Maternal rank influence on rank acquisition and social integration in wild dispersing male vervet monkeys

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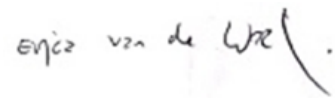Pashan, Pune 411008, INDIA

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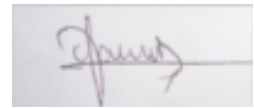South Africa.

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Certificate

This is to certify that this dissertation entitled "Maternal rank influence on rank acquisition and social integration in wild dispersing male vervet monkeys" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Varun Manavazhi at the Inkawu Vervet Project under the supervision of Dr Erica van de Waal, Director, Inkawu Vervet Project during the academic year 2019-2020.

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Declaration

I hereby declare that the matter embodied in the report entitled "Maternal rank influence on rank acquisition and social integration in wild dispersing male vervet monkeys" are the results of the work carried out by me at the Inkawu Vervet Project, under the supervision of Dr Erica van de Waal and the same has not been submitted elsewhere for any other degree.

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Abstract

Juvenile life is marked by behavioural and physiological changes that are shaped by the physical and social environment that an individual experiences. In mammals, an individual's social experience is closely linked with that of its mother. This study investigated the effects of maternal dominance rank and juvenile social experience on later life rank attainment and social integration in male vervet monkeys. Maternal ranks of ten study subjects were calculated during their juvenile period in their natal groups. The ranks that they attained and their extent of social integration - degree, strength and eigenvector centrality - were calculated one year after immigration into their new groups. The results indicated that maternal rank significantly predicts later life rank attainment. Individuals with high-ranking mothers showed negative power trajectories and attained lower ranks, and individuals with low-ranking mothers showed positive rank trajectories and attained higher ranks. No significant relationship was observed between maternal rank and social integration in this sample but high rank attainment and degree measures were observed to correlate. These results support the idea of birth sex ratio bias as low-ranking females would benefit more from having sons rather than daughters whereas high-ranking females would benefit more from having daughters rather than sons.

Acknowledgments

This thesis is dedicated to the memory of Pyongyang, the most adorable monkey there was, and ever will be in all of Mawana

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Chapter 1

Introduction

1.1 Maternal Effects

An individual's phenotype is defined as the sum of the interactions between the individual's genotype and its environment, leading to significant phenotypic variation within species. Since phenotypic variation is necessary for evolution by natural selection, the causes and consequences of phenotypic variation are of interest to evolutionary biologists. What is often overlooked though is that apart from the individual's own experience of its environment, the environment experienced by other individuals in the population, especially that of the individual's mother, also influences the individual's phenotype (Mousseau, 1998). Maternal effect is broadly defined as that effect which occurs when a mother's phenotype directly affects the phenotype of her offspring, independent of offspring genotype (Arnold, 1994; Bernardo, 1995). The environment that the mother experiences can lead to variation in her growth, physiological state, and hormone levels, which can in turn influence offspring phenotype through heritable, non-genetic cytoplasmic factors (yolk amount, hormones, mRNA and protein deposition) in the egg. Furthermore, in group-living animal societies, the mothers' social environment can influence the juvenile life of the offspring.

1.2 Social Groups

The major driving forces for the evolution of sociality are thought to be improved foraging efficiency and reduced predation risk (Wood et al., 2007). Living in groups, at the same time, has costs such as kin competition and detrimental effects of inbreeding associated with it. Social organisation combats some of these costs. Social organisation in an animal society refers to the number of individuals in the group, the behavioural and genetic relationships between them, and the way reproduction is partitioned between the constituent individuals (Ross et al., 1995; Krause, 2002). Certain fundamental features of animal societies such as dominance and dispersal strategies determine their social

organisation. In many species, social organisation has notable effects on the survival (Silk et al., 2010), reproductive success (Gilby, 2013), mate choice (Oh and Badyaev, 2010), information transmission (Fewell, 2003) and pathogen propagation (Hamede et al., 2009; Drewe, 2010) of the constituent individuals.

Dispersal is a mechanism of inbreeding avoidance (Itani 1972; Harcourt 1978; Packer 1979; Greenwood 1980). It is defined as any movement that has the potential to facilitate gene flow. Apart from its effects on the fitness of the individual, dispersal also has implications on population dynamics (Dunning et al., 1995), population genetics (Hanski & Gilpin, 1997) and species distribution (Hanski, 1999). Dispersal is observed to be sex biased across different mammalian orders. In most mammals, including Old World primate species, dispersal is male biased and females are philopatric, i.e. males disperse on attaining sexual maturity while females remain in their natal group. In primate societies, dispersal is of two types: natal dispersal and secondary dispersal. The movement of juvenile males from their birth group upon attaining sexual maturity to a potential breeding group is termed as natal dispersal. Subsequent dispersal events to other groups are called secondary dispersals.

A strategy that decreases the costs of within group competition is dominance. Dominance is defined as a consistent outcome in favour of one member of a dyad during repeated agonistic interactions between them, and a default yielding of the other individual rather than escalation (Drews, 1993). The consistent winner is termed dominant, and the consistent loser subordinate. A dominance hierarchy is the linear arrangement of individuals in a group from the relatively dominant to the relatively submissive. The prevalence of dominance hierarchy has been explained by the benefits gained and costs incurred by the dominant and submissive individuals (Clutton-Brock & Harvey, 1976; Deag, 1977). By choosing not to engage in fights on every encounter, individuals benefit from conserving energy which can instead be used for foraging or reproduction (Lack, 1966). High dominance rank has been found to correlate with fitness benefits for the individual (Côté & Festa-Bianchet 2001; von Holst et al., 2002; Widdig et al., 2004; Engelhardt et al. 2006). High ranked individuals benefit from preferred access to foraging patches, sleeping sites, mates and other resources that are limiting. They may also have more freedom to engage in social interactions. On the other hand, low ranked individuals may benefit from retreating before injury as it minimizes loss of fitness. It may also be of benefit to the loser to submit to the older individuals in the group until mature enough to challenge them to gain rank at a later time (Deag, 1977). Dominance ranks are subject to change when a subordinate individual challenges a dominant one (Chase, 2009). The position that an individual attains in the dominance hierarchy is determined by several factors like genetic influence (Craig et al., 1965), age

(Clutton-Brock et al., 1982) and body size (Goodall, 1986). Dominance hierarchies are prevalent across taxa including birds (Kurvers et al. 2009), mammals (Keiper & Receveur 1992), and insects (Kolmer & Heinze 2000).

In societies with male-biased dispersal and female philopatry, maternal rank is a critical determinant of dominance rank in the natal group. New offspring, both female and male, assume positions in the dominance hierarchy adjacent to those of their mothers; this is called maternal rank inheritance (Horrocks & Hunte, 1983). Maternal rank inheritance has been documented in macaques (genus *Macaca*), baboons (genus *Papio*) and vervet monkeys (genus *Cercopithicus*), and also in spotted hyenas (*Crocuta crocuta*) (Holekamp, 1991). A well-developed social learning ability, overlap of individuals over several generations in space and time, and clustering of resources are understood to be necessary conditions for maternal rank inheritance. Females retain their maternal rank throughout their lives, while for males this retention holds true only until their dispersal. It is possible that dispersed males could use socially learned strategies from their juvenile life to attain and/or maintain their dominance rank in their new groups. Hence, it is interesting to look at rank acquisition of dispersed males in their new groups in the context of their maternal rank.

1.3 Social Ties

Apart from the general benefits of living in groups, there are specific adaptive benefits of differentiated, cooperative and affiliative social ties in animals within the group (Lin & Michener, 1972; Silk, 2007). Maintenance of social ties increases fitness, survival and reproductive success of group members across taxa: in cetaceans, primates, rodents and ungulates (Thompson, 2019). In non-human primates, measures of social ties that correlate with individual fitness are categorised into three: gregariousness, bondedness and social integration (Thompson, 2019). Social integration is defined as the process during which new individuals are incorporated into the social structure of the host society (Alba, 1997). It is a measure of how socially connected to other individuals of the group they are. Individuals well integrated into the social network have been shown to have increased lifespan and offspring survival rate (Silk et al., 2003). McFarland et al. (2015) demonstrated that social integration directly influences thermoregulatory ability. Integration is also understood to confer females with better ability deal with social stress (Crockford et al., 2008; Silk et al., 2010; Brent et al., 2011). Recent research on vervet monkeys has found differences in how juvenile males and females integrate into their natal social network (Jarrett et al., 2018), but male social integration into adult social networks post migration remains unexplored.

1.4   Aim of Study

Due to the frequency of female-bonded primate societies, female sociality has received considerable research attention (Seyfarth, 1977; Wrangham, 1980; Silk et al., 2003; Cheney, 2016), partly due to their permanent group membership which allows individuals to be followed easily throughout their lives. On the other hand, since males disperse from their natal group, it is more difficult to keep track and continue to study them once they disperse and join new groups. Juvenile males also inherit rank from their mothers, but as they disperse their ranks are highly variable in different groups over their lifetime. When males disperse, they are met with a new social environment, which creates the challenge of integrating into the social structure of the new group. Fairbanks et al. (2004) studied rank acquisition by males after emigration and integration into new groups in captive populations by simulating female philopatry and male dispersal. Their study determined that behavioural, morphological, and neurochemical factors predict male rank acquisition in the immigration group. However, they found no significant effect of maternal rank on male rank acquisition. The age at which males disperse vary in the wild, but in captive studies manual transfer of subjects are usually done at fixed ages. Males in the wild also often disperse with a peer which may be difficult to simulate in captive studies. Although effects of morphological and neurochemical factors on male rank accquisition may be difficult to study in the wild, studies of behavioural effects and maternal rank influence are feasible. Male rank acquisition and integration after dispersal in the wild still remain unexplored. This study aims to investigate the effects of maternal rank and juvenile social experience on post-dispersal rank acquisition and social integration into adult social networks by wild male vervet monkeys.

Chapter 2

Materials and Methods

2.1 Data Collection

2.1.1 Study Species

Several factors make vervet monkeys (*Chlorocebus pygerythrus*) a suitable species in which to study social integration. They are Cercopithecine primates native to and widespread throughout the southern and eastern parts of Africa. Furthermore, their terrestrial nature makes them relatively easy to observe. They live in multi-male multi-female groups, resembling the common mammalian social structure of female philopatry and male dispersal (Greenwood, 1980; Pusey, 1987). Philopatric vervet monkey females form strict matrilineal hierarchies and female rank is relatively stable. Daughters tend to inherit their mother's rank in the inverse order of age, i.e., the youngest of the females' offspring attains a higher rank that her older siblings (Koyama 1967; Sade 1972; Fairbanks 1980; Bramblett et al. 1982). Females are considered adults once they give birth for the first time, and males once they complete their natal dispersal. Males disperse at the onset of adulthood to avoid inbreeding and to facilitate gene flow. They generally disperse to neighbouring groups with overlapping territories, alone or in parallel with other known males from the same group, and they disperse multiple times throughout their lives (Cheney, 1983). This situation provides males with the challenge of integrating into their newly dispersed groups. Furthermore, their terrestrial nature makes them relatively easy to observe.

2.1.2 Study Site

The project was carried out at the Inkawu Vervet Project (IVP), a research site established in 2010 by a team of researchers from Switzerland and the UK. It is located in the Mawana Game Reserve in the province of Kwazulu-Natal, South Africa (28°00' S, 31°12' E). According to the Köppen-Geiger classification (Peer et al., 2007) the vegetation of the area is classed as savannah biome, consisting of mainly of thickets and bushveld. Two distinct seasons are observed in a year: a hot, wet season from November to April and a cold, dry season from May to October. The study focused on four groups of wild vervet

monkeys with highly overlapping home ranges, habituated to researcher presence, namely, Ankhase (AK), Baie Dankie (BD), Noha (NH), and Kubu (KB). Group sizes ranged from 20 to 68 individuals.

2.1.3 Social Data Collection

Behavioural data were collected according to established data collection protocols since 2011 (Altmann, 1974) on mobile devices using Pendragon Forms® data collection software. The monkeys were followed six days a week for 8 hours up to a full day. Observers were trained to identify individual monkeys of the groups using unique facial and bodily features and natural markings. One adult female in each group was fitted with an active VHF radio collars that was used in locating and monitoring the groups. Grooming and agonistic interactions were recorded *ad-libitum*, i.e., on an 'as-and-when-seen' basis. The directionality of these interactions was recorded as well. Conflict data were used to construct dominance hierarchies (see 2.2.1), while grooming data were used to calculate social network metrics (see 2.2.2).

2.1.4 Demographic Data Collection

From the long term database, ranging from 2011 to present, males who were born in one of the study groups and whose natal dispersal was into another study group, were shortlisted. In this study, only natal dispersal events were looked at (and not subsequent secondary dispersal events) as from our hypothesis, the behaviour of males after their first dispersal should be the one most influenced by his social experience with his mother, whereas subsequent dispersals might by influenced by the experience that the male gained in other groups. A male was considered to have completed migration after it spent at least two months in the new group. Only those males were selected whose maternal identity was known, and whose mothers were present between one to three years of their juvenile period. Ten males met these criteria (Table 2.1). After dispersal, a period of one year in the new group for the males was deemed to be sufficient time (Teichroeb et al., 2011) to compute social network metrics, hierarchical ranks attained and the power trajectories (see 2.2). Another reason one-year post-dispersal was chosen was so that potential seasonal variability of ranks during the birth season (September-February) and during the mating season (March-August) were captured. This also made comparisons between individuals possible as the residence length in the first immigration group was highly variable across individuals.

Table 2.1: **List of study subjects**

No	Study Subject	Mother	Natal Group	Immigration Group	Birth Year	Date of Immigration	Date of Departure
1.	Hlokoloza	Hleka	AK	BD	2012	16.05.2017	20.11.2019
2.	Hwahwaza	Hamba	AK	BD	2011	08.06.2016	11.12.2017
3.	Mvula	Mamoobi	AK	BD	2010	13.06.2015	17.12.2016
4.	Nyoni	Nkosikasi	AK	BD	2013	16.05.2017	19.11.2018
5.	Rheban	Roma	NH	BD	2012	05.12.2017	29.02.2020
6.	Toronto	Troia	NH	BD	2009	16.06.2014	13.02.2016
7.	Ububhibhi	Ulaka	AK	BD	2011	28.05.2016	29.02.2020
8.	Wolfie	Wietnie	BD	AK	2010	20.07.2015	24.05.2018
9.	Yangtze	Yenissei	KB	NH	2013	14.05.2018	11.11.2019
10.	Zurich	Zara	NH	BD	2009	03.06.2014	15.02.2016

AK= Ankhase, BD= Baie Dankie, NH= Noha, KB= Kubu

2.2 Data Analyses

2.2.1 Dominance Hierarchy

Dominance hierarchies were constructed using the package "Elo Rating" in R (Neumann et al., 2011). An individual's Elo rating is a value that increases or decreases based on the outcome of the conflicts that it takes part in. Ad libitum conflict data composed of aggressive and submissive behaviours (Table 2.2) were used to determine the 'winner' and 'loser' for each dyadic interaction. After each conflict, the winner gets points from the loser, the value of which is determined by the difference in the ratings of the individuals at the start of the interaction. That is, in an interaction between a high-rated winner and a low-rated loser, the winner will gain only a few points from the loser. On the other hand, if the low-rated individual wins, it would gain a much larger number of points from the winner. The number of points that can be transferred is determined by the 'k' value, which was set to 100 as per Neumann et al. (2011). Only those interactions in which a clear 'winner' and 'loser' could be determined were used to construct the dominance hierarchy; inconclusive interactions or 'draws' were discarded.

2.2.2 Maternal Rank

In order to calculate the males' maternal ranks, dominance hierarchies between the adult females were constructed. Although adult dominance hierarchies are interdigitated between the sexes (Young et al., 2017), only female-female hierarchies were constructed here as they are sufficient for maternal rank determination. The *ad libitum* conflict data of the study subjects' mothers (between the juvenile ages of one to three years of the males)

Table 2.2: **IVP Ethogram of behaviours**

Type	Behaviour	Description
Aggressive behaviours	Stare	Popping up the eyelids so white above eyes is visible. Often combined with attack
	Attack	Forward motion of the body, or lunge
	Grab	Grabbing another individual
	Take place	Individual displaces another and takes their place, usually combined with approach
	Bite	Biting another individual
	Hit	Hitting another individual
	Chase	Running after another individual who is fleeing
	Aggressive call	Aggressive vocalisation
	Steal food	Take another individual's food
	Hand-on-head	One individual places their hand on the head of another, sometimes pushes it down (not whilst grooming)
Submissive behaviours	Avoid	Head or body movement away from an aggressor, or stopping previous behaviour
	Jump aside	Jump aside to avoid something or someone
	Crouch	Bow down to an aggressor while looking at them
	Leave	Walk away from an interaction partner (or potential partner)
	Retreat	Quickly leave the proximity of another individual – not pursued as in a chase
	Flee	Run away from an aggressor as they chase
	Scream	Distress call

were chosen to calculate maternal ranks. Years one to three were chosen because juveniles are observed to spend more time in proximity to their mothers during this period of their lives (Fairbanks, 1985). In their later juvenile years, proximity to their mothers decline and they become more independent. This period of two years also gave sufficient time for the Elo rating calculations to stabilise and the female-female hierarchy to be distinct. The standardised Elo ratings of the mothers (at the end of the 3rd juvenile year of the male) were calculated using *scale_elo* function from the Elo Rating package. Standardisation of the ratings made direct comparisons between groups of varying size possible (Henzi et al., 2013).

2.2.3 Male Power Trajectory and Rank Attained

A male's power trajectory is determined by the difference between its Elo rating on its first day in the immigration group and by its Elo rating at the end of one year. It is expressed

at the slope of the line that connects them. A positive slope indicates an increase in power, while a negative slope indicates a decrease. The magnitude of the slope captures the rate of increase/decrease.

Since vervet monkeys display linear dominance hierarchies in which females and males are co-dominant (Young et al., 2017), a single, interdigitated adult dominance hierarchy was constructed for study males in their new groups after dispersal. Dominance hierarchies were constructed for each group, starting from one year before the first immigration to one year after the last study male's immigration. Data from each group prior to the first immigration of a study male was used to allow the Elo ratings of the immigration group to stabilise. For each male, one-year of ad libitum conflict data post-dispersal were used to calculate:

1. Rank attained

   For rank attained after one year, standardised Elo ratings were calculated, just as in the case of maternal rank.

2. Male Power Trajectory

   The function *traj_elo* from the package Elo Rating was used to calculate the power trajectory.

2.2.4 Network Degree

Network degree (hereafter degree) is a measure of partner diversity for social interactions. Degree of an individual is defined as its total number of unique partners. Since grooming network is being used in this study, this is the total number of unique grooming partners. Degree is further classified into in-degree (number of unique partners from whom grooming was received) and out-degree (number of unique partners groomed). Dyadic grooming interactions were used to generate grooming matrices with all the individuals of the group for the duration of one year post-dispersal for each male. Grooming interactions between all the individuals were considered because integration is a group level phenomenon. The network degrees of the study subjects in the immigration group were calculated using the function *degree* from the R package "igraph" (Csardi & Nepusz, 2006). The degree values of the study subjects were standardised by dividing the values by the average degree of the group to make between group comparison possible.

2.2.5 Eigenvector Centrality

Measures of centrality have been found to correlate with fitness outcomes in several studies (Brent, 2015; Ostner & Schülke, 2018). They are useful measures that capture the ability of constituent individuals to disseminate information, influence, and disease (Brent, 2015). A high eigenvector score for an individual means that the individual is connected to many other individuals who themselves have high connectivity. The same input

grooming matrices used to calculate network degrees were used to calculate eigenvector centrality as well. The grooming eigenvector centrality of the the study subjects in the immigration group were calculated one year post-immigration using *eigen_centrality* function from the R package "igraph".

2.3 Statistical Analyses

All statistical analyses were performed in R (R Core Team, Version R 3.3.2, 2016), using the following packages: stats, fbasics (Wuertz et al., 2020), and igraph. All significance levels were set to α two-tailed = 0.05. We constructed four linear mixed models (Table 4) using the function *lm* from the R package "stats" to test whether maternal rank predicted male rank attained, male power trajectory, degree, and eigenvector centrality. We performed Pearson's correlation tests between i) male rank attained and degree, ii) male rank attained and eigenvector centrality (Table 5) using the function *cor.test* from the R package "stats".

Table 2.3: **List of simple linear models constructed**

Model	Response Variable	Predictor Variable
1.	Power Trajectory	Maternal rank
2.	Male rank attained	Maternal rank
3.	Network Degree	Maternal rank
4.	Eigenvector Centrality	Maternal rank

Table 2.4: **List of pairs for which Pearson's correlation test was performed**

Model	Response Variable	Predictor Variable
1.	Network Degree	Male rank attained
2.	Eigenvector Centrality	Male rank attained

Chapter 3

Results

3.1 Female-female dominance hierarchy was observed to be relatively stable over time

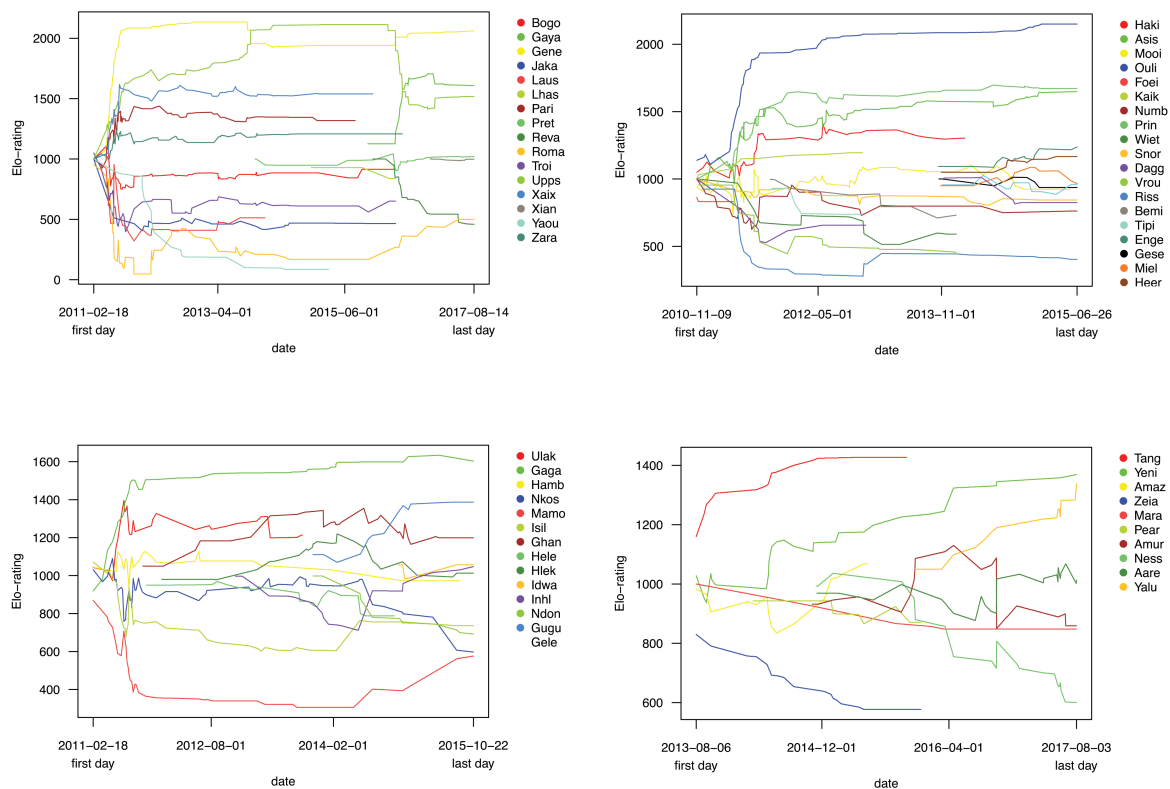Figure 3.1: Female-Female Elo rating plots of the four study groups.

It took around six months for the Elo rating to stabilize and for a distinct pattern to emerge (Figure 3.1). Using the long-term data, we extracted the maternal ranks of the study subjects at the end of their third juvenile year (Table 3.1).

Power trajectories and male ranks attained were calculated after one year in the immigration group (Table 3.2)

Table 3.1: **Maternal ranks of the study subjects**

No.	Study Subject	Mother	Maternal Elo Rating	Maternal Rank
1	Hlokoloza	Hleka	1013	0.421
2	Hwahwaza	Hamba	1030	0.525
3	Mvula	Mamoobi	354	0.000
4	Nyoni	Nkosikasi	607	0.042
5	Rheban	Roma	169	0.000
6	Toronto	Troia	606	0.215
7	Ububhibhi	Ulaka	1214	0.732
8	Wolfie	Wietnie	598	0.088
9	Yangtze	Yenissei	1345	1.000
10	Zurich	Zara	1137	0.487

Table 3.2: **Male rank attained and male power trajectory of the study subjects**

No.	Study Subject	Elo Rating	Male Rank attained	Power Trajectory
1	Hlokoloza	744	0.372	0.001
2	Hwahwaza	922	0.352	-0.535
3	Mvula	1040	0.611	0.338
4	Nyoni	790	0.405	-0.170
5	Rheban	1099	0.612	0.546
6	Toronto	936	0.330	0.105
7	Ububhibhi	797	0.176	-0.482
8	Wolfie	1106	0.701	0.616
9	Yangtze	624	0.183	-1.063
10	Zurich	892	0.290	-0.572

3.2 Maternal rank is a significant predictor of male power trajectory during the first year in the group of immigration

A simple linear regression found that maternal rank was a significant negative predictor of male power trajectory (n=10, $F_{(1, 8)}$= 55.9, R^2 = 0.86, $p < 0.05$; Figure 2). Male power trajectory can be predicted from maternal rank by the following formula: Male power trajectory = (-1.509 ± 0.202) x Maternal rank + (0.442 ± 0.096). Residuals were found to be normally distributed by performing the Jarque-bera normality test (X-squared = 0.6376, p = 0.727)
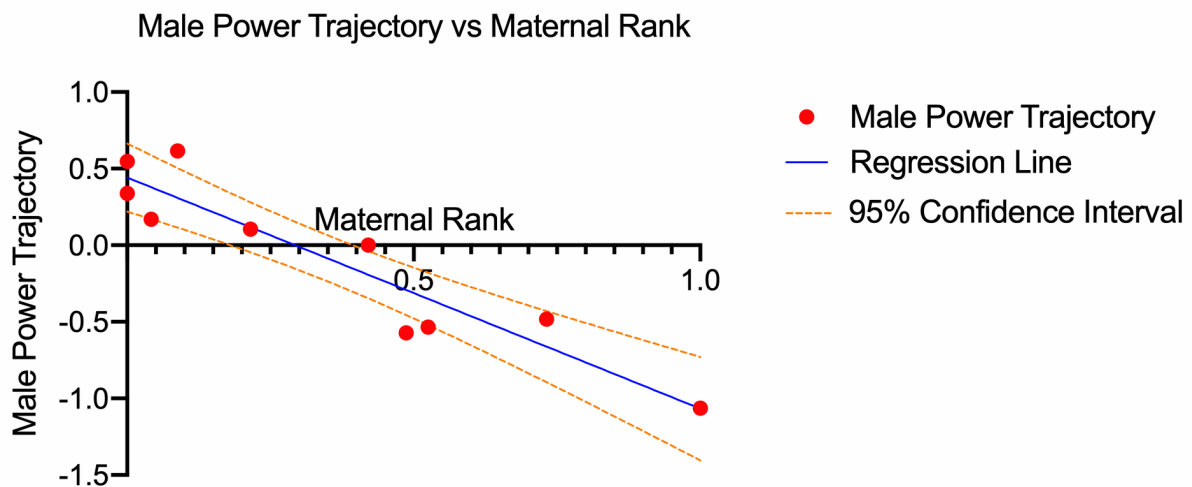
Figure 3.2: Maternal rank predicts male power trajectory (Model 1).

Individuals with maternal rank <0.293 will show a positive rank trajectory while individuals with maternal rank >0.293 will show a negative rank trajectory.

3.3 Maternal rank is a significant predictor of male rank attained after one year in the immigration group

Maternal rank was found to be a significant negative predictor of male rank using a simple linear regression (n= 10, $F_{(1, 8)}$= 19.7, R^2 =0.68, $p < 0.05$; Figure 4). Male rank attained can be predicted from maternal rank using: Male rank attained= (-0.449± 0.101) x Maternal rank + (0.561± 0.048). Jarque-bera normality test was performed and the residuals were found to be normally distributed (X-squared = 0.1801, p = 0.9139)
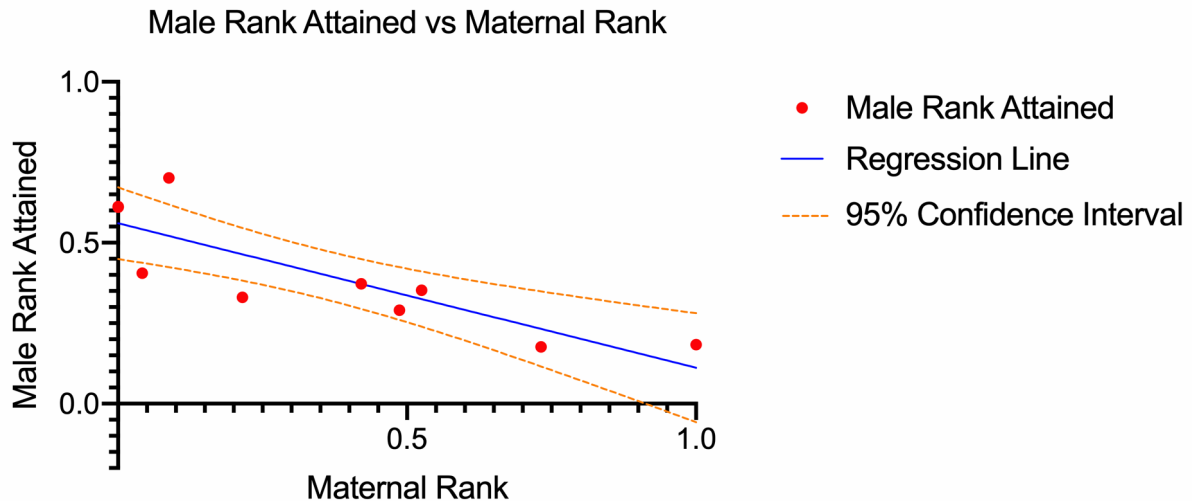
Figure 3.3: Maternal rank predicts male rank attained.(Model 2)

Individuals with maternal rank <0.387 attain ranks higher than their maternal ranks while individuals with maternal rank >0.387 attain ranks lower than their maternal ranks.

3.4 Maternal rank does not significantly predict degree and eigenvector centrality

Maternal ranks of the study subjects does not significantly predict degree (n=10, $F_{(1, 8)}$ = 0.61, R^2 = -0.045, p = 0.458), and eigenvector centrality (n=10, $F_{(1, 8)}$= 0.105, R^2 = -0.110, p= 0.755) measures after one year in the immigration group.

3.5 Male rank attained and degree were found to be significantly correlated

A significant correlation was found between the ranks attained by the study subjects in the immigration group and the degree after one year in the group (Pearson r = 0.6514, df = 8, p = 0.041) (Figure 3.4).

3.6 Male rank attained does not have a significant correlation with eigenvector centrality

No significant correlation was found between the ranks attained by the study subjects in the immigration group and their eigenvector centrality (Pearson r = 0.4564, df = 8, p = 0.185).
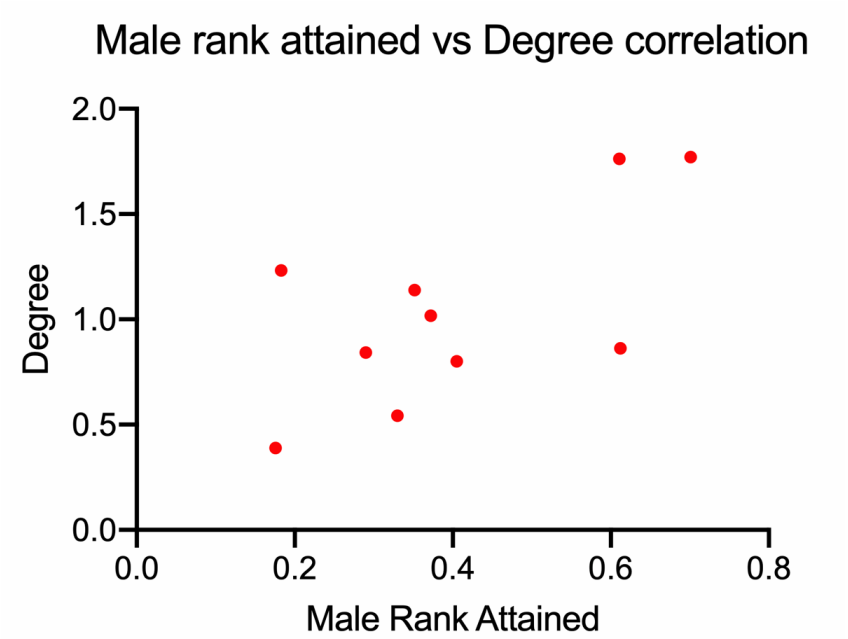
Figure 3.4: Male rank attained vs Degree correlation

Chapter 4

Discussion

This study investigated the effects of maternal rank and juvenile social experience on the post-dispersal rank acquisition and social integration into adult social networks by male vervet monkeys. In agreement with previous studies (Fairbanks, 1986), the female-female dominance hierarchy was observed to be stable over time. Maternal rank was a significant inverse predictor of male power trajectory and male rank attained after one year in the immigration group post-natal dispersal. Individuals with low-ranking mothers showed positive power trajectories and attained a higher rank in the immigration group while individuals with high ranking mothers showed negative power trajectories and attained lower ranks. Maternal rank had no significant effect on social integration of the immigrated male, characterised by network degree, strength and eigenvector centrality measures. The ranks attained by the males were significantly correlated with their degree measures after one year in the immigration group.

Our results are in contrast with Fairbanks et al., (2004) and show that maternal rank does have a significant effect on rank acquisition in the immigration group. This could be due to the advantage of using the Elo rating system to calculate dominance hierarchies that allowed the creation of distinct linear arrangements of the constituent individuals with standardised numeric values of rank while they had used categorical classification of low, mid and high ranks. The contrasting results could also be because of differences between wild and captive populations of vervet monkeys.

The different rank fates of immigrated males in the context of their maternal ranks may be explained by the different social environment that they experienced and the mechanisms that were involved in them attaining their maternal rank. Even before an infant starts taking part in agonistic interactions, it may observe the interactions between its mother and other individuals in the group, both agonistic and non-agonistic, and learn its position in the hierarchy. Studies have shown that the experiences an infant of a high-ranking mother undergoes is different from that of an infant with a low-ranking mother (Gouzoules,

1975; Ransom and Rowell, 1972; Altmann, 1980). The behaviour of other individuals of the group towards an infant is dependent on whether it outranks the infant's mother or not.

High-ranked adult females have been shown to be more aggressive than low-ranked females, even after taking into account that low ranked females have fewer individuals ranked below them that they can show aggression towards. Horrocks and Hunte (1983) suggest the frequent aggression by adult females towards young juveniles, termed as 'harassment', as a possible mechanism by which juveniles get incorporated into the dominance hierarchy of the group. High-ranked females behave aggressively towards the offspring of low-ranked females accessing a food resource, especially if the high-ranked females' offspring is within reach of said resource. With repeated instances of aggression, the offspring of the low-ranking mothers are put in constraints of movement and access to resources. Over time, these constraints reinforce deference behaviour from the offspring of low-ranked mothers. As deference behaviour by offspring of low-ranking mothers gets established, aggressions from an offspring of a high-ranking mother towards the former result in submission from the offspring of a low-ranking mother, in apprehension of potential intervention by the high rank's mother (Cheney, 1977). The offspring of high-ranking mothers may, therefore, be more used to favourable outcomes from the interactions in their natal group owing to support from their mother. On the other hand, offspring of low-ranking mothers are used to deferring and being opportunistic in resource utilisation.

Offspring of a high-ranking mother after dispersal may employ the strategy of going for resources that they want to, expecting the other individuals of the group to be deferent. Unlike in the natal group, the individuals in the new group have no reason to be deferent towards the new immigrant from the outset. This could lead to the offspring of a high-ranking mother being involved in more conflicts in their new group compared to the offspring of a low-ranking mother. Fully grown natal dispersers are a rarity (Cheney & Seyfarth 1983), and hence they face a disadvantage in conflicts with resident males of their immigration group, owing to smaller body size. This scenario might have resulted in the offspring of high-ranked mothers losing many fights which could explain why they showed negative power trajectories and attained lower ranks. On the other hand, the offspring of a low-ranked mother may continue to follow strategies of deference and engage in less conflicts after dispersal, resulting in fewer losses. This could explain why they showed positive power trajectories and attained higher ranks.

Male rank attained and degree measures correlation was expected as high ranked individuals have been found to be more integrated into the social network (Jarrett et al., 2018). In further analyses, it will be interesting to look at correlations between

male rank attained with in-degree, and male rank attained with out-degree. We expect out-degree to correlate with male rank attained, as males of low-ranking females may be more strategic in using grooming to be integrated, whereas males of dominants, used to being groomed as juveniles, may not modify their behaviour strategically after dispersal.

Trivers and Willard (1973) hypothesised that mothers could benefit from skewing birth sex ratio of their offspring that results in maximum fitness. This idea has been supported by studies in invertebrates (West et al., 2000) but studies in invertebrates are inconsistent (Clutton-Brock, 1991; Clutton-Brock and Iason, 1986; Hewison and Gaillard, 1999). Schino (2004) performed a meta-analysis on published studies in primates and observed a relationship between birth sex ratio and dominance rank, under the specific conditions of high resource availability and low sexual dimorphism. Attaining higher ranks is known to confer fitness benefits. Since our results show that offspring of low ranking mothers attain higher ranks and offspring of high ranking mothers attain lower ranks, it reinforces the idea that low ranking adult females benefit more from having sons rather than daughters and high ranking adult females benefit more from having daughters rather than sons.

Because of the constraints of needing to know the maternal identity, and for the males to disperse between the groups that were under study, the number of males that fit into our criteria over the ten years of the project were only ten. It will be worth repeating the study with a larger sample size, over a longer longitudinal study. It may also be important to control for parallel or solo dispersal events as parallel dispersers seem to be better integrated than solo dispersers. This was not possible in our study as the sample size was small. In future studies, whether it is the juvenile social experience or the experience in the first group of immigration that dictates the behaviour and strategies in subsequent groups of immigration from secondary dispersals may be looked at. It would also be interesting to test if sons of high-ranking females behave more aggressively and have a higher frequency of aggression towards new group members (especially towards juveniles that are lower in size) than the sons of low-ranking females. Looking at these differences between the levels of aggression in offspring of high-ranking mothers versus that of offspring of low-ranking mothers could explain the mechanisms through which maternal rank predicts rank acquisition.

Chapter 5

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