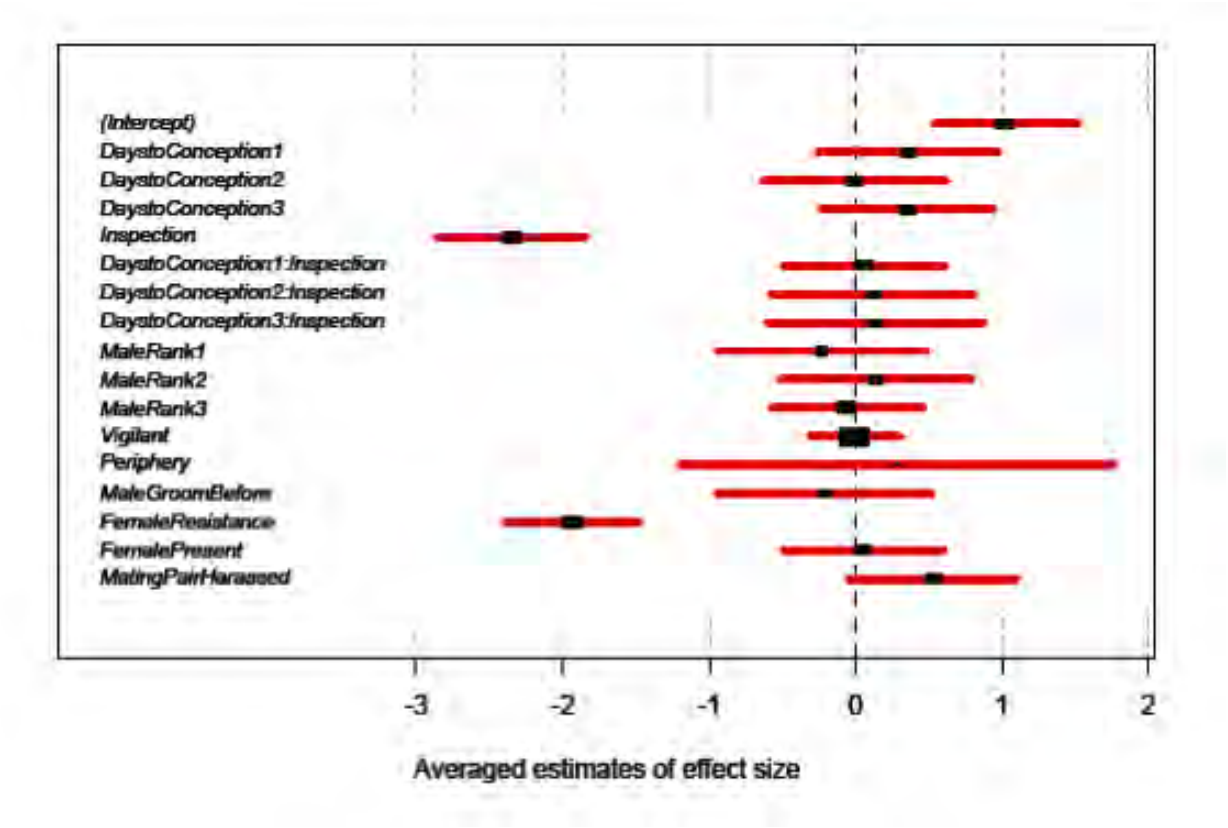

Figure 29: Estimates of effect size, precision and confidence for all variables averaged across all models. The black boxes indicate point estimate for each variable, with the size of the box being proportional to the precision (1=se2) of this estimate. The red lines describe the 95% confidence interval for each estimate.

The baseline for comparison when interpreting estimates for DC is all copulations occurring more than 15 days before or after the estimated date of conception, with DaystoConception1, DaystoConception2 and DaystoConception3 indicating the effect of

mating between 15 and 10 days, 10 and 5 days and 5 to 0 days before or after conception, respectively. I used the same intervals before and after conception because copulations appear to be distributed evenly either side of conception (see Figure 30). Ultimately, model-averaged estimates tell us that successful copulations are more likely to occur the closer they are to the day of conception, but that the extent of the variance does not suggest that it would be replicated in another sample.

In contrast to Days to Conception (DT), the occurrence of male inspection (MI) before a copulation attempt had a clear and well identified effect (Figure 29). When a male inspected a female prior to a copulation attempt, the probability that a copulation attempt would be successful was substantially reduced (Figure 30). The close correspondence between the predicted effect of male inspection made by the top model and the observed probability of copulation success across male inspection strongly suggests that the effect of male inspection is robust, all the more so, given that the effect predicted by the top model was almost identical to the model-averaged estimate. Figure 30 also confirms the negligible effect of days to conception (DC), which had little or no bearing on the effect of male inspection.

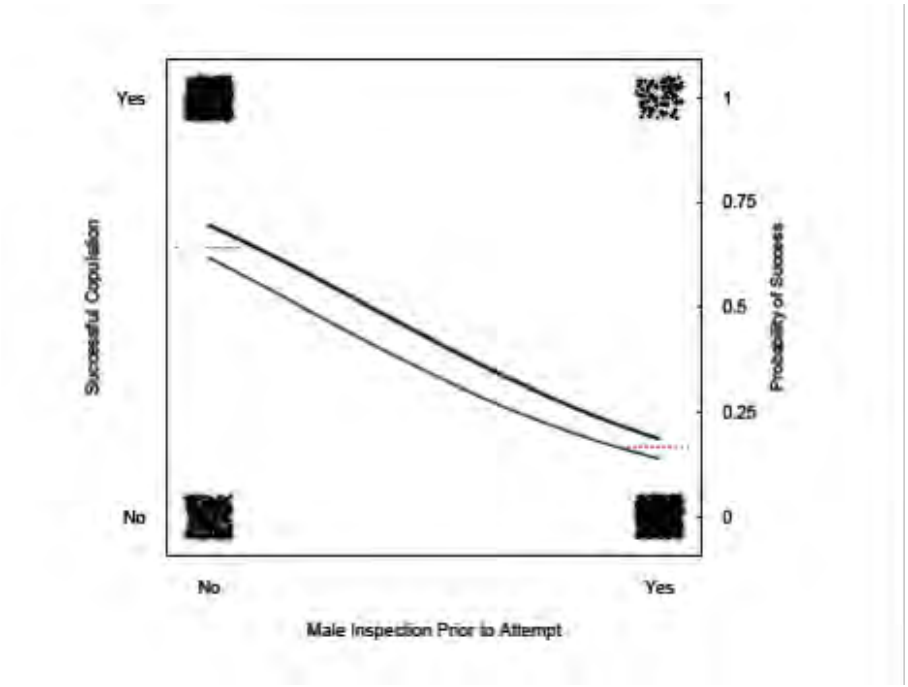

Figure 30: Relationship between copulation success and the occurrence of male inspection prior to the copulation attempt. The offset clustered points indicate observed successful and unsuccessful copulations distributed across male inspection. Points are offset to give sense of the relative weight of the data across the four possible 'cells'. Dashed red lines indicate the observed probability of success relative to the occurrence of male inspection. The black lines indicate the effect, predicted by the top model, of male inspection on the probability of copulation success. From top to bottom the three black lines indicate the relationship predicted by the top model when the probability of conception was high, mid and low, respectively.

While the occurrence of anogenital presentation by females was present in all top models, suggesting it may be salient, model-averaged estimates imply that its effect was negligible (Figure 29 and Figure 31). This was confirmed by the data (Figure 31), with little difference being seen between the observed probability of a successful copulation when a presentation was and was not seen to precede the copulation attempt. The weak effect of female presentation may, in part, be attributable to the fact that it was relatively rare. Females were observed presenting to males in only 12.0% (130/1083) of copulation

attempts. Interestingly, however, when they did present they had a high rate of success, with 56.2% (73/130) of presentations leading to mating success.

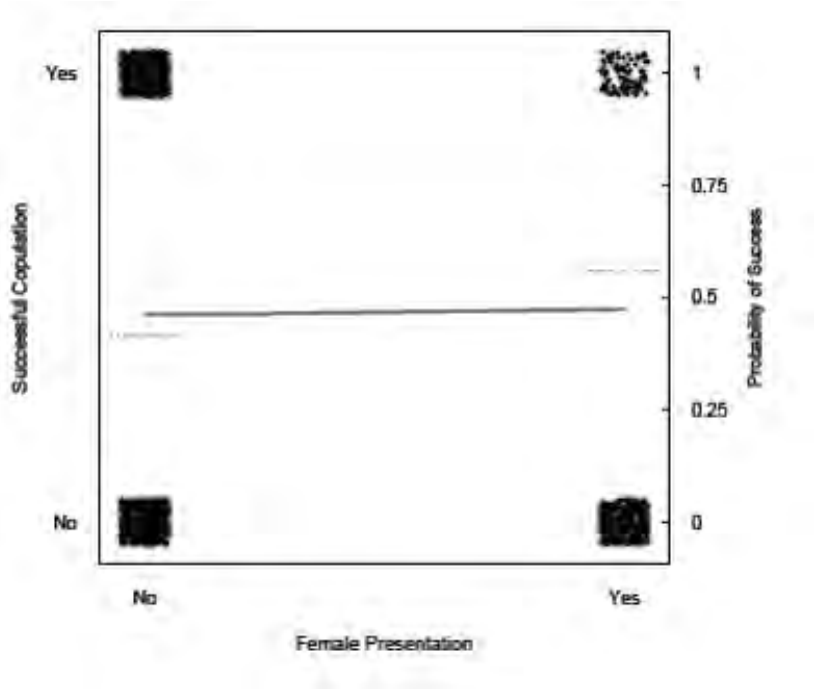

Figure 31: Relationship between copulation success and the occurrence of anogenital presentation by females. The offset clustered points indicate observed successful and unsuccessful copulations distributed across female presentation. Points are offset to give sense of the relative weight of the data across the four possible 'cells'. Dashed red lines indicate the observed probability of success relative to the occurrence of anogenital presentation by females. The black lines indicates the effect, predicted by the top model, of female presentation on the probability of copulation success. From top to bottom the three black lines indicate the relationship predicted by the top model when the probability of conception was high, mid and low, respectively.

The effects of female resistance to copulation attempts were strong, clear and unambiguous. As predicted by the models, the occurrence of female resistance to male copulation attempts was associated with a dramatic reduction in the success of those attempts (Figure 32). Females resisted 34.6% (365/1056) of all copulation attempts made by males and did so successfully in nearly 20% (71/365) of cases. Thus, while resistance

was not guaranteed to prevent copulation, it did have a reasonable success rate. Note that Figure 32 once again confirms the lack of any effect on the probability of conception on the relationship between copulation success and female resistance

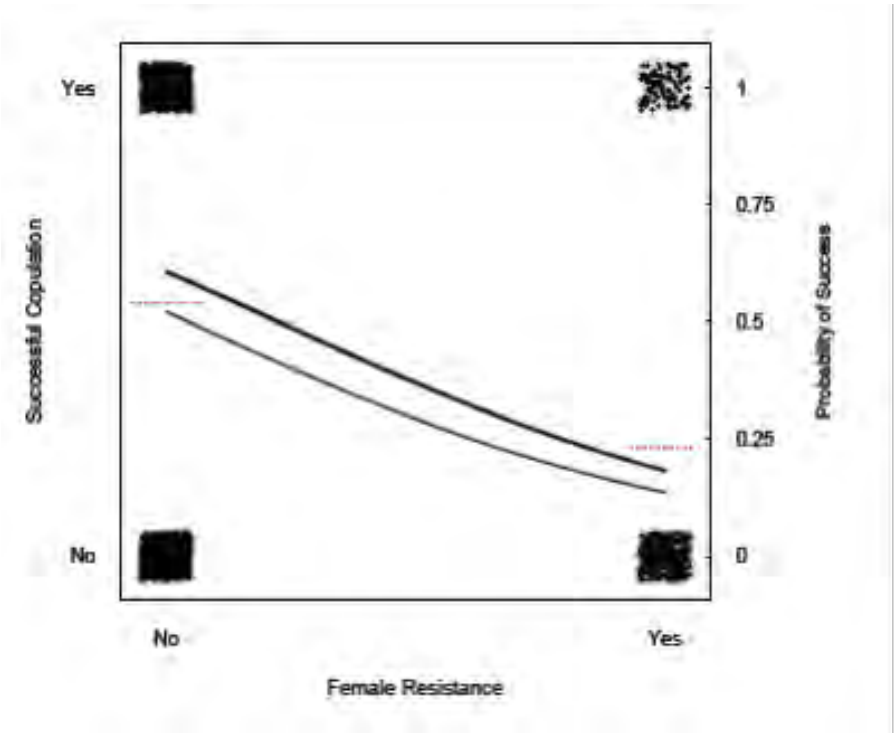

Figure 32: Relationship between copulation success and the occurrence of female resistance. The offset clustered points indicate observed successful and unsuccessful copulations distributed across female resistance. Points are offset to give sense of the relative weight of the data across the four possible 'cells'. Dashed red lines indicate the observed probability of success relative to the occurrence of female resistance. The black lines indicate the effect, predicted by the top model, of female resistance on the probability of copulation success. From top to bottom the three black lines indicate the relationship predicted by the top model when the probability of conception was high, mid and low, respectively.

Nearly all the top models include an effect of the harassment of mating pairs by third parties (H). Model averaged estimates (Figure 29) confirm that it did have a relatively strong positive effect on the probability that a copulation attempt would be successful; although, the confidence intervals may caution against generalising the effect

too much. The fact that the effect was positive suggests that (i) 3rd parties tended to intervene in copulation attempts that seemed to be going well and (ii) their attempts to disrupt mating was largely unsuccessful. That is, there is little causative association between the probability of copulation success and harassment and, instead, the association appears to be little more than a correlation.

Male rank, grooming effort, the occurrence of vigilance and mating on the periphery all appeared to have little effect on the probability of mating success. The negligible effect of being on the periphery is undoubtedly, in part at least, due to the fact that it was rarely observed: 1.6% (21/1338) of samples. In contrast, male rank, grooming effort and the occurrence of vigilance were all well sampled, however. Therefore, their lack of effect is likely to be genuine and have little to do with the nature of the dataset

Male Rank	Female Rank 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Grand Total
1	8	11	10	9	8	3	4	2	4		7	4			3	2		4		4	1	84
2	2	8	19	4	8	10	4	5		2	3	1	2		4	1		2	1	3		79
3	3	1	6	4	5	8		2	1	3	4	3		10				2		1	2	55
4	7	1	2	1	4		5	1	2		3	5	1	2	1		1		1	4		41
5		1	2	1	2	1				2	1	1		6			1	1		5		24
6	6	1			2	9			3	1	1		1	2								26
7	3	1	2	1	1	1	2		1	1	1						1				2	17
8	9	1	2	2	4	1	5	3		1	1	2	1		2							34
9	8	2	3	5	5	7	2	3	6	2	4	5		6	2	1	2		1	2	2	68
10	3	2		4	1		3	2	3		2	2		2			1	2	4			31
11		1	1		3	1									1						1	8
12	2		1		1				1	1	1		1				1				1	10
13	5	1		1	1	1	3		2		2	2	1	2					1	1		23
14	3	2					1					1		1			1				2	11
15	3	1	2				4					3	2			1			1		2	19
16		1	1				1		1	1	1		1					1			1	9
17							1															1
18										1				1								2
	62	35	51	32	45	42	35	18	24	15	31	29	10	32	13	5	8	12	9	20	14	542

Figure 33. Successful copulations for both males and females, with corresponding rank ranging from highest to lowest.

To determine the mating success by males according to rank (Figure 33), a Spearman's rank correlation was run and a significant negative relationship was found between male rank and frequency of successful copulations (Rho=-0.841, N=16, P<0.01). When successful copulations were narrowed to the conception window (with 5 days either side of estimated day of conception), rank was significantly negatively correlated with successful copulations (Rho=-0.568, N=15, P<0.05). There was no trend evident for number of female copulation partners each male rank for RST (Figure 34), and a slight trend was evident for RBM males with high ranking males copulating with a higher frequency of females. Female rank played a role in frequency of male copulation partners

(Figure 35), with RBM females showing a steeper trend of high ranking females have more copulation partners, than RST females.

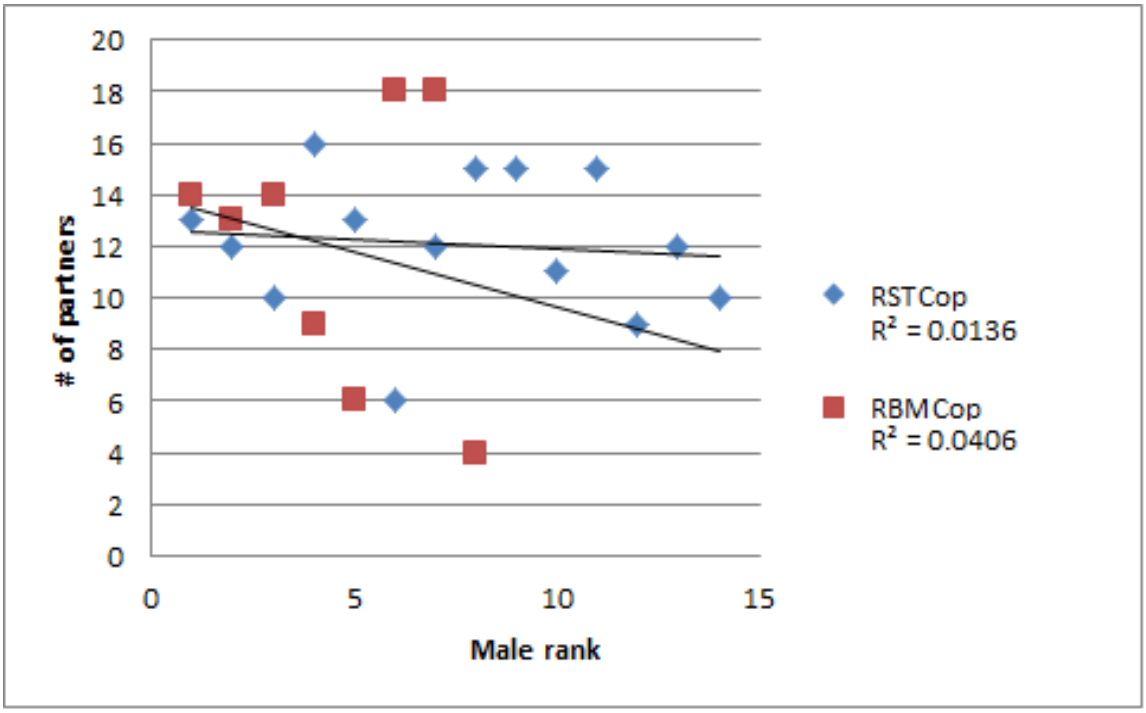

Figure 34. Number of female copulation partners per rank for both RST and RBM males.

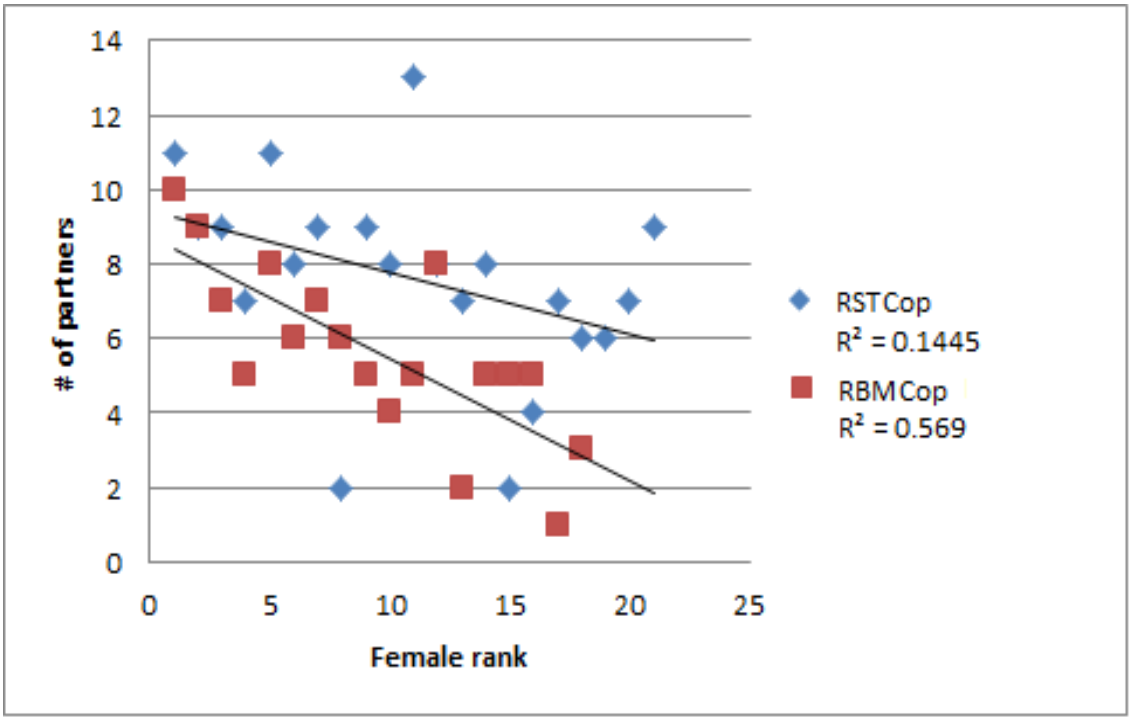

Figure 35. Number of male copulation partners per rank for both RST and RBM females.

Discussion

The analyses presented in this chapter indicate evidence for male reproductive tactics that are directed both at other males, in order to reduce the likelihood of their mating as well as at females, in order, presumably, to improve mating opportunities. Those tactics directed at males include the expression of dominance, which was manifest primarily in the harassment of mating males and in the spatial associations of males and females, where higher ranking males had correspondingly higher association indices (see also Baldellou, 1991). In this regard, the maintenance of association after the breeding season suggests the possibility that males are, as it were, preparing for the next breeding season although the low absolute values of male-female AI and the decline in AI prior to the breeding season do not support this possibility. The decline in AI is likely to be due to the arrival of a number of new males and the tenor of male interactions at this time.

Female-directed mating activity is essentially represented by olfactory investigation. Surprisingly and interestingly, this was not associated with female-directed grooming by males and was likely therefore only to be opportunistic. More broadly, I found no evidence for grooming as a commodity that could be traded directly for access to mating opportunities. The data on grooming indicate, too, that rank-based male association with females did not translate into increased grooming. There was, instead, a weak indication that lower ranking males were more likely to groom with females, itself a possible response by such males to their spatial exclusion from females by high ranking males, and a strong effect that indicates that male grooming was associated with female grooming.

The occurrence of female grooming was a very strong positive predictor of the occurrence of male grooming. The degree of coincidence between the two was reduced during the breeding season, however. Male rank and number of receptive females present in the group had no discernible impact on the probability of male grooming. This all suggests that the social engagement of the sexes was driven by females and that females were able to express their own preferences for sexual partners. This is supported by the analyses of copulation success, where the best predictors were female resistance to male initiated mating and olfactory investigation, both of which were associated with a decreased likelihood of mating. This is unexpected but, together with the absence of any effect for days to conception and the persistence of copulation after conception (as seen also in other guenons) indicates that males are not well placed - or able - to detect ovulation in this species, which corroborates Andelman's (1987) findings, and that females have much better control of their reproductive careers than do baboon females,

for example. Nevertheless, 25% of all copulation events involved males not continuing the sequence after olfactory investigation, indicating that they can detect cues to ovulation, even if only crudely.

Finally, the absence of two effects - that of male dominance and commodity trading - needs some discussion. While male rank was found to be significantly negatively correlated with copulation success, the lack of 2010 paternities prevents a conclusion if male rank increases reproductive success. While it is likely that the lack of better mating outcomes (as measured by copulation success) for higher ranking males may be a robust finding as it has been observed in other populations (Henzi, 1982), pointing to the exercising of mate choice by females, there has to be the possibility that it reflects the absolute size of the male and female cohorts as well as the fact that most females were sexually active in 2010. Henzi & Lawes (1987, 1988) have shown in blue monkeys that the presence of lots of males in a season where most females were receptive, led to the alpha male not contesting reproductive access by other males. Put simply, there may have been some kind of confusion effect operating. If so, this might also explain the absence of trade between males and females (Stopka &MacDonald, 1999; Gumert, 2007). This possibility can be assessed by collecting data in this population during seasons when fewer females are receptive, as was the case in the 2011 season (Sashaw, pers. comm.).

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