
Strategic social behaviour in wild vervet monkeys

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TABLE OF CONTENTS

<u>GENERAL ABSTRACT</u>	1
<u>GENERAL INTRODUCTION</u>	3
I.1. The complexity of group living	3
I.2. The development of sophisticated decision rules	4
I.3. The Social Brain Hypothesis	6
I.4. The Machiavellian intelligence hypothesis	8
I.5. Is cooperation incompatible with the Machiavellian intelligence hypothesis?	13
I.6. Study species and study site	15
I.7. PhD thesis topic	16
I.8. Thesis chapters	16
I.9. References	19
	31

CHAPTER I: SOCIAL NETWORKS AND THEIR DYNAMICS

1. THE INFLUENCE OF DEMOGRAPHIC VARIATION ON SOCIAL NETWORK STABILITY IN WILD VERVET MONKEYS	31
1.1. Abstract	31
1.2. Introduction	32
1.3. Material and methods	34
<i>1.3.1. Study site and population</i>	<i>34</i>
<i>1.3.2. Data collection</i>	<i>35</i>
<i>1.3.3. Data and statistical analyses</i>	<i>35</i>
1.4. Results	37
<i>1.4.1. Correlations between periods for the grooming network</i>	<i>37</i>
<i>1.4.2. Centrality within the grooming network</i>	<i>38</i>
<i>1.4.3. Strength of dyadic relationships within the grooming network</i>	<i>39</i>
1.5. Discussion	39
<i>1.5.1. Correlations indicate group differences</i>	<i>40</i>
<i>1.5.2. The influence of sex, hierarchy and migration on individual centrality</i>	<i>40</i>
<i>1.5.3. The influence of demographic variation on the strength of dyadic relationships</i>	<i>41</i>
<i>1.5.4. Similarities and differences among groups</i>	<i>42</i>
<i>1.5.5. Dynamic social network analyses: a new method to quantify social complexity?</i>	<i>43</i>
1.6. Conclusion	45
1.7. References	47
Figures and Table	53
1.8. Supplemental results, figures and tables	55
<i>1.8.1. Correlations between periods within proximity networks</i>	<i>55</i>
<i>1.8.2. Centrality within the proximity networks</i>	<i>55</i>
<i>1.8.3. Strength of dyadic relationships within the proximity networks</i>	<i>56</i>

2. INTERGROUP VARIATION OF SOCIAL RELATIONSHIPS IN WILD VERVET MONKEYS: A DYNAMIC NETWORK APPROACH	61
2.1. Abstract	61
2.2. Introduction	62
2.3. material and Methods	65
2.3.1. <i>Study site and population</i>	65
2.3.2. <i>Data collection</i>	66
2.3.3. <i>SIENA model and statistical analyses</i>	66
2.4 Results	70
2.4.1. <i>Triadic closure and degree popularity effects</i>	70
2.4.2. <i>Homophily: Covariate-similarity effect</i>	70
2.4.3. <i>Network rate analyses: How quickly are relationships modified?</i>	70
2.5. Discussion	70
2.5.1. <i>Limited triadic closure and degree popularity effect</i>	71
2.5.2. <i>Homophily within relationships</i>	72
2.5.3. <i>Among-group differences in relationships stability</i>	73
2.5.4. <i>Methodological considerations</i>	73
2.6. Conclusion	74
2.7. Acknowledgments	74
2.8. References	75
Figures and Table	79

CHAPTER II: HIERARCHY KNOWLEDGE

3. THIRD-PARTY RANKS KNOWLEDGE IN WILD VERVET MONKEYS (CHLOROCEBUS AETHIOPS)	81
3.1. Abstract	81
3.2. Introduction	81
3.3. Material and Methods	83
3.3.1. <i>Study site and population</i>	83
3.3.2. <i>Experimental design</i>	83
3.3.3. <i>Data and statistical analyses</i>	84
3.3.4. <i>Ethical note</i>	84
3.4. Results	85
3.5. Discussion	85
3.5.1. <i>Females know the whole female hierarchy</i>	85
3.5.2. <i>Methodological considerations and perspectives</i>	85
3.6. Acknowledgments	87
3.7. References	89
Figure	91
4. AGE/SEX DIFFERENCES IN THIRD-PARTY RANK RELATIONSHIP KNOWLEDGE IN WILD VERVET MONKEYS, CHLOROCEBUS AETHIOPS	93
4.1. Abstract	93
4.2. Introduction	94
4.3. Material and Methods	96
4.3.1. <i>Study site and population</i>	96

4.3.2. <i>Experimental design</i>	96
4.3.3. <i>Playbacks simulating conflicts between two males</i>	97
4.3.4. <i>Playbacks simulating conflicts between two females</i>	97
4.3.5. <i>Data and statistical analyses</i>	98
4.3.6. <i>Ethical note</i>	99
4.4. Results	99
4.4.1. <i>Female knowledge about male hierarchy</i>	99
4.4.2. <i>Male knowledge about female hierarchy</i>	99
4.4.3. <i>Juvenile knowledge about female hierarchy</i>	100
4.5. Discussion	100
4.5.1. <i>Females know about the male hierarchy</i>	101
4.5.2. <i>Males do not seem to know about the female hierarchy</i>	101
4.5.3. <i>Juveniles do not seem to know about the female hierarchy</i>	102
4.5.4. <i>Methodological considerations</i>	103
4.6. Conclusion	104
4.7. Acknowledgments	104
4.8. References	107
Figures and Tables	111

CHAPTER III: INDIVIDUALISED BOXES EXPERIMENTS

5. WILD VERVET MONKEYS TRADE TOLERANCE AND SPECIFIC COALITIONARY SUPPORT FOR GROOMING IN EXPERIMENTALLY INDUCED CONFLICTS	115
5.1. Abstract	115
5.2. Introduction	116
5.3. Material and Methods	117
5.3.1. <i>Training</i>	117
5.3.2. <i>Data collection</i>	118
5.3.3. <i>Data and statistical analyses</i>	118
5.4. Results and Discussion	119
5.4.1. <i>Effect of grooming on tolerance</i>	119
5.4.2. <i>Effect of grooming on coalitionary support</i>	120
5.5. General conclusions	121
5.6. Acknowledgments	123
5.7. references	125
Figures	129
5.8. Supplemental experimental procedures	131
5.8.1. <i>Study site and group composition</i>	131
5.8.2. <i>Training</i>	131
5.8.3. <i>Experimental design</i>	131
5.8.4. <i>Assessment of relationships quality</i>	132
5.9. Supplemental references	133
Supplemental figures and table	133

6. EVIDENCE FOR FINE-TUNED DECISIONS ON TOLERANCE VERSUS CONFLICT IN WILD VERVET MONKEY FEMALES	135
6.1. Abstract	135
6.2. Introduction	135
6.3. material and Methods	138
6.3.1. <i>Study site and population</i>	138
6.3.2. <i>Training</i>	138
6.3.3. <i>Data collection</i>	139
6.3.4. <i>Data and statistical analyses</i>	139
6.4. Results	140
6.4.1. <i>Audience effect on tolerance</i>	140
6.4.2. <i>Effect of bondedness and kinship</i>	141
6.4.3. <i>Audience effect on emission of vocalisations during a conflict</i>	141
6.4.4. <i>Punishment from the audience?</i>	141
6.5. Discussion	141
6.5.1. <i>Audience effect on tolerance and vocalisations</i>	142
6.5.2. <i>Interaction between grooming and audience effects</i>	143
6.5.3. <i>Punishment or image scoring?</i>	143
6.6. Conclusion	143
6.7. Methodological considerations and future perspectives	144
6.8. Acknowledgments	144
6.9. References	145
Figures	147
7. TESTING FOR AWARENESS IN RECIPROCITY DECISION RULES: AN EXPERIMENTAL APPROACH IN WILD VERVET MONKEYS	149
7.1. Abstract	149
7.2. Introduction	150
7.3. Methods	153
7.3.1. <i>Study site and species</i>	153
7.3.2. <i>Training</i>	153
7.3.3. <i>Data collection</i>	153
7.3.4. <i>Data and statistical analyses</i>	154
7.4. Results	155
7.4.1. <i>Vervet monkeys do not seem to be aware of increased tolerance</i>	155
7.4.2. <i>Awareness of coalitionary support or audience effect?</i>	155
7.5. Discussion	155
7.5.1. <i>Methodological considerations</i>	156
7.5.2. <i>Implications of potential future positive results</i>	157
7.6. Conclusion	158
7.7 Acknowledgments	158
7.8. References	159
Figures	163
<u>GENERAL DISCUSSION</u>	165
D.1. Summary	165
D.2. The Big picture	167
D.2.1. An experimental approach to cognition and cooperation	167

D.2.2. Dynamic social network analyses: a new way of quantifying social complexity?	168
D.2.3. Knowledge about third party rank relationships might be sex and age dependant	170
D.2.4. Evidence for strategic social behaviour in vervet monkeys	172
<i>D.2.4.1. Evidence for direct reciprocity</i>	<i>172</i>
<i>D.2.4.2. Evidence for audience effect</i>	<i>173</i>
<i>D.2.4.3. No evidence for awareness about decision rules</i>	<i>174</i>
D.3. Methodological considerations	175
D.4. Future research	176
D.5. References	179
<u>GENERAL ACKNOWLEDGMENTS</u>	183

GENERAL ABSTRACT

In comparison to other vertebrates, primates have a large brain in relation to their body size. It has been hypothesised that the degree of social complexity is the major predictor for such variation. In group living species, individuals face various social challenges which can include finding the right balance between cooperation and competition with other group members. Thus to survive and reproduce individuals would have to show an adapted cognitive flexibility. Following this argument, two parallel hypotheses emerged; the “Machiavellian intelligence” and the “Social brain” hypotheses propose that the social complexity of group living selected respectively for advanced cognitive abilities and an increase in relative brain/neocortex size (i.e. complexity). However, finding a positive correlation between the complexity linked to social life, corresponding advanced cognitive processes and brain size/complexity remains challenging. First, adequate proxies of social complexity that could be applied to various taxa remain to be found. Second, examples of strategic social behaviour such as proposed by the Machiavellian intelligence have been described in many taxa suggesting that more comparative studies are needed to distinguish between advanced cognitive processes and those that could rely on associative learning. Finally, a potential link between cognitive abilities and brain/neocortex size remains largely unexplored.

By studying wild vervet monkeys (*Chlorocebus aethiops*) in South Africa, the aim of this thesis was to test for the presence of some social knowledge facets in their behaviour. I also wanted to assess their ability to use such knowledge strategically in both cooperation and competition contexts. Vervet monkeys represent an ideal species as they are highly social, have a strict linear female and male hierarchies and are usually very willing to participate in set-up experiments involving food.

In Chapter I, I tested the effect of natural migration, births and deaths on the individual centrality and strength of dyadic relationships within the grooming, 1m and 5m proximity social networks (i.e. method 1). I also used a new method (i.e. SIENA; method 2) to test both the network structure and the relationships dynamics. With both methods, I found a strong among-group variation. In addition, results suggest that females and juveniles have more influence than males on the stability at both the individual and dyadic levels, especially within the grooming network. Social relationships might be subject to frequent and significant changes often linked to natural demographic variation. Thus, social network analyses have the potential to capture important aspects of the cognitive social challenges an individual has to cope with. In Chapter II, I conducted rank reversal playbacks to test vervet monkeys’ knowledge about the entire group’s hierarchy. I found that females know about both female and male hierarchies while males and juveniles seem to lack such knowledge about the female hierarchy. Results therefore suggest

sex and developmental differences in the extent of third party rank relationships. In Chapter III, I first trained females to consistently approach their personalised boxes to obtain a food reward, which allowed staging potential conflicts by placing two boxes next to each other. With such experiments I could show that subordinates trade grooming for tolerance and coalitionary support and that such trading is modified by the composition of the audience (i.e. individuals within 10m). However data also suggest that subordinates are not able to incorporate the effect of their grooming on dominants' decision-making to their own advantage.

In summary, the results of this thesis provide important insights on vervet social strategies and underlying cognitive processes. The introduced methodological advances regarding social network analyses and experimentation to reveal social strategies offer a basis for future research on other primate species for comparison. Such data would then be amenable for correlative studies that link the results to brain evolution. In such a way, one can hope to make important progress regarding the major quest: to assess how social complexity, strategic social behaviours and brain size are interlinked.

GENERAL INTRODUCTION

I.1. THE COMPLEXITY OF GROUP LIVING

In vertebrates, there is a great variation in both absolute and relative brain size (Jerison 1973). Primates generally have a large brain for to their body size in comparison to other taxa. A potential explanation relies on the hypothesis that the ecological/physical environment selected for larger brain size (Clutton-Brock and Harvey 1980; Gibson 1986). Primates indeed have to navigate successfully through extended home ranges, learn and recall where and when food is available and potentially use tools in order to get it. Positive correlations between diet and brain size have been found in non-human primates (Clutton-Brock and Harvey 1980), bats (Eisenberg and Wilson 1978) but not in birds (Bennett and Harvey 1985) suggesting some potential flaws to the ecological hypothesis. For example, while group size positively correlates with home range size in primates (Barton et al. 1992), this one does not correlate with the neocortex size (Dunbar 1992). In average, frugivorous species have larger brains than folivorous species (Clutton-Brock and Harvey 1980; Barton 1996) and it has been suggested that frugivory is more complex in the sense that individuals have to remember the spatial but also temporal distribution of fruits. However, recent studies indicated that such arguments are also valid for folivores (Snaith and Chapman 2007; Sayers 2013). Interestingly, folivorous species generally live in smaller groups than frugivorous ones (Janson and Goldsmith 1995). Many species live in stable social groups which has been suggested to be the response of an ecological challenge. Group living provides many advantages, such as a decrease of predation risk and also an increase in competitiveness against other groups of conspecifics over resources (Alexander 1974; van Schaik 1983; Wrangham 1980). As a consequence an individual's fitness strongly depends on its social interactions (Silk et al. 2003, 2009, 2010). Building upon previous work from Jolly (1966) and Humphrey (1976) an alternative to the ecological hypothesis emerged. It suggests that the complexity of a species' social environment might have been one important factor that promoted the evolution of brain size. In order to survive and reproduce an individual living in a social group has to find the right balance between intragroup competition, usually over food and mate, and cooperation with other group members, for example against predators. An additional level of difficulty is that an individual has to interact with group members who are also flexible in their decisions to compete or cooperate, leading to a natural selection based on social challenges. In figure 1, I present a summary of how "intelligence" might be linked to social complexity and which proxies of social complexity correlate with cognitive mechanisms and functions.

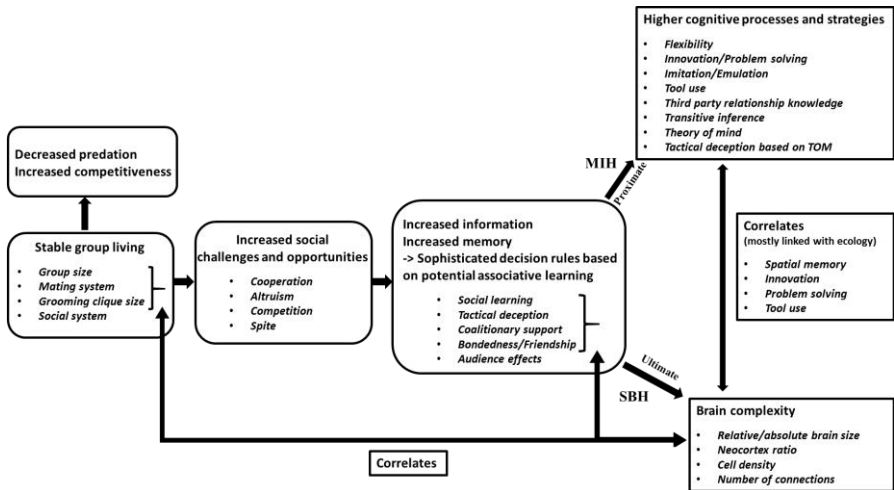


Figure 1. Summary of how social complexity selected for greater “intelligence”. The Machiavellian Intelligence Hypothesis (i.e. MIH) relies on the development of advanced cognitive abilities while the Social Brain Hypothesis (i.e. SBH) focuses on the functional processes which correspond to brain complexity.

I.2. THE DEVELOPMENT OF SOPHISTICATED DECISION RULES

As group size increases, the amount of information an individual needs to process increases accordingly. For example, individuals would have to remember more group members and more relationships, consequently selecting for a greater memory. To be socially competitive, individuals might have to develop more sophisticated decision rules based on social knowledge as they would have to face more potential competitors or co-operators. However, some of these abilities might rely on associative learning and might not need advanced cognitive processes. One of the challenges of group living also relies on the capacity to cooperate with other group members. Cooperation can depend on the quality of kin and non-kin relationships which has been referred as “friendship” (Silk 2002; Seyfarth and Cheney 2012) or “bondedness” (Shultz and Dunbar 2007, Dunbar and Shultz 2010). Such relationships are important in the sense that 1) an individual has to remember its own relationships with other group members which might be cognitively challenging in large groups and 2) they have an influence on an individual’s fitness (Silk et al. 2003, 2009, 2010). For example, coalition formation, which is the alliance of two or more individuals against a third party, might be used to increase access to mates and food, or to challenge or maintain a dominance rank (reviewed in Bissonnette et al. 2015). This latter case is largely supported by the enormous amount of coalitions across taxa that involved a target

subordinate to both coalition partners (Bissonnette et al. 2015). Such behaviour is considered as a low-cost and opportunistic way of reinforcing dominance rank and preventing own injury as the target is rather unlikely to retaliate (Cheney 1977; Watts 2002). Interactions usually take place within a communication network (McGregor 2005) adding a level of social complexity. So called “audience effect”, in the sense that an individual alters its behaviour according to the audience composition, is a capacity that seems to be present in various taxa (Matos and Schlupp 2005; Zuberbühler 2008). Audience could be used to increase social prestige or to encourage it to intervene. For example, in a client-cleaner fish interaction, cleaners (*Labroides dimidiatus*) seem to be more cooperative with their client if another potential future client is eavesdropping (Bshary and D’Souza 2003). Such behaviour has been observed in both cooperative (Pinto et al. 2011; Wedekind and Milinski 2000) and competitive contexts (Dzieweczynski et al. 2005; Slocombe and Zuberbühler 2007). Relationship quality could also influence how knowledge is transferred among group members. So called social learning, which is “the learning that is influenced by observation of, or interaction with, another animals or its products” (Heyes 1994) allows the creation of group-level behaviours and potentially traditions. For example, in primates, knowledge about food processing techniques is transferred from mother to infant (van de Waal et al. 2012). Social learning ability is wide spread and has been described in many taxa including mammals, birds, fish and insects (Galef and Laland 2005; reviewed in Galef and Heyes 2004). Similarly, tactical deception has been considered as an advanced cognitive process. It is defined as “acts from the normal repertoire of an agent, deployed such that another individual is likely to misinterpret what acts signify, to the advantage of the agent” (Byrne and Whiten 1988). For example, despite the absence of food, male chickens (*Gallus gallus*) sometimes produce food calls to attract females to increase their mating opportunities (Gyger and Marler 1988). Such deceptive behaviour seems to be rather elaborated and potentially intentional but could also be based on simple associative learning. Besides primates (Byrne and Whiten 1985; Whiten and Byrne 1997), examples of tactical deception that might rely on associative learning are present in birds (Bugnyar and Kotrschal 2002; Flower et al. 2014), fish (Bshary 2011) and cephalopods (Brown et al. 2012). While it is necessary to distinguish between simple cognitive abilities from more advanced ones, it remains challenging to design experiments that would allow testing for the presence/absence of intentionality.

Although all these behaviours and abilities might rely on basic associative learning, they seem to have been developed to cope with the complexity of a social environment and to increase an individual’s own fitness. Such arguments are part of the two major hypotheses that attempt to explain the differences in brain size

and advanced cognitive abilities across taxa: the “Social brain” (Dunbar 1992; Barton and Dunbar 1997) and “Machiavellian intelligence” (Byrne and Whiten 1988; Whiten and Byrne 1997). Initially, it was assumed that these hypotheses were relevant only to primates. However, several analyses suggested that they might also apply to other mammals such as cetaceans, carnivores and bats (Marino 1996; Dunbar and Bever 1998; but see Schultz and Dunbar 2007 for carnivores). Although both hypotheses rely on the idea that the social challenges of group living might be the prerequisite of the evolution of cognitive skills, which were developed to increase an individual’s own fitness, together with larger brains/neocortex, they may emphasise different aspects of sociality and cognition. While the Social brain hypothesis focuses on the relationship between social complexity and brain size or parts of it, the Machiavellian intelligence suggests that the complexity of a social life selected for advanced cognitive abilities, which could be related to “intelligence”. This corresponds to the development of some strategic behaviours such as manipulation and tactical deception (Byrne and Whiten 1988; Whiten and Byrne 1997), while de Waal (1982, 2007) used the term “Machiavellian” to describe some subtle manoeuvring to gain alliances in chimpanzees (*Pan troglodytes*).

I.3. THE SOCIAL BRAIN HYPOTHESIS

The Social Brain hypothesis (Dunbar 1992; Barton and Dunbar 1997) focuses on adaptive function of social complexity which corresponds to an increased brain/neocortex size. The neocortex (i.e. part of the cerebral cortex) is involved in higher function such as sensory perception, spatial reasoning, conscious thought and language. Studies sometimes evaluate the neocortex ratio which is the ratio of the neocortex size compared to the rest of the brain. Positive correlations between brain size or part of it and some parameters meant to represent social complexity have been found. In primates, neocortex (Dunbar and Shultz 2007) and relative brain size (Shultz and Dunbar 2007) correlates with group size and neocortex size also positively correlates with grooming clique size (Kudo and Dunbar 2001). In carnivores, bats (Dunbar and Bever 1998) and cetaceans (Marino 1996) neocortex ratio correlates with group size, while a following study found that in carnivores, ungulates and bats (Shultz and Dunbar 2007) relative brain size is much more strongly associated with pair-bonding. Deaner et al. (2007) found a positive correlation between absolute brain size and general learning abilities in primates. In birds, relative brain size is much more strongly associated with pair-bonding and social cohesion rather than group size (Emery et al. 2007; Shultz and Dunbar 2010a). In fish, some studies suggest that brain size differences might correlate with mating system, parental care type, habitat complexity and interspecific

competition (Pollen et al. 2007; Shumway 2008; Gonzalez-Voyer et al. 2009), but also that social environment selects for larger brain parts (i.e. tecta optica) compared to individually reared fish (Gonda et al. 2009). The enormous amount of positive correlations across taxa makes a general interpretation rather difficult. Other puzzling results suggest that social complexity might not have been the only factor selecting for larger brain size. For example, within carnivores, relative brain and neocortex size are bigger within the highly solitary bear family, than within some other much more gregarious families (Dunbar and Bever 1998). Whilst group size correlates with brain size in primates (Kudo and Dunbar 2001), it does not in birds (Beauchamp and Fernandez-Juricic 2004). It is therefore possible that another factor, such as the ecological/physical environment, might have co-selected for larger brains.

What also remains challenging is finding an accurate method to quantify social complexity. A majority of the studies used “group size” as a quantitative measurement (Dunbar 1992, 1995). Others made some qualitative comparisons between different social systems, such as fission-fusion (Barrett et al. 2003; see also Aureli et al. 2008) or mating patterns (Shultz and Dunbar 2006; 2007), while some focused on more precise social components linked with the complexity of relationships such as bondedness (Shultz and Dunbar 2007; Dunbar and Shultz 2010), rate of coalitions (Dunbar and Shultz 2007; Connor 2007) or deception (Byrne and Corp 2004). An interesting study found a positive correlation between grooming clique size based on social network analyses and neocortex ratio (Kudo and Dunbar 2001). Although social network analyses are a promising tool to study the complexity driven by the social environment only few studies applied it in relation to a more cognitive aspect (Lehmann and Dunbar 2009; Lehmann and Ross 2011; Pasquaretta et al. 2014). Despite some new propositions and ideas, the measurement of social complexity remains challenging. While it has been largely used across taxa, the proxy group size might not truly reflect the social complexity as group members might not interact similarly with each other if interacting at all. Other measures might be unfortunately limited to some species, preventing some necessary comparative studies, while others might not be directly linked with cognition. Similarly to social complexity, the measurement of intelligence or cognitive abilities has been largely debated (Shultz and Dunbar 2010b). Most studies linked to the Social brain hypothesis focused on the absolute (Deaner et al. 2007) or relative brain size (Amstrong 1985) or eventually the size of specific parts of it. It includes the neocortex in mammals (Dunbar 1992, 1995), the forebrain (Beauchamp and Fernandez-Juricic 2004) and hippocampus (Krebs et al. 1989) in birds. Therefore, there seems to be a disagreement on what needs to be measured to quantify “intelligence”. Some indeed suggest that measuring the whole brain might

not help to understand how specific behaviours were developed, while some raised the issue that some studies focused on part of the brain that were potentially not responsible for the tested cognitive behaviour (see Healey and Rowe 2007 for a review). For example, when considering relative brain size, shrews, which are the smallest mammals, have up to 10% of their body mass while for humans it represents 2% (van Dongen 1998). However, more recently, new technological advances allow considering other parameters such as cell density, cortical thickness or number of connections to quantify “intelligence” (Roth and Dicke 2005; Schnack et al. 2015). Future studies should reveal if one of them represent an accurate measurement.

I.4. THE MACHIAVELLIAN INTELLIGENCE HYPOTHESIS

The Machiavellian intelligence hypothesis in its broader term regroups a large list of advanced cognitive processes through which an individual could exploit its social environment (Byrne and Whiten 1988; Whiten and Byrne 1997), although some of these adaptations might be interlinked with the challenges proposed by the physical environment (see Figure 1). This for example includes flexibility, innovation, social learning, imitation, culture, social problem solving, self-awareness, social knowledge and theory of mind. A refined form of the hypothesis emphasises the development of strategic capacities to increase an individual’s own fitness, such as coalition formation and tactical deception (de Waal 1982). Here I present a brief review of the cognitive abilities proposed by the Machiavellian intelligence hypothesis and discuss the implication of the results at the end. As mentioned previously, social learning, coalition formation, audience effect and tactical deception might rely on associative learning. I do not discuss them below in further detail unless they clearly rely on some advanced cognitive processes.

A basic adaptation is to possess some cognitive flexibility which is “the ability to adapt the cognitive processing strategies to face new and unexpected conditions in the environment” (Cañas et al. 2003). Classic examples include task switching, multitasking, finding a new solution to a problem, creating new knowledge or eventually tools. Cognitive flexibility has been demonstrated in primates (see Reader and Laland 2011 for a review), cetaceans (Marino et al. 2007), bats (Ratcliffe et al. 2006) and other mammals (Kappeler et al. 2013), birds (Sol et al. 2005; Watanabe 2006; Bond et al. 2007), fish (Bshary 2011; Bshary et al. 2014; Patton and Braithwaite 2015), reptiles (Leal and Powell 2012 but see Vasconcelos et al. 2012) and invertebrates (Menzel et al. 2007; De Marco and Menzel 2008; Pahl et al. 2010) and seems therefore very widespread (see Roth 2015 for a review). However, not all these studies are comparable as they used different methodologies to test for the presence of cognitive flexibility.

Innovation has been defined as “a solution to a novel problem or a novel solution to an old problem” (Kummer and Goodall 1985; Reader and Laland 2003), for example, the creation of a tool to get access to previously inaccessible food. Innovations are scarce and rather unpredictable and therefore very difficult to observe or test. As a result, most successful studies came from anecdotal observations from the literature, including mammals, birds and fish (Reader and Laland 2003) or potentially from captivity (Manrique et al. 2013). Few recent studies, however, manage to implement an experimental approach in a natural environment in birds (Webster and Lefebvre 2001; Morand-Ferron et al. 2011) and mammals (Benson-Amram and Holekamp 2012; Thornton and Samson 2012; Huebner and Fichtel 2015). Innovation from an individual might spread to others by social learning (Galef and Heyes 2004) which in turn can be developed through imitation (Hurley and Chater 2005) or teaching (Caro and Hauser 1992). A tradition has been defined as a learned behaviour by multiple individuals that persists across time and potentially generations (Fragaszy and Perry 2003). Similarly to social learning, the presence of traditions has been found in mammals, birds, fish and insects, including very well-known examples such as the potato washing in Japanese macaques (*Macaca fuscata*) (Kawai 1965), the opening of milk lids by blue tits (*Cyanistes caeruleus*) (Hinde and Fisher 1951) or the song dialects in white-crowned sparrows (*Zonotrichia leucophrys*) (Marler and Tamura 1964) and whales (reviewed in Rendell and Whitehead 2001). Examples often rely on observational data (Hobaiter et al. 2014) or experiments in captivity (Whiten and Mesoudi 2008) but two recent experimental studies demonstrated the spread of traditions in the wild (vervets: van de Waal et al. 2013; great tits (*Parus major*): Aplin et al. 2014). While the idea of social learning and traditions is largely accepted, the term “culture” in animals is more debated and to this day the definition depends mostly on the authors (Whiten et al. 2011).

Innovation could emerge from the capacity of problem-solving, in the sense that the individual understands and solves a novel problem. Such capacity has been found in mammals (primates: Völter and Call 2012; Seed et al. 2009; bottlenose dolphins (*Tursiops truncatus*): Kuczaj et al. 2015; meerkats (*Suricata suricatta*): Thornton and Samson 2012; spotted hyenas (*Crocuta crocuta*): Benson-Amram and Holekamp 2012) but also in birds, especially corvids (Taylor et al. 2009 but doubt about causal reasoning), and parrots where a species living in a fission-fusion society (*Forpus conspicillatus*) outperformed three other species (Krasheninnikova et al. 2013), and more recently in a tropical lizard species (*Anolis evermanni*) (Leal and Powell 2012, but see Vasconcelos et al. 2012). However, many studies emphasised the fact that such capacities might be depend

upon individual traits and again completely excluding associative learning remains challenging.

Self-awareness is considered as a highly cognitive ability and usually tested with a mark on the animal's body that can only be seen with the help of a mirror. Such capacity has been successfully demonstrated in apes (Gallup 1970; Suarez and Gallup 1981; see Anderson and Gallup 2015 for a review), bottlenose dolphins (Reiss and Marino 2001), killer whales (*Orcinus orca*) (Delfour and Marten 2001), Asian elephants (*Elephas maximus*) (Plotnik et al. 2006) and most recently magpies (*Pica pica*) (Prior et al. 2008) and ants (Cammaerts and Cammaerts 2015). However, this was successfully demonstrated only in few individuals and usually interest was lost very quickly, while results on gorillas (*Gorilla gorilla gorilla*) provided contradictory results (Swartz and Evans 1994; Posada and Colell 2007) throwing a doubt about the level of understanding. Strong critics suggest that individuals do not have to integrate a sense of self to pass the mirror test. According to them a positive reaction might be due to a connection between seeing the same body moves as its own and if there is a spot on the body in the mirror then there might be a spot on its own body (Povinelli and Cant 1995).

Similarly to self-awareness, theory of mind (Premack and Woodruff 1978) is one of the most cognitively evolved capacities and is the ability to attribute a state of mind to another individual, which suggests some understanding of intentionality or causality. Except for humans, such capacity has been shown in chimpanzees (see Call and Tomasello 2008; Heyes 2014 for a review). However, positive results have been largely debated because simpler explanation could not be ruled out (Povinelli and Vonk 2003), because of the artificial design of the experiments, the involvement of humans as partners or the small sample size. The theory nowadays covers a wide range of social cognitive processes (Tomasello et al. 2003) rather than the strict definition of attribution to beliefs and desires. For example, recent studies tested whether chimpanzees know what others see (Hare et al. 2000) or know (Crockford et al. 2012; Schel et al. 2013). Scrub-jays (*Aphelocoma californica*) hide food multiple times after being observed by a potential pilferer and do so only after having experienced a thieving experience, while naïve birds do not show such behaviour (Emery and Clayton 2001). However, even such results might be criticised because individuals could respond to the identity of the partner rather than their perception or simply because of an inappropriate experimental design. For example, a chimpanzee taking food that an opponent cannot see might do so because of some understanding of the relationship between seeing and knowing or because of some basic learning that the opponent is motivated to defend the food it is looking at. Gaze following is a behaviour that could allow interpreting mental states and therefore is well studied. Apart from apes, such

behaviour is present in other primates (Tomasello et al. 1998; Flombaum and Santo 2005), mammals (Bräuer et al. 2004; Kaminski et al. 2005; Tschudin et al. 2001; Held et al. 2001), in corvids (Bugnyar 2013; von Bayern and Emery 2009) and even tortoises (Wilkinson et al. 2010; see Seyfarth and Cheney 2015 for a review). However, how social complexity is linked with gaze following is still poorly understood and there is still little evidence that animals have the capacity to make a connection between seeing and knowing.

Social knowledge is a broad subject that regroups multiple capacities such as some already cited above, but also individual and kin recognition, third party and third party rank relationship knowledge. Third party relationship knowledge is an important basic requirement for sophisticated social strategies and is the knowledge not only of one's own relationships with all other group members but also of the relationships between other group members. In general, individuals obtain such information through 'eavesdropping' on social interactions in a communication network (McGregor 2005). Individual (Tibbetts and Dale 2007; Wiley 2013) and kin (Hepper 2005) recognition is widespread across taxa. In some species, for example, after a conflict, redirection of aggression occurs often against an aggressor's kin, which suggests some strategic retaliation (primates: Cheney and Seyfarth 1990; Cheney and Seyfarth 1999; Schino and Marini 2014; hyenas: Engh et al. 2005). Examples of recognition of each other's associative patterns or bondedness might be more limited but is present in primates (Bachmann and Kummer 1980; Cheney and Seyfarth 1990; Tomasello and Call 1997; Crockford et al. 2007; Wittig and Boesch 2010; Wittig et al. 2014) and birds (Galef and White 2000; Mennill et al. 2002). Using playbacks experiments, Crockford et al. (2007), showed that subordinate male baboons (*Papio hamadryas ursinus*) can assess consortships temporally and spatially and achieve mating with the females that are separated from the dominant male, which indicates some awareness about the quality of some relationships even if transient. Recognition of the entire dominance hierarchy within a group is present in various taxa and is usually gained through transitive inference: if A is above B and B is above C, then deduction can be made that A is above C. Evidence has been provided for mammals (Davis 1992; Engh et al. 2005), birds (Paz-y-Miño et al. 2004; Massen et al. 2014) and even fish (Grosenik et al. 2007). However, so far, a lot of studies focused on primates (Gillian 1981; Cheney and Seyfarth 1990; Cheney et al. 1995; Silk 1999; Bergman et al. 2003; Schino et al. 2006; Slocombe and Zuberbühler 2007). Coalition formation based on third party rank relationships is considered as cognitively complex because to be highly successful, individuals have to choose the most appropriate partner, which may differ from one situation to the next. A focus has been particularly given to primates (reviewed in Bissonnette et al. 2015) but

coalitionary support also exists in other mammals, such as dolphins, some carnivores, elephants and birds (reviewed in Smith et al. 2010; Bissonnette et al. 2015).

Finally, tactical deception is the most strategic behaviour described by the Machiavellian intelligence hypothesis (Byrne and Whiten 1988; Whiten and Byrne 1997). It is however very difficult to prove the consciousness of such behaviour and although many anecdotal studies suggest its presence in various species (Byrne and Whiten 1988; Whiten and Byrne 1997). Wheeler's study (2009) on capuchins (*Cebus apella nigrinus*) relies on an interesting experimental design but again, associative learning could not be ruled out. So far the best example has been found in chimpanzees, where victims exaggerate their screams in the presence of an audience that outranks or has a similar rank of this of the aggressor (Slocombe and Zuberbühler 2007).

Some of the capacities described above fit without any doubt the Machiavellian intelligence hypothesis and positive results on social learning, culture, social knowledge and also cooperation are abundant. However, the lack of systematic comparative studies between species still prevents to explain the presence of such big variation in brain size/complexity even between social species. The few studies that tested how advanced cognitive processes are linked with brain size/"intelligence" and the usual measurement of social complexity such as group size found puzzling results. A brand new experimental study described a positive correlation between relative brain size and capacity of problem solving (Benson-Aram et al. 2016) although the problem (i.e. puzzle box) was not intrinsically linked with social complexity. While deception rate (Byrne and Corp 2004) and coalition formation (Dunbar and Shultz 2007) also correlate with the neocortex ratio, frequencies of social learning, innovation and tool use correlate with absolute and relative volume of executive brain (i.e. neocortex plus striate cortex) (Reader and Laland 2002). Interestingly no correlation between group size and social learning was found (Reader and Laland 2002). In birds, frequency of tool use and innovation are positively correlated with relative brain size (Lefebvre et al. 2002, 2004; Sol et al. 2005). Although some of these results seem to support the Machiavellian intelligence hypothesis, the correlation between deception rate and neocortex ratio seems rather meaningless saying that small brained species such as fish and some birds seem to use it regularly (Munn 1986; Bshary 2011; reviewed in Evans 1997). In fish there is also little evidence that strategic behaviour correlates with an enlarged brain (Chojnacka et al. 2015). The study from Byrne and Corp (2004) relies on a large panel of anecdotal studies which reliability might be discussed due to the lack of systematic in the data collection. For example, Wheeler (2009) found a higher frequency of deception in capuchins than

previously reported in studies based on anecdotes. Most importantly, as previously mentioned, tactical deception in its simpler form might rely on associative learning and likely to be well spread while intentional tactical deception seems to be rare in non-human species. Although positive correlations were found between brain size and innovation, tool use or problem solving, such abilities are more related to physical/ecological complexity rather than the social one. The lack of correlation between group size and social learning again suggests that group size might not be accurate enough to quantify social complexity. For example, capuchin monkeys show a good capacity of tool use and cooperation compared to baboons and macaques which live in much larger groups. Therefore, it would be important to focus on the study of abilities that correspond to social complexity and develop a powerful methodology that quantifies such complexity across diverse taxa.

Advanced cognitive processes defined by the Machiavellian intelligence hypothesis seem to be widespread within vertebrates and to some extent within invertebrates making results difficult to interpret. The lack of systematic data collection makes it unfortunately impossible to demonstrate if such abilities are somehow linked with brain complexity or “intelligence”. Positive evidence in one species might reflect an adaptation to its ecology while in another the same cognitive process might have evolved because of the complexity of its social environment. It becomes important to develop multiple experiments in a systematic way that could be applied to various species and the remaining challenge would be to quantify the different processes for correlational analyses with brain size/complexity.

1.5. IS COOPERATION INCOMPATIBLE WITH THE MACHIAVELLIAN INTELLIGENCE HYPOTHESIS?

Within an evolutionary context, explaining helping behaviours that benefit the recipient at some cost to the donor (i.e. helping based on investments) has been a great challenge. Both the kin selection (Hamilton 1964) and the reciprocity (Trivers 1971) concepts provide an evolutionary explanation to helping, respectively within related and unrelated individuals. While evidence for kin selection seems to be strong and wide spread (reviewed in Dugatkin 1997), it remains challenging to test for cooperation in the sense that both partners invest mutually in a contingent way and some previous studies might have described a so called “pseudo-reciprocity” rather than direct reciprocity (Wilkinson 1984; Milinski 1990; Hemelrijk 1994; Barrett et al. 1999; Schino and Aureli 2010; Cheney and Seyfarth 2010; reviewed in Raihani and Bshary 2011). Another theory that attempts to explain the evolution of helping behaviours for direct benefits (further termed cooperation) is the generalised reciprocity theory (Hamilton and

Taborsky 2005; Pfeiffer et al. 2005; Rutte and Taborsky 2007). In contrast to direct reciprocity, generalised reciprocity does not require advanced cognitive skills such as partner recognition or memory of previous interactions. Such reciprocity indeed implies that an individual is more likely to help a random partner after having experienced helping from another random partner. Positive examples have been so far found in humans (Yamagishi and Cook 1993; Bartlett and De Steno 2006), primates (chimpanzees: Claidière et al. 2015; capuchins: Leimgruber et al. 2014) and rats (*Rattus norvegicus*) (Rutte and Taborsky 2007). However, this theory remains largely unexplored and some other studies that attempted to test it failed to find positive results (Milinski et al. 1990; de Waal 1997), which suggests that it might evolve, but only under particular conditions. Recently, primatologists in particular have argued that primates might make decisions based on emotional states rather than on precise book-keeping of previous events. Following this theory, helping may lead to return helping either due to a short-term increase in positive emotions ('attitudinal reciprocity'; de Waal 2000), or because long-term bonds lead to increased helping due to general positive emotions ('emotional book-keeping'; Schino 2007). However, what remains well accepted is that group living individuals have to choose between cooperation, competition or a potential neutral behaviour when interacting with each other. This requires individual recognition, assessing current and remembering previous interactions (i.e. bookkeeping) and the ability to assess the situation context to select appropriately from the behavioural repertoire. This latter capacity has been developed in more detail in the concept of social competence (Taborsky and Oliveira 2010; Bshary and Oliveira 2015). In conclusion, cooperation is also an important part of the Machiavellian intelligence hypothesis.

Allogrooming (i.e. grooming hereafter) is a behaviour used in various species to remove ectoparasites (Mooring et al. 1996; Zamma 2002), but also to create and maintain social bonds (Kosfeld et al. 2005; Soares et al. 2010; Madden and Clutton-Brock 2011). Studies suggest that grooming could be exchanged for other commodities such as grooming itself (Silk et al. 1999; Barrett et al. 1999; Henzi and Barrett 1999; Schino et al. 2009), food (de Waal 1997), mating opportunities (Hemelrijk et al. 1992; Gumert 2007; Norscia et al. 2009), tolerance (Henzi and Barrett 1999; Watts 2002; Ventura et al. 2006; Port et al. 2009; Tiddi et al. 2011) and coalitionary support (Seyfarth 1977; Seyfarth and Cheney 1984; Hemelrijk 1994; Cheney et al. 2010; Schino 2007). Given that such trading increases an individual's own benefit, it can be studied within the Machiavellian intelligence hypothesis framework. However, most of the previous studies rely on correlational data or on experiments in captivity and experimental studies in the wild still remain largely unexplored.

I.6. STUDY SPECIES AND STUDY SITE

As it stands, baboons and chimpanzees are large brained species no matter which criteria are used (neocortex ratio: Dunbar 1992, 1998; absolute brain size: Deaner et al. 2007). Therefore, the question arises in how far detailed knowledge about the relationships between other group members is restricted to large brained species. Here, I studied vervet monkeys (*Chlorocebus aethiops*), which with respect to brain size are an average guenon (Stephan et al. 1989) and hence quite an average Old World monkey. Vervet monkeys' distribution is spread from central Africa to the South and their home range size varies from 0.1 to a few square kilometres (Struhsaker 1967). Group size average for this thesis was around 40 individuals with a sex ratio biased towards females. All three groups lived in overlapping home ranges which should prevent any environmental factor of having an influence on the study. Vervets represent an ideal species to run field experiments as they are usually kin on participating in experiments involving food and they have strict and linear female and male hierarchies. Both rank hierarchies were regularly assessed with the help of behavioural observations during conflicts in natural and experimental contexts. During the thesis, I had the opportunity to see few females spontaneously leaving their natal group, but generally females remain in their natal group throughout their lives and form close bonds (i.e. matriline) with their offspring. Males on the other hand migrate multiple times from sexual maturity and throughout their lives (Cheney and Seyfarth 1990). The monkeys were habituated to observers since the beginning of the project in 2010. All individuals were identified by facial characteristics. Data collection and experiments were all conducted in the private game reserve of Mawana, Kwazulu Natal, South Africa.

Published evidence suggests that vervets may already be quite sophisticated in their social strategies. They know the matriline membership of other individuals (Cheney and Seyfarth 1980; Cheney and Seyfarth 1986), females recognise the voice of their own offspring and of others', social learning is used to transfer knowledge to the new generation and matriline seem to be the key unit for social transmission (van de Waal et al. 2010, 2012, 2013). Vervets also form coalitions (Walters and Seyfarth 1987; Cheney and Seyfarth 1983, 1990), and an early playback experimental study suggests that recent grooming interactions might have an influence on the formation of coalitions (Seyfarth and Cheney 1984). Interestingly, it has been documented that, during a conflict, similarly to various species (Chapais et al. 1991; Watts 2002; Schino et al. 2007) support is usually given to the high-ranking individual (Cheney 1977; Cheney 1983). Such strategy might be developed to prevent any injury to itself (Cheney 1977).

I.7. PHD THESIS TOPIC

Using MIH and SBH as conceptual frameworks, the main aim of this PhD thesis was to study various aspects of social cognition in vervet monkeys which would be transferable to multiple species. By applying the same methodology on different species/taxa, one could finally think about testing correlations between social complexity, advanced cognitive processes and brain/neocortex size. Although they may emphasise different aspects of sociality and cognition, the “Social brain” and the “Machiavellian intelligence” hypotheses agree on the prediction that social complexity promoted the evolution of larger brains or “intelligence”, which somehow is thought to be correlated with brain size or parts of it. While new technological advances allows us to consider other parameters such as cell density or number of connections to measure “intelligence”, the alternatives proposed to quantify social complexity have been limited. Interestingly, many studies focused on cooperation, but the “Machiavellian” or strategic parts of the Machiavellian intelligence have been rather neglected. Finally, the studies that did focus on this aspect provided rather little convincing evidence that the cognitive abilities proposed by the hypothesis are positively correlated with an enlargement of brain/neocortex size. In consequence, the aim of this study was to 1) propose new methods based on dynamic social network analyses which could be used to quantify social complexity, 2) test some aspects of the social knowledge of the studied species and 3) assess if they use this knowledge strategically as suggested by the Machiavellian intelligence hypothesis.

I.8. THESIS CHAPTERS

In Chapter I, I tried to identify new parameters that can be measured in different taxa to provide an indicator of social complexity. I therefore proposed two potential methods of social network analyses which integrate some temporal dynamics that is a consequence of a constant natural demographic variation. In many species, one sex migrates at sexual maturity to prevent inbreeding and usually integrates into a new group. Migration can happen multiple times throughout life. New generations regularly also integrate into the group, while other individuals disappear naturally, which in consequence might drastically modify the group composition. Such dynamics correspond to the social complexity described by Jolly (1966) and Humphrey (1976) in the sense that social environment is not only less predictable than the physical one because it does not only depend on the different partners but also on the quality of their relationships (i.e. kinship, rank, bondedness). The cognitive challenge related to keeping track of these relationships should be smaller if these are stable over time than if they are highly variable. Social network analysis is a recent methodology and also a

powerful tool that enables describing and quantifying relationships among individuals within a social group. Some studies on female baboons (*Papio cynocephalus ursinus*) strongly suggest that maintaining strong and stable relationships correlates with increased offspring survival (Silk et al. 2003, 2009) and longevity (Silk et al. 2010). Interestingly, in the same species, females form stable bonds with their preferred partners while these bonds are more prone to variation with less preferred partners (Silk et al 2012). While these studies suggest how important the management of relationships is, they also allow realising how complex this management could be if the group composition is regularly modified. As a consequence, I analysed the influence of immigration, emigration, births and deaths on the individual centrality and on the stability of dyadic relationships strength over periods of three months and during two years (i.e. method 1). I also assessed the social networks structure and stability with the RSiena method that allows analysis of the creation and destruction of the relationships within a network according to various individual attributes such as sex, matriline, hierarchy and age (i.e. method 2). This method is capable of analysing the dynamics of a social network and may help understanding the evolution of the different relationships with time.

The aim of Chapter II was to assess what vervet monkeys know about third party relationships. Such knowledge may be an important prerequisite for strategic decision making, which was the topic of Chapter III. As it stands, individual recognition is a basic requirement which has been demonstrated in many taxa (Tibbetts and Dale 2007; Wiley 2013), similarly to kin recognition (Mateo 2004). Third party relationships knowledge, on the other hand, might be more limited to some species or taxa, including mammals, birds and fish. Such knowledge would make many strategic decisions more efficient, like adjusting behaviour to audience composition in reputation-making interactions, to pick most suitable partners for grooming and coalitions and also for some forms of tactical deception. Within despotic (i.e. with a strict hierarchy) societies in particular, knowing the whole hierarchy within a social group would be of a great benefit. I therefore reproduced a playback experiment successfully performed on baboons (Bergman et al. 2003) to assess if vervet monkeys know the whole hierarchy within their group. The idea was to play to a subject two sequences of conflicts. The control sequence involved a conflict in line with the hierarchy where the dominant produces vocalisations to aggress a subordinate which, because of the stress, produces a distress call. The experimental sequence involved a rank reverted conflict in which the subordinate aggresses the dominant. By analysing how long the subject spent looking towards the speakers, I could tell if the subject found the sequence in line with the reality or not. With this experimental set up I could test: 1) the females' knowledge about the

female hierarchy, 2) the females' knowledge about the male hierarchy, 3) the males' and 4) the juveniles' knowledge about the female hierarchy.

The aim of Chapter III was to test what individuals do with their knowledge of kinship, hierarchy and potentially bondedness that is in line with the strategic capacities described by the Machiavellian intelligence. Some studies suggest that cooperation in primates relies strongly on emotions, build up from long-term bonds (i.e. emotional bookkeeping (Schino 2007)) or eventually short-term positive interactions (i.e. attitudinal reciprocity (de Waal 2000)). However, as studies usually focus on one or the other, it is difficult to assess the relative importance of each of them. To test how individual use their social knowledge and potentially developed strategic capacities, I present a new experimental design. Adult females were first trained to approach a personal box, identifiable by unique, coloured patterns, to access high quality food. During the experiments, two boxes were placed next to each other to induce the potential for a conflict through forced proximity. The major questions asked in this Chapter are: 1) Do vervets trade grooming for other commodities such as tolerance or support? 2) Do they manipulate their behaviour according to who is around (i.e. audience effect)? 3) If grooming is indeed exchanged for other commodities, are they aware of it and therefore capable of manipulating their grooming partner for present or future benefit? The results of this study describe cognitive abilities in vervet monkeys and might help to understand if tactical strategies are more developed within a competition or a cooperation context. The results also encourage similar experiments to be run in different species. This may be only through the comparison of different capacities in multiple species/taxa that a clear correlation between these abilities and brain size or parts of it could be tested.

In summary, the social network analyses should allow us to describe how complex the social system of vervet monkeys is. Both experiments should give us a better idea of their cognitive abilities and if they can make use of these in a more strategic way. Taken together, these analyses should draw a general picture of the relation between social complexity and some cognitive processes proposed in the Machiavellian Intelligence Hypothesis. This could lead to further between-species comparative studies to better understand the evolution of cognitive abilities and how these are linked with social complexity and, ultimately, brain size.

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THE INFLUENCE OF DEMOGRAPHIC VARIATION ON SOCIAL NETWORK STABILITY IN WILD VERVET MONKEYS

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1.1. ABSTRACT

From a cognitive point of view, management and knowledge of social relationships is thought to be very challenging. This is because of ecological and demographic constraints relationships are likely prone to variation and hence need constant updating. Social network analysis is a potent tool that allows determining the position and therefore the importance of an individual within its group. However, despite the multiplication of studies on social networks, only few focused on the dynamics of such networks and how they evolve across time. Here we present a study on three wild groups of vervet monkeys (*Chlorocebus aethiops*) that analyses the modification of centralities as well as the strength of dyadic relationships within both grooming and proximity networks during two years, incorporating natural demographic variation. As females are the philopatric sex and usually remain in the natal group, while males migrate, we tested whether the former had more influence on a network dynamics than the latter. Our results document that demographic variation has a significant influence on both centralities and strength of dyadic relationships, particularly when individuals enter the group. In addition, females and juveniles had a stronger influence than males, especially within the grooming network. Interestingly, we also found important among-group variation with no obvious link to ecological or demographic differences. Our findings

support the idea that a network is a dynamic structure that varies through time, leading to an important cognitive challenge for group living species in order to keep track of the various relationships and their changes within their social group.

1.2. INTRODUCTION

Based on pioneering work by Jolly (1966) and Humphrey (1976), the Machiavellian intelligence hypothesis proposes that the social complexity of group living promoted the evolution of advanced cognitive processes, and correspondingly large brains (de Waal 1982; Whiten and Byrne 1997). Indeed, Humphrey (1976) argued that while the physical environment is highly predictable, interactions with social agents are not. Therefore, individuals have to keep track of their own social relationships as well of the third-party relationships that exist between group members in order to compete successfully within their group (Harcourt 1988). Usually such information is obtained through eavesdropping on social interactions within a communication network (McGregor 2005). It has been shown that such third party relationship knowledge ability is widespread throughout various taxa (Cheney and Seyfarth 1990; Davis 1992; Cheney et al. 1995; Bshary 2002; Paz-y-Mino et al. 2004; Engst et al. 2005; Grosenick et al. 2007; Slocombe and Zuberbühler 2007). In primates, previous studies showed evidence for the recognition mother-offspring relationships (Cheney and Seyfarth 1990), third-party rank relationships (Silk 1999; Bergman et al. 2003; Schino et al. 2006; Borgeaud et al. 2013, Chapter II) as well as consortships (Bachmann and Kummer 1980; Crockford et al. 2007). There is also some largely anecdotal evidence that primates use this knowledge in strategic behaviours such as coalition formation, manipulation or tactical deception (Kummer 1967; Cheney and Seyfarth 1990; Whiten and Byrne 1997; Slocombe and Zuberbühler 2007). Such capacities have been proposed to be increasingly cognitively demanding as group size increases as the number of dyads to be monitored increases exponentially with group size (Dunbar 1992; Lehmann et al. 2007; Sueur et al. 2011a).

Recent studies strongly suggest that successful management of social relationships increases an individual's fitness. For example, maintaining strong and stable social bonds correlates with increased offspring survival (Silk et al. 2003) and longevity (Silk et al. 2010) in female baboons. A recent study documented that female baboons form stable social relationships with preferred partners while these relationships are more prone to variation with less preferred partners (Silk et al. 2012), suggesting that individuals make indeed strategic decisions about relationship management. Such studies show how important it is to study the different relationships and their development through time. Social network analyses have become increasingly popular in the last decade and have been

employed in many studies of various taxa (Krause et al. 2007; Whitehead 2008; Croft et al. 2008), including nonhuman primates (Flack et al. 2006; Sueur and Petit 2008; Henzi et al. 2009; Sueur et al. 2011b). Networks analyses investigate the position that an individual occupies within its group and therefore the importance of its social role, for example within a hierarchy or within a grooming network (Brent et al. 2011; Sueur et al. 2011c). Centrality measure is a way to quantify an individuals' importance in a group according to its position in the network. Previous studies found that individuals from the philopatric sex are more central within a network as they form strong and long lasting bonds with their kin (Smuts 1985; Matsuda et al. 2012). It also has been shown that related individuals spend more time in proximity of each other (Lehmann and Ross 2011). Furthermore, previous studies found that high-ranking individuals occupy a more central place within a grooming network as they receive more grooming, especially in despotic societies (Sade 1972; Watts 2000; Kanngiesser et al. 2011; Sueur et al. 2011c; see Schino 2001 for a meta-analysis). A potential explanation for such asymmetric grooming patterns is that grooming can be exchanged against coalitional support and therefore high-ranking individuals are more solicited as they are of better support (Seyfarth 1977). However, some studies found a negative correlation between the rank and the amount of grooming received (O'Brien 1993; Linn et al. 1995; Henzi et al. 2003), suggesting that high-ranking individuals' attractiveness might be species or even population specific.

So far, social network analyses have been used to test for the development and the evolution of complex social systems. However these studies examined static social networks, while relationships between individuals are dynamic processes that can be modified over time according to external conditions such as ecological and social variation. Indeed, the composition of nonhuman primates groups is constantly subject to variation as new generations get integrated regularly, while old generations disappear, and individuals migrate. However, only few studies integrated such dynamics in their analyses (Croft et al. 2008; Blonder and Dornhaus 2011; reviewed in Pinter-Wollman et al. 2013). The ones that did investigated how dyadic association patterns are modified according to seasonal or resources variation (chacma baboons (*Papio hamdryas ursinus*): Henzi et al. 2009; Asian elephants (*Elephas maximus*): de Silva et al. 2011; spotted hyenas (*Crocuta crocuta*): Holekamp et al. 2012), how simulated and natural individual knock-outs influence the whole social network (Barrett et al. 2012; Kanngiesser et al. 2012) or the temporal stability of dyadic relationships (bottlenose dolphins (*Tursiops truncatus*): Connor et al. 2001; spider monkeys (*Ateles geoffroyi*): Ramos-Fernandez et al. 2009; monk parakeets (*Myiopsitta monachus*): Hobson et al. 2013). More of such studies are needed, with the ultimate aim to investigate in how

far species differences in network dynamics reveal differences in their Machiavellian intelligence capacities.

Here we present a study of grooming and proximity networks dynamics on three wild groups of vervet monkeys during two years. Both grooming and proximity between individuals are considered to be meaningful measures in order to assess the social relationships quality among non-human primates, especially in despotic societies (Cords 1997; Silk et al. 2006; Gilby and Wrangham 2008). To test the relative stability of the different relationships we first performed correlations between three months periods within the grooming, 1m and 5m proximity networks. As the number of individuals, especially females, varied between our three study groups of varying size, we also conducted explicit comparisons of network dynamics between groups. Following Dunbar (1992), we expected individuals of larger groups to yield higher correlation coefficients between time periods. This is because members of larger groups interact longer with fewer individuals, which should lead to potential more stable relationships (Lehmann et al. 2007). As vervets have strict female and male hierarchies (Cheney and Seyfarth 1990), we tested whether rank affects attractiveness in terms of grooming and proximity. As females are the philopatric sex and form long lasting bonds with their kin and other females (Cheney and Seyfarth 1990), we expected them to be more central within the grooming and proximity network compared to males. Similarly, adult females should be more central than juveniles because they have longer established relationships and a higher fighting ability. Males on the other hand migrate multiple times throughout their lives (Cheney and Seyfarth 1990), causing variation in group composition that may also have important effects on social networks. Additional variation in network structure should be caused through the integration of new generations of juveniles and the disappearance of individuals through death. Therefore, we tested how new incoming (i.e. immigrating or new generation) and leaving (i.e. emigrating or dying) individuals influence the social network in two ways: in terms of centrality at the individual level and in terms of strength of dyadic relationships. For both variables, we expected that individuals entering and leaving the group would cause disturbances. Nevertheless, as females are the philopatric sex, we expected changes in their presence and that of their kin to have a bigger impact on the dynamics of the network than migrating males.

1.3. MATERIAL AND METHODS

1.3.1. Study site and population

The study was conducted from January 2012 until December 2013 at the Inkawu Vervet Project, Mawana game reserve (S 28° 00.327; E 031° 12.348), Kwazulu

Natal, South Africa. Subjects were members of three groups of wild vervet monkeys that were habituated to the presence of human observers since 2010 (van de Waal et al. 2013a). All individuals were recognised individually through facial and body features. We considered females as adult as soon as they had their first infant, while males were scored as adult once they migrated from their natal group. Individuals were scored as infants as long as they were less than one year old and as juveniles (i.e. sub-adults included) between one and the adult age. The size of the Ankhase (AK) group excluding infants varied from 26 to 33 individuals (including from 4 to 7 adult males, 6 to 8 adult females and 12 to 19 sub-adults and juveniles), the one of the Baie Dankie (BD) group 36 to 48 individuals (4 to 5 adult males, 11 to 14 adult females and 19 to 33 sub-adults and juveniles) and the one from the Noha (NH) group 25 to 41 individuals (2 to 7 adult males, 11 to 12 adult females and 11 to 25 sub-adults and juveniles). Hierarchy was assessed by the creation of matrices based on dyadic aggressive interactions (i.e. winner-loser) occurring either in a natural context or around various food experiments. Rank relationships were assessed through the “de Vries” (1998) methodology. Juveniles’ ranks were considered as similar to their mothers’ but when a female became adult she got given her own rank according to her place within the hierarchy. The female hierarchy remained stable during the whole study period, while the male one was more prone to variation.

1.3.2. Data collection

Grooming as well as 1m and 5m proximity data were collected with scan sampling (Altmann 1974) during two full days per week per group. Every 30 minutes and during a window of 10 minutes, observers walked within the group to collect the behaviour of a maximum of individuals (except infants). For each scanned individual the identity of all the individuals present within 1m and 5m of it was also recorded. As data were collected by multiple observers, an inter-observer reliability test was performed for each observer and for each category of data to reduce variation in the data due to observer bias. The threshold of reliability was set to a minimum of 80%. In the AK group we collected 31’661 scans, in BD 28’548 and in NH 28’448. Data were collected on handheld computers (Palm Zire 22 or TX, PDA 32 and Pocket pc HP Travel Companion iPAQ rx5935) equipped with the Pendragon 5.1 software.

1.3.3. Data and statistical analyses

Only the individuals present during the 8 observation periods have been considered for the following analyses, which represents 17 individuals for AK, 28 for BD and 22 for NH. These individuals were the constant ‘core’ in the group and help to understand how permanent individuals within the group get influenced or not by

demographic changes over time. For each one of them, we calculated the weighted and normalized eigenvector for the 8 networks, each network being on a period of three months, using the software UCINET 6.375 (Borgatti et al. 2002). We did this for grooming interactions, 1m and 5m proximity networks. For each network, the link between two nodes (individuals) is the number of times scanned individuals were seeing together (grooming, 1m or 5m). The normalized eigenvector is the eigenvector divided by the maximum difference (expressed as a percentage). Thus it includes both temporal intragroup and intergroup variance. The eigenvector centrality index is the sum of the connections to its neighbors weighted by their degree. It provides a metric with which to determine the individual centrality relative to the rest of the network and the individual's "influence" on the network (connected to high-degree nodes) and thus, on the social structure. Additionally, it would appear to be a more pertinent centrality metric for non-human primate groups (Kasper and Voelkl 2009). For an overview of the weighted network metrics and their calculations, see: Croft et al. (2008), Kasper and Voelkl (2009), Wasserman (1994), Wey et al. (2008), Whitehead (2008).

To analyse the stability of the links in the network over time, we conducted a QAP (Quadratic Assignment Procedure) analysis (Mantel 1967). The QAP analysis allows studying the probability of the existence of a tie (in a matrix X) depending on the existence of another tie (in a matrix Y). To determine the correlation between two given matrices (with the same actors) we calculated a Spearman's rank correlation coefficient. We generated a p-value by comparing the observed coefficient to a distribution of coefficients produced by a null model. Edge-level permutations in the null matrices were made, values were permuted randomly between dyads. Statistical parameters of interest (e.g. model estimates, p values) were compared between the observed and randomised data. Thus, we studied the probability of the existence of a tie in regards of time.

To study the variation in individuals' eigenvector (centrality) or links (i.e. behavioural frequencies between two dyads) over time depending on their attributes (gender, age), their hierarchical rank and demographic variations (entries and leaving of the group), we used Generalized Linear Mixed Models (GLMM) with restricted maximum likelihood method, controlling for random effect of individuals and with permutation test (Croft et al. 2011; Gear et al. 2009; Otterstatter and Thomson 2007; Wey and Blumstein 2010). Weighted network metrics allow to take into account the weight of the links. GLMM (through the random effect) structures the error to enable the analysis of repeated samples of individuals in time and experimental units without committing pseudoreplication (Hurlbert 1984). The permutation procedure allows to trade with the intrinsic nature of the collected data (interactions between same-group individuals)

underlying the non-independence of the data required by inferential statistical techniques (Wasserman and Faust 1994; Krause et al. 2009; Brent et al. 2011).

GLMM models analyse a variable Y (dependent) in function of one or several explanatory variables. In this case, variables Y are whether the links or the eigenvector, and explanatory variables are the individual attributes (gender, age), hierarchical rank and demographic variations. This allows the examination of gender, hierarchical rank, demographic and age-related changes in the eigenvector or links.

Each GLMM model pattern consists in using the eigenvector or links as dependent variable and individual attributes and demographic variations of the group as independent and fixed factors. Therefore, we conducted three models for each group for the three types of network (grooming and individual proximity of 1m and 5m). This modelling method provides a comparison of the influence of explanatory variables between the groups.

Furthermore, we created another three models that include the three groups for the three networks. In these models we controlled for the random effect of groups. This modelling method provides an analysis of the influence of explanatory variables to study this phenomenon at the level of the species.

Afterwards, for each group we realized two GLMM models for the three types of network, in function of the two types of demographic variation (males or females/juveniles), as independent fixed factors and the eigenvector or links as dependent variable.

All analyses were performed in SPSS (version 20). For the correlational data we set the significance $\alpha = 0.007$ according to the Bonferroni correction, because each period was correlated 7 times with the others. We are aware that this might not be the most accurate way of dealing with multiple comparisons. However, the coefficients of correlation are of higher importance for the general aim of this paper rather than the level of significance. For the GLMM analyses as we run three analyses within each data set, we set the significance $\alpha = 0.016$.

1.4. RESULTS

For reasons of conciseness, we present only the grooming network analyses in the main paper. The analyses of the 1m and 5m distance networks are presented in the supplementary material.

1.4.1. Correlations between periods for the grooming network

When correlating all periods with each other during the two years, we found that (Table 1) the AK group, unlike the two other groups, did not have many correlated

periods within the grooming network, stressing the imprecision involved in predicting the strength of a link according to its state in a past time or to predict its future state based on its current state. In the AK group indeed only 7 out of 28 periods (25%) of the periods were significantly correlated with each other and significant correlations only involved a maximum of two periods following each other. In both the BD and NH groups, 24 periods out of 28 (85.7%) were significantly correlated with each other. In both groups the level of correlation between each period was rather stable. However, while the BD group indicated coefficients of correlation that were usually lower than 0.4, a majority of the coefficients within the NH group were higher than 0.4.

1.4.2. Centrality within the grooming network

The simultaneous analysis of the three groups highlighted a significant role of sex as females were more central than males ($F_{1,56}=29.73$; $P<0.001$). Furthermore, individuals entering decreased the centrality of the individuals already present in the group ($F_{1,484}=12.525$; $P<0.001$) (Fig. 1 for variation of centrality through time ; Appendix I: Table 1).

We also noted that results disclosed a relatively high variation among groups ($F_{2,117}=4.97$; $P=0.008$) but we also found a significant interaction between group and hierarchy ($F_{2,76}=4.626$; $P=0.013$). When analysing the groups separately, the NH group was the only group in which hierarchy had a significant effect on centrality (AK: -0.309 ; $t=-0.353$; $P=0.72$; BD: -0.375 ; $t=-1.183$; $P=0.366$; NH: -2.252 , $t=-4.147$; $p<0.001$).

Analyses of the effect of females and juveniles movements (e.g. deaths and new generation), indicated that for all three groups together, the number of entries significantly decreased the individuals' centrality that are already present in the groups ($F_{1,456}=13.412$; $P<0.001$) (Appendix I: Table 2). Interestingly, there was generally a difference among groups in the centrality of the individuals, AK having a higher mean centrality than the other groups, and a post hoc test revealed that AK and BD groups were significantly different from each other (Mean difference= 9.735 ; $SE=3.201$; $P=0.003$). Male migration did not seem to have much influence on the individuals' centrality within the grooming network when all three groups were analysed together (Appendix I: Table 3). However, we found again a variation among groups ($F_{2,141}=5.331$; $P=0.006$) but most importantly an interaction between group and the number of males leaving ($F_{2,456}=5.544$; $P=0.004$). When considering the groups separately, there was indeed a significant negative influence of the number of males leaving only in AK group (-4.845 , $t=-2.60$, $P=0.013$).

1.4.3. Strength of dyadic relationships within the grooming network

When considering the influence of migration on the strength of dyadic relationships in all three groups, we found a significant positive influence of the number of individuals leaving the group ($F_{1,10046}=28.947$; $P < 0.001$) (Fig. 2 for variation of relationships' strength through time; Appendix II: Table 1). However, there was a significant interaction between group and the number of individuals entering ($F_{2,10046}=7.58$; $P=0.001$) and leaving ($F_{2,10046}=6.375$; $P=0.002$). Analyses on each group revealed that the number of individuals entering decreased the dyadic strength significantly only in the NH (-6.23^{-5} , $t=-4.32$, $P<0.001$) group, while individuals leaving increased the strength of relationships in all three groups (AK: 1.89^{-4} , $t=2.79$, $P=0.005$; BD: $5.59e^{-5}$, $t=3.45$, $P=0.001$; NH: 2.93^{-4} , $t=3.50$, $P < 0.001$).

Our results also indicate that there is a sex difference within the grooming network. Indeed, the number of females and juveniles leaving ($F_{1,10046}=13.419$; $P<0.001$) influence significantly and positively the strength of grooming relationships (Appendix II: Table 2), while males generally do not have any influence on the grooming network. However, there was again a significant group effect for both females/juveniles (AK-BD: Mean difference: 0.001; $SE<0.001$; $P<0.001$; BD-NH: Mean difference: -0.001; $SE<0.001$; $P<0.001$) and males (AK-BD: Mean difference=0.001; $SE<0.001$; $P<0.001$; BD-NH: Mean difference<0.001; $SE<0.001$; $P=0.011$) and in all cases the AK group had a higher mean of dyadic relationships strength (Appendix II: Table 3).

1.5. DISCUSSION

In group living species, individuals face various social challenges which include finding the right balance between cooperation and competition with other group members. The social environment is indeed less stable than the physical one as group members have their own goal and have to interact with each other on multiple occasions. To survive, reproduce and increase its own fitness, an individual would have to develop sophisticated cognitive processes based on social knowledge. For example, kin recognition or third-party relationship knowledge might be a necessary prerequisite to cope with a complex social environment and such knowledge might be used in a strategic way to gain personal benefit (Whiten and Byrne 1997). However, it remains challenging to quantify social complexity as this might not only depend on the quantity but also on the quality of social bonds. Here we present a study of social network analyses on three wild groups of vervet monkeys to test how stable an individual's centrality and the strength of dyadic relationships are within a group, according to the natural demographic variation. We used grooming, 1m and 5m proximity networks data and analysed their

stability over time. Our results indicate that natural demographic variation has a strong influence on both individual centrality and dyadic relationships strength. Because individuals would have to keep track of the various relationships to be competitive, our results suggest that the complexity of the social environment might indeed have selected for advanced cognitive processes (Whiten and Byrne 1997) and potentially greater brain complexity (Dunbar 1992).

1.5.1. Correlations indicate group differences

Correlational analyses of three months period indicated similar results for the grooming and proximity networks within each group. However, there was a strong among-groups variation indicating that, the smallest group AK has the least stable relationships between individuals that remained in the group during the two years of the study. To some extent our results confirm that in larger groups, individuals interact with fewer partners but that these relationships are very stable (Dunbar 1992; Lehmann et al. 2007). However, the NH group that showed the stronger correlations was of middle size and not the largest group (i.e. BD). Our results contrast with a study on baboons that found that females living in larger groups had less stable relationships (Silk et al. 2012). Although we did not calculate how strong each dyadic relationship is, our results suggest that in both BD and NH, individuals are forming either strong or weak bonds that remain stable through time, implying some individual clustering, while within the AK, individuals seem to interact with each other on a more fluctuating basis. These results reflect the among-group differences observed in the field and found in another study (Borgeaud et al., submitted, Chapter I). In the AK group, most of the individuals regularly groom each other independently of the hierarchy, which is reflected by a higher level of tolerance within the group (Borgeaud and Bshary 2015, Chapter III), while in both BD and NH, individuals tend to interact mostly with individuals of similar rank (Borgeaud et al., submitted, Chapter I). While we are confident that such variation among groups reflects the field observations, it would be interesting to test other correlations to get a precise idea of the method accuracy. For example we could split periods into two and group each half with another half period to assess if results remain similar.

1.5.2. The influence of sex, hierarchy and migration on individual centrality

Similarly to previous studies, our network analyses on the three groups indicate that females, which are the philopatric sex, are significantly more central than males within both grooming and proximity networks (Smuts 1985; Lehmann and Ross 2011). Female vervet monkeys are likely to represent a good source of knowledge for the juveniles and the new integrated males (van de Waal et al. 2010, 2013a, 2014; Renevey et al. 2013) so that they can learn where the different food

sources are located as well as what species or items are edible. We also found that individuals entering the group, contrary to individuals leaving, have a significant negative influence on the group members' centrality within the grooming and the 1m proximity network, suggesting an active process to bond with current group members. Such bonding seems to promote social competition and as a consequence modifies individuals' position within a network, while broken bonds are replaced by new ones without drastically altering the network.

As individuals' integration to the group seem to have a strong influence on the individual centralities, while emigration or disappearance seem to have a weaker effect, we tested if such effect were more due to the adult males' migration (which occurs regularly) or to the integration/disappearance of females and juveniles. Females usually remain in their natal group throughout their whole life and sub-adult males start migrating around the age of 4 (Cheney and Seyfarth 1990). Our results indicate that new generations of juveniles integrating the group have a significant effect on all the different networks, while immigrant males did not (but see below for discussion about group differences). As expected, this suggests, that male migration has little impact on the stable group members' centrality in comparison to juveniles joining the network due to reaching the minimal age threshold, who form strong and long-lasting social bonds with their natal group members. It is indeed very likely that a mother would favour bonding with her offspring which as a consequence would decrease the quality of her other relationships at least with some individuals. Yet another potentially contributing factor might be that juvenile age cohorts typically join our network analyses within a narrow time window because the existence of an about three months lasting birth season synchronises their birth dates. Male migration on the other hand is usually spread over more months (February until June) and involves fewer individuals.

1.5.3. The influence of demographic variation on the strength of dyadic relationships

Although we could not find any general influence of natural demographic variation on the dyadic relationships strength, similarly to centrality, our results indicated a sex difference. While females and juveniles disappearing had a significant positive effect on the strength of dyadic relationships within the grooming network, males' migration on the other hand had an influence only on the 1m proximity network. Interestingly, within this network the number of males entering and leaving had respectively a positive and negative influence on the dyadic relationships strength. It is very likely that immigrant males first attempt to spend time in proximity of valuable group members such as females before being completely accepted by the group members, and hence any effect on the grooming network would occur with delay. To the contrary, males leaving had a negative influence on the proximity

dyadic relationships of the stable group members, which seems rather surprising. However, we noticed in the field that juveniles spend a lot of time in close proximity of adult males and more particularly the dominant male. It is possible that for juvenile/sub-adult males spending time in their proximity might help some form of social learning. As a result, juveniles might learn some behaviours that are crucial their future social challenges. It could also be due to the fact that adult males might provide some protection towards other adult males. If a rather central adult male leaves the group it is likely that this would lead to competition between other males to be more integrated and as a consequence might create some instability within the proximity network. However, such hypotheses would have to be tested in future studies.

1.5.4. Similarities and differences among groups

Some factors played a consistent role when we compared groups. For example, results indicated that high-ranking individuals were more central in all three groups within the 1m proximity network and when looking at the juvenile influence, we found that there was a significant negative influence of the number of juveniles entering on the individual centrality in all three networks. The general picture that emerges from these analyses is that despite the among-group differences, females and juveniles generally have a strong influence on a network stability, especially for the grooming and 1m proximity, while males have the tendency to have an influence only on the proximity networks. Individuals entering the group usually decrease the individual centrality and the strength of bonds between individuals within a grooming network but results for individuals leaving were not as consistent. As for the proximity networks, the general patterns were also less obvious. Taken together, these results again emphasise the importance of bonds between philopatric females as well as mother-offspring (matrilineal) bonds (Silk et al. 2003, 2010, 2012).

Somewhat unexpectedly, some analyses did not provide any general pattern across groups considering the high number of significant interactions. However, two general differences emerged. First with respect to analyses of centrality, we found a significant interaction between group and hierarchy within all networks. When we analysed the groups separately, results indicated that within the grooming network, NH is the only group in which high-ranking individuals were more central. This results contrast with Seyfarth's model (1977) which suggests that, within a grooming network, high-ranking individuals should be more attractive as they confer better support during conflicts. Second, the average centrality and bonds strength was generally higher within the AK group especially within the grooming and 1m network. A previous study showed that females of this group were generally more tolerant towards each other (Borgeaud and Bshary 2015,

Chapter III) and a parallel one (Borgeaud et al. submitted, Chapter I) support these results in the sense that individuals seem to bond with each other independently of the hierarchy. Such variation among groups may seem rather surprising as all three groups live in similar overlapping home ranges, rendering an ecological explanation less likely. One potential explanation could be linked with the variation of group size. It has been indeed proposed that as group size increases, networks within the group become smaller, and thus increases the likelihood of group fission (Dunbar 1992; Williamson and Dunbar 1999; Watts 2000; Lehmann et al. 2007). However, again, such explanation seems unlikely in our study, as, for example, both AK and NH groups, which showed extreme opposite results about the hierarchy had a similar group size throughout the two years.. Another explanation could rely on kinship as some groups might be more genetically related than others. However, as no genetics results are available at the moment, we were unfortunately unable to test this theory. Taken together these results suggest some interesting differences among groups. Previous studies also found that groups of the same species can show a variation in their network structure (Madden et al. 2009; Cronin et al. 2014; Dey and Quinn 2014) which might depend on demographic, ecological and potentially social variables. Furthermore, the results fit other studies on vervet monkey groups belonging to the same population with adjacent home ranges, where important variation was found with respect to diet (Tournier et al 2013), negotiation over grooming (van de Waal et al 2013b) and conflict behaviour (van de Waal in prep).

1.5.5. Dynamic social network analyses: a new method to quantify social complexity?

Social network analysis is a powerful tool which allows assessing the structure (i.e. how individuals are interconnected) and strength of relationships between individuals within a social group. However, only few studies focused on the actual dynamics of a network (Connor et al. 2001; Henzi et al. 2009; Ramos-Fernandez et al. 2009; de Silva et al. 2011; Barrett et al. 2012; Holekamp et al. 2012; Hobson et al. 2013). In a parallel study we also looked at how bonds (i.e. friendship) between individuals were created according to various individual attributes (i.e. sex, matriline, hierarchy and age) but also how these bonds fluctuate according to the natural demographic variation (Borgeaud et al. submitted, Chapter I). Similarly to this study we found a strong among-group variation and could not find any general pattern concerning how quickly relationships are modified according to the different individual attributes. Here we provide a second method to analyse and potentially quantify social network stability by integrating the same demographic variation. We propose that such measurement could be used to quantify social complexity. Both the Social brain (Dunbar 1992) and the Machiavellian

intelligence hypotheses (Byrne and Whiten 1988; Whiten and Byrne 1997) rely on the argument that the complexity of a social environment selected for the higher “intelligence” found in primates and later on in other species. The finding of an accurate proxy for social complexity would allow testing how this one is linked with advanced cognitive processes and ultimately brain complexity. For example, Kudo and Dunbar (2001) found a positive correlation between grooming clique size and neocortex size. Running comparative studies between species would then allow seeing to what extent the social environment complexity is responsible for the evolution of larger brains. Our correlational results between periods allow a first step in this direction as the effect size provided by the analyses could be compared to other species if similar data were collected. However, the strong among-group variation indicates that it would be very important if not necessary to integrate multiple groups per species within the study. After all, the ability to keep track of varying social relationships might be one of the important indicators for social complexity. For example, a male migrating from one group to another would have to show some cognitive flexibility to adapt to his new group if in this one relationships stability differs from its previous group. More generally, we note that first correlations between network features and brain features will be highly exploratory. For example, it seems impossible to predict whether relationship instability should correlate positively or negatively with brain measures. A positive correlation might be expected because relationship instability increases the need for updating information. On the other hand, relationship instability might indicate the inability to form lasting bonds and the inability to counteract the advances of competitors towards partners, and hence a lack of strategic abilities that should lead to a negative correlation with brain measures.

Taken together, our results document that natural demographic variation has an important effect on social network stability. The existence of network instability sets the stage for the evolution of sophisticated social strategies that allow individuals to exploit the emerging opportunities. Keeping track not only of its own relationships (kin, rank or bonds) but also of those that exist between other group members (Harcourt 1988) are important prerequisites of social strategies. Therefore, the social environment is likely to be complex in the sense that important components of social strategies cannot be encoded genetically but must rely on learning and memory, and might have promoted the evolution of advanced cognitive processes (Byrne and Whiten 1988; Whiten and Byrne 1997) and ultimately brain complexity (Dunbar 1992). The documented variation between groups might also support this hypothesis, as, an adult male migrating would indeed have to show some cognitive flexibility to adapt himself to the specifics of his new social environment. As a feedback, complex cognitive capacities may

result in more complex societies (Whiten and van Schaik 2007; Pasquaretta et al. 2014).

1.6. CONCLUSION

Our study indicates that the analyses of the dynamics of social network are a potent tool to describe the challenges individuals face if they want to successfully manage own relationships as well as keep track of third party relationships within their group. Our analyses suggest that social networks are indeed rather unstable over time, hinting at cognitive challenges in the social domain that are indeed different from physical cognition. As a future step, dynamic social network analyses should be conducted with various species, so that a comparative approach can be used to test whether any network features correlate with variation in brain complexity/features.

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FIGURES AND TABLE

Table 1. Networks QAP test for the grooming network. Each period of observations correspond to the number 1 to 8. Numbers indicate the coefficient of correlation. Grey cells represent significant correlations ($P>0.007$) while white ones represent non-significant ones.

	AK								BD								NH							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0.73	0.75	0.07	0.1	-0.04	-0.08	-0.12	0	0.4	0.39	0.33	0.24	0.19	0.31	0.13	0	0.63	0.68	0.6	0.55	0.64	0.65	0.39
2	0	0.66	0.02	0.18	-0.05	-0.06	-0.01	0	0.34	0.17	0.31	0.2	0.36	0.22	0	0.73	0.44	0.58	0.54	0.59	0.42			
3	0	0	-0.08	0.05	-0.1	-0.08	-0.12	0	0.22	0.24	0.26	0.46	0.31	0	0.62	0.51	0.77	0.76	0.21					
4	0	0	0.22	0.59	0.46	0.14	0	0.08	0.11	0.17	0.17	0	0.45	0.65	0.57	0.23								
5	0	0	0.37	0.23	0.23	0	0.2	0.29	0.3	0	0.24	0.24	0	0.44	0.53	0.28								
6	0	0	0.51	0.06	0	0.24	0.24	0	0.24	0.24	0	0.7	0.16											
7	0	0	0.11	0	0.33	0	0.33	0	0.33	0	0.23													
8	0	0	0	0	0	0	0	0	0	0	0													

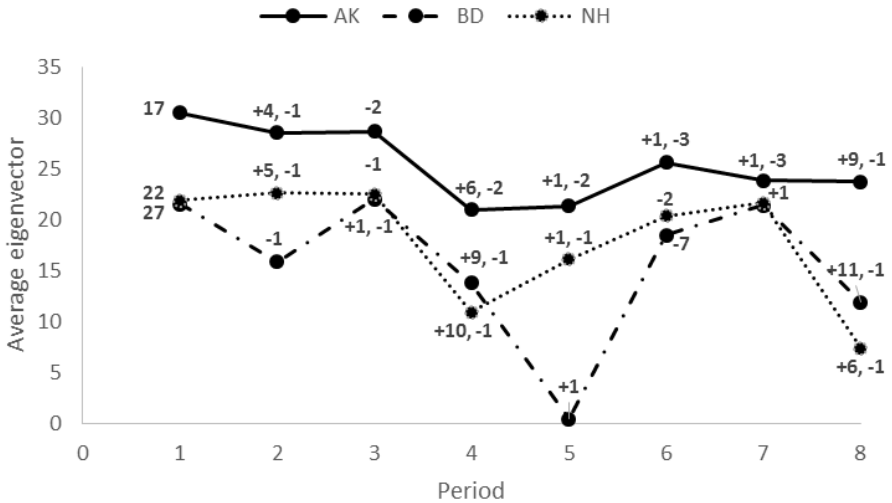


Figure 1. Variation of the eigenvector average for the grooming network throughout the 8 periods for each group according to the demographic variation. The number of group members at the beginning of the study is indicated at period 1. The number of individuals entering the group at each period is represented by “+” and the number of individuals leaving by “-”.

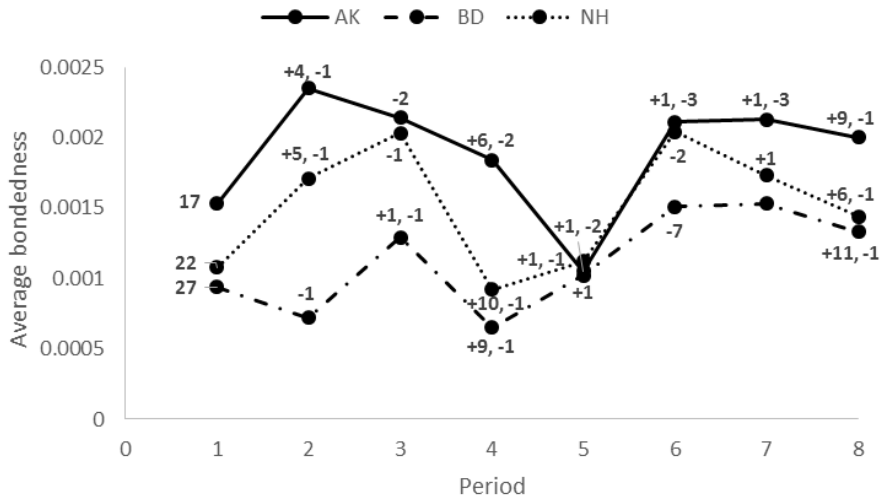


Figure 2. Average of dyadic relationships strength according to the demographic variation within the grooming network. The number of group members at the beginning of the study is indicated at period 1. The number of individuals entering the group at each period is represented by “+” and the number of individuals leaving by “-“.

1.8. SUPPLEMENTAL RESULTS, FIGURES AND TABLES

1.8.1. Correlations between periods within proximity networks

Similarly to the grooming network results, the QAP analysis (Table S1) indicated a strong difference among groups. Indeed, in the AK group, only 12 out of 28 periods (42.9%) significantly correlated with each other within the 1m proximity network, while in the 5m proximity network, there were only 6 out of 28 (21.42%). In the BD group, within both the 1m and 5m proximity networks, all periods correlated with each other. Finally in the NH group, within both 1m and 5m networks, 22 out of 28 periods correlated with each other (78.6%). While the coefficients of correlations are stronger within the proximity networks than the grooming network, in average, the NH group still has stronger correlations coefficients than the other two groups.

Table S1. Networks QAP test for 1m and 5m proximity networks. Each period of observations correspond to the number 1 to 8. Numbers indicate the coefficient of correlation. Grey cells represent significant correlations while white ones represent non-significant ones.

		AK								BD								NH							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1m	1	0	0.7	0.8	0.08	0.09	-0.18	-0.04	0.08	0	0.44	0.49	0.4	0.41	0.32	0.37	0.29	0	0.65	0.72	0.56	0.5	0.61	0.64	0.3
	2		0	0.72	0.04	0.1	-0.18	-0.1	0.07		0	0.49	0.33	0.31	0.31	0.4	0.36		0	0.73	0.55	0.48	0.58	0.64	0.26
	3			0	-0.01	0.05	-0.15	-0.07	-0.01			0	0.48	0.37	0.45	0.5	0.42			0	0.75	0.58	0.77	0.8	0.24
	4				0	0.65	0.46	0.5	0.47				0	0.33	0.31	0.37	0.29				0	0.56	0.68	0.66	0.29
	5					0	0.3	0.49	0.5					0	0.23	0.26	0.33					0	0.47	0.53	0.23
	6						0	0.51	0.16						0	0.41	0.31						0	0.76	0.23
	7							0	0.41							0	0.54							0	0.28
	8								0								0								0
5m	1	0	0.75	0.79	0.17	-0.02	-0.17	-0.07	0.03	0	0.47	0.47	0.48	0.52	0.34	0.34	0.41	0	0.67	0.69	0.57	0.5	0.57	0.6	0.21
	2		0	0.74	0.15	-0.07	-0.18	-0.07	-0.01		0	0.63	0.53	0.39	0.33	0.47	0.41		0	0.74	0.67	0.56	0.7	0.71	0.24
	3			0	0.22	-0.06	-0.21	0.02	0.02			0	0.49	0.37	0.49	0.58	0.53			0	0.73	0.53	0.73	0.76	0.18
	4				0	0.04	-0.2	0.02	0.02				0	0.57	0.49	0.41	0.48				0	0.58	0.71	0.71	0.29
	5					0	0.5	0.55	0.53					0	0.35	0.31	0.35					0	0.54	0.5	0.23
	6						0	0.58	0.33						0	0.58	0.51						0	0.78	0.29
	7							0	0.49							0	0.62							0	0.21
	8								0								0								0

1.8.2. Centrality within the proximity networks

Females were significantly more central than males within both 1m ($F_{1,54}=8.877$; $P=0.004$) and 5m ($F_{1,50}=6.224$; $P=0.016$) networks (Appendix I: Table 1). Within the 1m proximity network, individuals entering significantly decreased the centrality of the individuals already present in the group ($F_{1,483}=16.898$; $P<0.001$). High-ranking individuals were more central than low-ranking ones in both 1m ($F_{1,95}=88.138$; $P<0.001$) and 5m ($F_{1,75}=0.39$; $P<0.001$). In both

networks there was also a difference among groups (1m: $F_{2,87}=20.431$; $P<0.001$; 5m: $F_{2,80}=17.371$; $P<0.001$). However, there was a significant interaction between group and hierarchy in both 1m ($F_{2,96}=31.524$; $P<0.001$) and 5m ($F_{2,90}=23.974$; $P<0.001$) networks and also an interaction between group and the number of individuals leaving within the 5m network ($F_{2,480}=4.711$; $P=0.009$). When groups were analysed separately, analyses indicated that for proximity distances of 1m, high-ranking individuals were significantly more central in all three groups (AK: -4.351 , $t=-6.89$, $p<0.001$; BD: -0.677 , $t=-1$, $p=0.013$; NH: -3.505 , $t=-6.72$, $p<0.001$; Fig 2), while within the 5m network, this was the case in both the AK and the NH groups (AK: -2.78 , $t=-5.11$, $p<0.001$; NH: 0.705 , $t=-2.31$, $p<0.001$).

Analyses of the effect of females and juveniles movements (e.g. deaths and new generation), indicated that for all three groups together, the number of entries influenced significantly and negatively the individuals' centrality within the 1m ($F_{1,456}=49.903$; $P<0.001$) and 5m ($F_{1,456}=24.535$; $P<0.001$) (Appendix I: Table 2). However, there was again an interaction between group and the number of entries within the 1m proximity network ($F_{2,456}=5.798$; $P=0.003$). Analysed separately, all three groups showed a significant negative effect of the number of juveniles entering on the individuals' centrality within the 1m proximity network (AK: -0.9788 , $t=-4.17$, $p<0.001$; BD: -0.870 , $t=-4.26$, $p<0.001$; NH: -0.282 , $t=-2.88$, $p=0.004$).

In the contrary to females and juveniles, males' migration did not seem to have much influence on the individuals' centrality, although emigration might have had a stronger impact than immigration (Appendix I: Table 3). Within the 1m proximity network, we found a significant negative effect of the number of males leaving on the centrality of the group members ($F_{1, 456}=11.573$; $P=0.001$) but there was again a significant interaction with the group identity ($F_{2,456}=6.613$; $P=0.001$). With the groups analysed independently, we found that there was a significant effect of males leaving only in the AK group (-5.082 , $t=-4.59$, $p<0.001$). Similarly, within the 5m network there was an interaction between the number of males leaving the group and the group identity ($F_{2,456}=4.572$; $P=0.011$) and with the analyses of groups separately, only NH indicated a positive effect of males leaving on the individuals' centrality (2.727 , $t=3.03$, $p=0.004$).

1.8.3. Strength of dyadic relationships within the proximity networks

When considering the influence of migration on the strength of dyadic relationships in all three groups, in contrary to the grooming network, we could not find any significant effect of demographic variation (Appendix II: Table 1). However, in both networks there was a significant group effect. Within the 1m network, the AK group had in average stronger dyadic relationships (AK-BD:

Mean difference=0.002; SE=<0.001; P<0.001; AK-NH: Mean difference: 0.002; SE<0.001; P<0.001) while BD and NH groups were not significantly different from each other. Within the 5m proximity network, the BD group had stronger dyadic relationships (AK-BD: Mean difference=-0.022; SE=0.003; P<0.001; BD-NH: Mean difference=0.022; SE=0.001; P<0.001), while AK and NH were similar to each other.

For the females and within the 1m network, we found a group effect ($F_{2,1942}=24.15$; $P<0.001$) but also an interaction between group and the number of females/juveniles leaving ($F_{2,10032}=34.492$; $P<0.001$) (Appendix II: Table 2). Separate analyses for groups indicated a significant effect of the number of individuals leaving in all groups but in contrary to AK ($-9.59e-1$, $t=-4.16$, $p<0.001$) and BD ($-2.48e-1$, $t=-6.13$, $p<0.001$), the NH group shows a positive effect (1.6 , $t=6.03$, $p<0.001$). Within the 5m network, we could only find a significant difference between groups, indicating that the BD group had stronger dyadic relationships (AK-BD: Mean difference=-0.022; SE=0.002; P<0.001; BD-NH: Mean difference=0.022; SE=0.002; P<0.001), while again AK and NH were not significantly different from each other.

Within the proximity networks, our results indicate that in contrary to the grooming network male migration might have an influence on the strength of dyadic relationships (Appendix II: Table 3). Interestingly, we found respectively a significant positive and negative effect of male entering ($F_{1,10030}=36.257$; $P<0.001$) and leaving ($F_{1,10030}=12.998$; $P<0.001$) but also a significant group difference ($F_{2,2460}=11.018$; $P<0.001$). A post hoc analyses revealed that in average the AK group had a stronger dyadic relationships (AK-BD: Mean difference=0.002; SE<0.001; P<0.001; AK-NH: Mean difference=0.002; SE<0.001; P<0.001) while BD and NH groups were not significantly different from each other. When looking at the 5m network, we found a significant group effect ($F_{2,4907}=49.885$; $P<0.001$) but also a significant interaction between the group identity and the number of males entering the group ($F_{2,5933}=7.49$; $P<0.001$). When analysing the group separately, we found that males entering significantly influenced the strength of relationships in all three groups (AK: $2.07e-3$, $t=6.91$, $p<0.001$; BD: $3.60e-3$, $t=8.78$, $p<0.001$; NH: $1.6e-3$, $t=8.91$, $p<0.001$).

APPENDIX I

Table 1. GLMM test synthesis table of fixed effects (with global demographic variation) for individual eigenvector index

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	120.85	131.83	<0.001	1	84.317	418.02	<0.001	1	78.258	627.37	<0.001
Group	2	117.5	4.969	0.008	2	86.697	20.431	<0.001	2	80.571	17.371	<0.001
Sex	1	56.529	29.734	<0.001	1	54.43	8.877	0.004	1	50.536	6.224	0.016
Age	1	74.408	0.978	0.326	1	80.046	0.607	0.438	1	74.696	0.39	0.534
Hierarchy	1	76.209	5.917	0.017	1	94.95	88.138	<0.001	1	89.067	72.084	<0.001
Entering	1	483.72	12.525	<0.001	1	483.39	16.898	<0.001	1	481.05	5.214	0.023
Leaving	1	480.4	1.358	0.244	1	481.04	1.242	0.266	1	478.56	1.27	0.26
Group*Sex	2	56.727	1.88	0.162	2	54.822	0.053	0.948	2	50.905	0.132	0.876
Group*Age	2	75.792	0.552	0.578	2	87.914	0.607	0.547	2	82.291	1.025	0.363
Group*Hierarchy	2	75.816	4.626	0.013	2	96.289	31.524	<0.001	2	90.432	23.974	<0.001
Group*Entering	2	477.58	1.285	0.278	2	475.83	1.613	0.2	2	472.92	0.014	0.986
Group*Leaving	2	483.03	1.497	0.225	2	482.4	3.385	0.035	2	480.03	4.711	0.009

Table 2. GLMM test synthesis table of fixed effects (with females and juveniles demographic variation) for individual eigenvector index

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	104.36	203.12	<0.001	1	72.616	294.21	<0.001	1	74.115	657.14	<0.001
Group	2	102.79	4.33	0.016	2	72.334	1.112	0.335	2	73.783	1.911	0.155
F&J entering	1	456	13.412	<0.001	1	456	49.903	<0.001	1	456	24.535	<0.001
F&J leaving	1	456	0.276	0.599	1	456	0.795	0.373	1	456	1.061	0.303
Group*F&J entering	2	456	2.517	0.082	2	456	5.798	0.003	2	456	2.314	0.1
Group*F&J leaving	2	456	0.256	0.774	2	456	0.53	0.589	2	456	0.6	0.55

Table 3. GLMM test synthesis table of fixed effects (with males demographic variation) for individual eigenvector index

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	147.48	177.04	<0.001	1	82.786	256.33	<0.001	1	85.306	573.8	<0.001
Group	2	141.38	5.331	0.006	2	82.447	0.883	0.418	2	84.855	1.82	0.168
Males entering	1	456	3.086	0.08	1	456	4.59	0.033	1	456	3.265	0.071
Males leaving	1	456	2.507	0.114	1	456	11.573	0.001	1	456	4.437	0.036
Group*	2	456	3.833	0.022	2	456	2.665	0.071	2	456	0.925	0.397
Males entering	2	456	5.544	0.004	2	456	6.613	0.001	2	456	4.572	0.011
Group*	2	456	5.544	0.004	2	456	6.613	0.001	2	456	4.572	0.011
Males leaving	2	456	5.544	0.004	2	456	6.613	0.001	2	456	4.572	0.011

APPENDIX II

Table 1. GLMM test synthesis table of fixed effects (with global demographic variation) for proximity links

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	3884.4	230.41	<0.001	1	3146	837.22	<0.001	1	5875.8	18.373	<0.001
Group	2	3472.2	2.816	0.06	2	2874.9	9.609	<0.001	2	5569.6	52.328	<0.001
Entering	1	10046	2.43	0.119	1	10032	0.448	0.503	1	5977.2	0.201	0.654
Leaving	1	10046	28.947	<0.001	1	10031	1.007	0.316	1	5972.5	0.237	0.627
Group*	2	10046	7.58	0.001	2	10032	0.971	0.379	2	5918.2	0.583	0.559
Entering	2	10046	7.58	0.001	2	10032	0.971	0.379	2	5918.2	0.583	0.559
Group*	2	10046	6.375	0.002	2	10031	1.467	0.231	2	5913.7	0.486	0.615
Leaving	2	10046	6.375	0.002	2	10031	1.467	0.231	2	5913.7	0.486	0.615

Table 2. GLMM test synthesis table of fixed effects (with females and juveniles demographic variation) for proximity links

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	2227.8	392.17	<0.001	1	1978	1133.7	<0.001	1	4294.4	38.961	<0.001
Group	2	2175	9.622	<0.001	2	1942.8	24.15	<0.001	2	4077	104.59	<0.001
F&J entering	1	10046	3.874	0.049	1	10032	1.195	0.274	1	5847	0.119	0.731
F&J leaving	1	10046	13.419	<0.001	1	10032	1.491	0.222	1	5889.9	0.175	0.676
Group*	2	10046	3.171	0.042	2	10031	0.017	0.984	2	5779.4	0.273	0.761
F&J entering	2	10046	3.171	0.042	2	10031	0.017	0.984	2	5779.4	0.273	0.761
Group*	2	10046	2.706	0.067	2	10033	32.492	<0.001	2	5906.1	0.399	0.671
F&J leaving	2	10046	2.706	0.067	2	10033	32.492	<0.001	2	5906.1	0.399	0.671

Table 3. *GLMM test synthesis table of fixed effects (with males demographic variation) for proximity links*

Factor	Grooming				1M				5M			
	Num	Den	F	Sig.	Num	Den	F	Sig.	Num	Den	F	Sig.
Intercept	1	2926.5	348.77	<0.001	1	2467.1	900.43	<0.001	1	5064.5	25.188	<0.001
Group	2	2896.4	5.953	0.003	2	2460.8	11.018	<0.001	2	4907.8	49.885	<0.001
Males entering	1	10046	4.052	0.044	1	10031	36.257	<0.001	1	5969.4	4.238	0.04
Males leaving	1	10046	0.59	0.442	1	10032	12.998	<0.001	1	5980.9	0.042	0.838
Group* Males entering	2	10046	0.597	0.551	2	10031	0.109	0.897	2	5933.4	7.49	0.001
Group* Males leaving	2	10046	1.607	0.2	2	10032	0.018	0.982	2	5901.9	0.085	0.918

INTERGROUP VARIATION OF SOCIAL RELATIONSHIPS IN WILD VERVET MONKEYS: A DYNAMIC NETWORK APPROACH

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CB collected the data, SS and CS run the analyses and all authors contributed to the writing.

2.1. ABSTRACT

Social network analysis is a powerful tool that enables us to describe and quantify relationships between individuals. So far most of the studies rely on the analyses of various network snapshots, but do not capture changes over time. Here we use a stochastic actor-oriented model (SAOM) to test both the structure and the dynamics of relationships of three groups of wild vervet monkeys. We found that triadic closure (i.e. the friend of a friend is a friend) was significant in all three groups while degree popularity (i.e. the willingness to associate with individuals with high degree of connections) was significant in only two groups (AK, BD). The structure and dynamics of relationships according to the attributes of sex, matriline and age differed significantly among groups. With respect to the structure, when analyzing the likelihood of bonds according to the different attributes, we found that individuals associate themselves preferably to individuals of the same sex only in two groups (AK, NH), while significant results for attachment to individuals of the same matriline were found also in two groups (BD, NH). With respect to the dynamics, i.e. how quickly relationships are modified, we found in two groups (AK, BD) that females' relationships were more prone to variation than

males'. In the BD group, relationships within high-ranking matriline were less stable than low-ranking ones while in the NH group, juveniles' relationships were also less stable than adults' ones. The intergroup variation indicates that establishing species-specific or even population specific characteristics of social networks for later between-species comparisons will be challenging. Although, such variation could also indicate some methodological issue, we are quite confident that data was collected similarly within the different groups. Our study therefore provides a potential new method to quantify social complexity according to natural demographic variation.

2.2. INTRODUCTION

Social network analysis is a method that is used to describe and quantify relationship patterns within a group. Such metrics can be applied at an individual, group or species level. During the last decade, social network analysis has become increasingly popular, especially in primatology (Flack et al. 2006; Sueur and Petit 2008; Henzi et al. 2009; Silk et al. 2003, 2010). However, most previous studies considered a network to be a static structure that does not vary over time. The few studies that integrated temporal variation focused on dyadic relationships or at the group level and compared networks at different periods (Silk et al. 2006 a; Henzi et al. 2009). Such a dynamic approach is necessary if we aim at quantifying network instability and hence the need of an individual to monitor and update its knowledge about its own and also third party relationships. One study tested the influence of natural "knock-outs" within the group (Barrett et al. 2012) and measured their effects in term of entropy. Another one used 20 years of data on a clan of spotted hyenas to understand the effect of rainfall and abundance of preys on the network structure (Ilany et al. 2015). In a parallel publication (Borgeaud et al. in prep) on wild vervet monkeys, we also made a first step forward towards the analysis of a network dynamics by considering the influence of demographic variation (i.e. the number of individuals entering and leaving the group) on the individual centrality and on the dyadic relationship stability. Results suggested that, despite some intergroup variation, demographic variation of females and juveniles have a stronger influence than males on both centrality and the relationship stability. This seems logical knowing that, in vervet monkeys, females remain generally in their natal group for their entire life and form strong and long-lasting bonds with their kin, while males migrate throughout their lives (Cheney and Seyfarth 1990). However, despite the development of new analytical methods, studies that took into consideration changes over time within a network remain scarce (see Pinter-Wollman et al. 2013 for a review).

Explaining cooperative behaviors that benefit the recipient at some cost to the donor (i.e. helping based on investments) has been a great challenge. Both the kin selection (Hamilton 1964) and the reciprocity (Trivers 1971) concepts provided an evolutionary explanation to helping, respectively within related and unrelated individuals. Social network analyses have been proposed as a powerful tool to describe how individuals influence each other within a network and how these relationships evolve over time. Ultimately understanding the dynamics of these relationships could help explain how cooperation evolves. For example, triadic closure (i.e. the hypothesis that an individual is more likely to create bonds with the friends of its friends) may facilitate the formation of cohesive sub-/groups and consequently cooperation within a social group (Granovetter 1973; Lusseau et al. 2006; Easley and Kleinberg 2010). The process that describes how individuals associate preferably to individuals with high centrality is called degree popularity (Barabási and Albert 1999) and some studies found that high-ranking individuals are usually more central within a grooming and proximity network (see Schino 2001 for a meta-analysis; Sueur et al. 2011; Kanngiesser et al. 2011; Borgeaud et al. in prep). This supports Seyfarth's theory (1977) which suggests that grooming could be exchanged against coalitionary support and that individuals should compete to associate with high-ranking individuals as they provided better support during conflicts or as tolerance in the vicinity of food resources increase with grooming exchanged. In this way, individuals attracted to central individuals might have a better fitness than other less strategic individuals. Another interesting measurement is the assortativity of relationships based on individual traits which is called homophily (see McPherson et al. 2001 for a review). Examples include space use in sea lions (Wolf et al. 2007), sex and age-related relationships in dolphins (Lusseau and Newman 2004) and personality in sticklebacks (Pike et al. 2008). Homophily might also increase an individual's fitness. For example, playing behaviour between juveniles decreases the risk of injuries (Shimada and Sueur 2014) and personality or sex segregation increases food research efficiency (Ruckstuhl and Kokko 2002; Dyer et al. 2009). In primates, some studies report that, except for kin who usually forms the strongest bonds (Chapais 2001; Silk et al. 2006 a, b, 2010, 2012), unrelated individuals of similar rank or age also form long-lasting relationships (Silk et al. 2006 a, 2010, 2012). Such bondedness could be explained through familiarity and eventually paternal kinship (Seyfarth and Cheney 2012) but also personality (Massen and Koski 2014). It has been reported that the quality of such bonds have an influence of an individual's fitness such as its longevity and offspring survival (Silk et al. 2003, 2009, 2010) resulting in the selection of such social strategies but a lot of studies analyzed such relationships as being part of a static network. Hence it would be important to apply a more

dynamic approach to the analyses of relationships quality which evolve naturally over time (Ilany et al. 2015).

One method that has been developed is the Siena model (for Simulation Investigation for Empirical Network Analysis, Snijders 2001; Blonder et al. 2012; Pinter-Wollman et al. 2013; Ilany et al. 2015; Pasquaretta et al. 2016), available in the R package RSiena. This stochastic actor-based model aims to give a realistic representation of the dependence between the formation and also termination of different network ties. It therefore allowed us to examine how network processes and covariates influence the probability of individuals changing their network ties according to their attributes over time (Burk et al. 2007; Snijders et al. 2010). By applying these analyses on three wild groups of vervet monkeys over a period of two years, we aimed at describing the dynamics of their social network (in terms of grooming and proximities relationships) according to the natural demographic variation. Vervet monkeys represent an ideal model as, in addition to natural disappearance, every year a new generation of infants gets integrated. Native sub-adult males leave the group once they have reached sexual maturity and adult males migrate throughout their whole life joining and leaving multiple groups (Cheney and Seyfarth 1990).

RSiena is a powerful program allowing us to answer many questions about the mutually dependent dynamics of networks and attributes (behavior, individual characteristics, etc.) of the individual actors in the network. The RSiena approach allows testing of a great variety of potentially interesting network characteristics such as triadic closure, homophily and rate effect which analyses the relationships' stability according to various individual attributes. This approach allowed us to assess how the relationships' quality (i.e. based on grooming and proximity data) evolves in function of the natural demographic variations. First, we tested the effect of triadic closure (Fig. 1a) and degree popularity as well as the temporal persistence of these effects. As vervet monkeys are a highly social species that shows some level of cooperation (Cheney and Seyfarth 1990; Borgeaud and Bshary 2015), we expected triadic closure to be present in all three groups. Specifically, the triadic closure effect will assess whether new coming individuals developing relationships with specific individuals will also develop relationships with their "friends". Triadic closure is a good model to understand how networks will evolve over time. While simple graph theory tends to analyze networks at one point in time, applying the triadic closure principle can predict the development of ties within a network and shows the progression of connectivity (Easley and Kleinberg 2010). We also tested the effect of degree popularity (Fig. 1b): as high-ranking individuals offer better support in case of conflict (Cheney and Seyfarth 1990) and could also confer some protection when spending time in their proximity

(Watts 2002; Cheney and Seyfarth 2008) they should be preferred targets for bonding attempts and hence should receive disproportionate amounts of grooming. Therefore, new incomers would challenge existing links between group members and in this case it might result in detectable variation of central/high ranking individuals' position within the network (Cheney and Seyfarth 1990; Borgeaud et al. in prep). We also tested homophilic bonds (Fig. 1c) to know if individuals preferably associate with individuals of similar attributes such as sex, matriline, hierarchy and age. As females are the philopatric sex and normally remain in their natal group throughout their lives (Cheney and Seyfarth 1990), we expected them to form stronger bonds between them rather than with males. As juveniles from the same generation spend at least four years within the same group before a potential migration (i.e. for the males) and as adult females have spent many years within the same group (Cheney and Seyfarth 1990), we expected individuals from similar age to form stronger bonds (Silk et al. 2010). We also expected individuals of similar rank in the hierarchy to form stronger bonds than individuals of distant rank as usually neighboring ranks are more closely related (Cheney and Seyfarth 1990). Furthermore, as hypothesized by Seyfarth (1977), if high-ranking females are indeed preferred grooming partners, competition may limit the access to high-ranking partners only to neighboring rank individuals (Silk 2006 a, b). Finally, we examined how the different group members' relationships according to the same individual attributes are prone to variation over time. As indicated by Silk et al. (2010), adult female baboons form strong and stable bonds with their kin and with females of similar age. We therefore expected the same for female vervet monkeys while males' relationships should be more prone to variation.

2.3. MATERIAL AND METHODS

2.3.1. Study site and population

The study was conducted from January 2012 until December 2013 at the Inkawu Vervet Project, Mawana game reserve (S 28° 00.327; E 031° 12.348), Kwazulu Natal, South Africa. Subjects were three habituated groups of wild vervet monkeys. All individuals were recognized individually through facial and body features. Observers were all requested to pass an identification test and data were collected only if the identity of the individual was certain. We considered females as adult as soon as they had their first infant and males once they migrated from their natal group. Individuals were considered as juveniles (including sub-adults) from the age of 1 until adulthood and as infants up to 1 year old. All three groups had been regularly followed since 2010, allowing us to have a good estimation of their age although for the analyses we considered only two age categories: adult or juvenile while infants were excluded. The size of the Ankhase (AK) group

excluding infants varied from 26 to 33 individuals (including from 4 to 7 adult males, 6 to 8 adult females and 12 to 19 juveniles), Baie Dankie (BD) group varied from 36 to 48 individuals (4 to 5 adult males, 11 to 14 adult females and 19 to 33 juveniles) and the Noha (NH) group varied from 25 to 41 individuals (2 to 7 adult males, 11 to 12 adult females and 11 to 25 juveniles) (see Table 1 for group composition). Hierarchy was assessed by the creation of matrices based on dyadic aggressive interactions (i.e. winner-loser) occurring either in a natural context or around various food experiments. Rank relationships were assessed through the “de Vries” (1998) methodology. The ‘I&SI’ method of de Vries (1998), in which parts of the hierarchy that are unresolved by the ‘I’ method (Slater 1961, which minimizes the number of inconsistencies) are decided by minimizing the sum of the rank differences between individuals whose ranks are inconsistent, gave us a list of individuals from the most to the less dominant one. The female hierarchy remained stable during the study period, while the male one was highly variable across three months periods.

2.3.2. Data collection

Grooming, 1m and 5m proximity data were collected through the method of scan sampling (Altmann 1974) during two full days per week per group. Every 30 minutes and during a window of 10 minutes, observers walked within the group to collect the behavior of a maximum number of individuals (except infants). For each scanned individual the identity of all the individuals present within 1m and 5m of it was also recorded. As data were collected by multiple observers, an inter-observer reliability test was performed for each observer and for each category of data to reduce any bias. The threshold of reliability was set to a minimum of 80%. In total we analyzed three months periods over two years which equals a total of 8 different periods. In the AK group we collected 31’661 scans, in BD 28’548 and in NH 28’448. Data were collected on handheld computers (Palm Zire 22 or TX, PDA 32 and Pocket pc HP Travel Companion iPAQ rx5935) equipped with the Pendragon 5.1 software.

2.3.3. SIENA model and statistical analyses

SIENA Model (Simulation Investigation for Empirical Network Analysis) (Snijders et al. 2010) is a loglinear dynamic model based on Markov processes that allows longitudinal network analysis. It uses an iterative stochastic simulation algorithm in three phases (calculating, updating and re-calculating) as a Diffusion model updating statistical values after each iteration, making it a powerful method to find significant effects (effects that are greater than expected based on random models) and decreasing probabilities to find false positives (an effect that does really not exist) or false negatives (absence of effect that should be present).

Concerning actors, the model is based on the purposive action. Actors are considered as aware of the state of the network as a whole. They make choices and they can opt for creating, maintaining or deleting an association in order to optimize their position within the group. These choices are done independently but can be constrained by endogen effects (i.e. relational structuring processes that depend on relational choices made by all the actors but independent from individual characteristics), hexogen effects (i.e. individual attributes such as sex or age) and some random effects.

As for the network, SIENA proposes a statistical model for longitudinal data analysis that requires at least two observations of the state of a network at two consecutive moments. The model supposes that some observations are missing between the two moments and that changes occur on a linear time basis through small steps between the two states observed. Thus, the model is based on Markov chains with linear time in which the future state of the network is linked to the previous state.

Siena only runs on binary matrices (existence or absence of links). In order to turn our valued matrices into binary matrices we used the protocol established by Fedurek (2013) to create a mutual preferred social patterns index based on multiple social indices (i.e. grooming and proximity). The first step of this protocol consists of establishing a threshold for each one of the 8 matrices for the three behaviors (grooming, 1m proximity and 5m proximity). The threshold is based on one-third standard deviation larger than the average for each behavioral matrix. The second and final step consists in considering the dyads as mutual preferred social partners if they were mutual associates for at least two of the three different behavioral matrices at a given time point (Fedurek et al. 2013; Levé et al. 2016). We repeated this protocol for each of the three groups.

The dependent variable here is the change in network relations with an analysis of factors influencing network changes over time. This network modelling aims to explain the network from the links and the actors it is composed of and also to explain the emergence, the pattern and the evolution of relations within the network. To determine whether effects are significant or not, RSiena applies a stochastic simulation algorithm. The procedure consists of simulating many networks to observe if the value of the effects in these simulated networks is different or not from the observed network. Simulation allows us to obtain two parameters, the estimate and the standard error. To obtain the significance of the effect we performed a Wald-type test (based on the parameter estimate and the covariance matrix). Under the null hypothesis that parameter is zero with approximately a standard normal distribution. See Ripley et al. (2011) for more information about this procedure.

The network evaluation function (analysis of the probability of changes in the links according to some patterns called factors in RSiena) for an actor I is defined by:

$$f_i^{net}(x) = \sum_k \beta_k^{net} s_{ik}^{net}(x) \quad (eq.1)$$

Where β_k^{net} are the parameters and s_{ik}^{net} are the effects chosen by the user (in this research the “TransTrip”, “InPop”, and “SimX” effects are described above respectively in *eq.2, eq.3, eq.4*).

The analytical protocol consisted in adding the effects one by one, and testing the significance of the effect after each addition. The effect was retained when significant, otherwise it was simply removed from the model.

The first effect tested in the model was one potential structural effects: the “TransTrip”, which give information about phenomenon of triadic closure process (TC): TransTrip (i.e. TC) effect analyses individuals’ transitivity (*i.e.*). It is calculated by the number of transitive triplets among relations of i (i is linked to j and h , and these are linked to each other). It describes the « friends of my friends are my friends » phenomenon. The TransTrip effect formula is as follows :

$$s_{ik}^{net}(x) = \sum_{j,h} x_{ij}x_{ih}x_{jh} \quad (eq.2)$$

For this effect the contribution of the relation $i \rightarrow j$ is proportional to the total number of transitive triplets formed, which can be ($i \rightarrow j \rightarrow h$; $i \rightarrow h \rightarrow j$; $i \rightarrow j$).

The second effect tested in the model was another potential structural effects: “InPop”, which give information about growth-preferential association (PA). The inPop (i.e. PA) effect analyses individuals’ « popularity » (*i.e.* defined by summing relations received by actors j (*degree*) whom i is linked to). In our case as the networks are undirected we can consider this effect as degree popularity. It is calculated by the sum of in-degrees of the individual whom i is linked to. Popularity effect discloses individuals’ preference to be linked to popular actors (*i.e.* individuals with highest degrees receive more incoming links). The inPop effect formula is as follows :

$$s_{ik}^{net}(x) = \sum_i x_{ij} \sum_h x_{hj} \quad (eq.3)$$

Then we investigated the influence of covariate factors one by one by analyzing the “SimX” effects according to sex, matriline hierarchical rank and age, which give information about the tendency of individuals to create relations with

individuals with similar attributes. This effect can be seen as an analysis of homophily or heterophily processes. Calculation details of this effect are described above and further information can be found in SIENA manual (Ripley et al. 2011). The covariate-related similarity (SimX) effect is the sum of centered similarity scores sim_{ij}^v between i and the other actors j to whom he is tied according to the covariate v . The SimX effect formula is as follows :

$$s_{ik}^{net}(x) = \sum_j x_{ij}(sim_{ij}^v - \widehat{sm}^v) \quad (eq.4)$$

Where \widehat{sm}^v is the mean of all similarity scores.

For each one of this ‘‘SimX’’ effects we added at the same time the ‘‘Covariate-ego x alter’’ effect in order to control unequal ties between groups. The ‘‘Covariate-ego x alter’’ effect is simply the product of I’s covariate and sum of his alters. To consider the effect as significant, both ‘‘SimX’’ and ‘‘Covariate-ego x alter’’ effects have to be significant.

Finally, we investigated the rate function effect according to sex, matriline, hierarchy and age one by one. The network rate function analyses how fast interactions change according to individual attributes (e.g. females have higher rate changes than males) for an actor i . This function is restricted to positive values as product of exponential elements. It can be defined by:

$$\lambda_i^{net}(\rho, \alpha, x, m) = \lambda_{i1}^{net} \lambda_{i2}^{net} \lambda_{i3}^{net}, \text{ for } x = x(t), t_m \leq t < t_{m+1} \quad (eq.5)$$

With $\lambda_{i1}^{net} = \rho_m^{net}$ representing the dependence of the period, $\lambda_{i2}^{net} = \exp(\sum_h \alpha_h v_{hi})$ representing the effect of actor covariates (v_{hi} as the factor and α_h as the dependence of the degree) and $\lambda_{i3}^{net} = \exp(\alpha_h + x_i)$ representing the contribution of the degree (actor’s personal network). Where ρ is the basic rate parameter, α is the dependence of the degree, m is the period (number of observation minus one), and t is the time point.

Models that included all the effects did not provide accurate goodness of fit analyses. For each group, we therefore realized a global model built up step by step by adding and testing the significance of one effect at a time. Once we obtained the final model for each group, we ran a goodness-of-fit test to assess if our model was significantly different from the observational data. We run a one-tailed Monte Carlo Mahalanobis distance test. After controlling for unequal ties between groups, such methodology led to the disappearance of the ‘‘hierarchy’’ attribute effect within the whole model and the ‘‘age’’ effect when testing the presence of homophilic bonds (Table 2). We therefore present only significant results below but discuss the absence of these effects within our model further below.

2.4. RESULTS

2.4.1. Triadic closure and degree popularity effects

First of all, the goodness of fit analyses indicated that our model selection was reasonably accurate for all three groups, AK (MHD = 156.51; P = 0.054), BD (MHD = 126.65; P = 0.425) and NH (MHD = 77.17; P = 0.434).

2.4.2. Homophily: Covariate-similarity effect

When analyzing the structure of the network, all three groups showed a significant effect of triadic closure (AK: $\chi^2 = 7.794$; DF = 1; $p = 0.029$; BD: $\chi^2 = 21.573$; ; DF = 1; P < 0.001; NH: $\chi^2 = 53.561$; DF = 1; P < 0.001, Table 2), while there was a significant effect of degree popularity in only two groups (AK: $\chi^2 = 3.918$; DF = 1; P = 0.048; BD: $\chi^2 = 4.228$; DF = 1; P = 0.039; Table 2).

2.4.3. Network rate analyses: How quickly are relationships modified?

With respect to the structure, when analyzing the likelihood of homophilic bonds according to the different attributes, we could not find any general pattern across all three groups. Only the AK ($\chi^2 = 8.615$; DF = 1; P = 0.003) and the NH ($\chi^2 = 21.719$; DF = 1; P < 0.001) group members showed a significant preference of association to individuals of the same sex while preference of association with the same matriline was present only in the BD ($\chi^2 = 41.833$; DF = 1; P < 0.001) and NH: $\chi^2 = 71.463$; DF = 1; P < 0.001; Table 2) groups.

Finally, when looking at the network dynamics with relationships variation over time, results indicated a strong intergroup variation. In the AK groups, we found that females experience a greater and quicker relationships' variation than males do ($\chi^2 = 9.048$; DF = 1; P = 0.003) while for the BD group there was a significant effect of sex and matriline, suggesting that males' relationships are more prone to variation than females' ($\chi^2 = 17.889$; DF = 1; P < 0.001) and that high-ranking matriline also experience a greater variation in their relationships stability ($\chi^2 = 12.276$; DF = 1; P < 0.001). Only in the NH group, we found that juveniles' relationships were more prone to variation than adults' ($\chi^2 = 11.334$; DF = 1; P < 0.001; Table 2).

2.5. DISCUSSION

In this study we tried to understand the dynamics of a social network through detailed analysis of the creation and destruction of relationships over time according to the following individual attributes: sex, matriline, hierarchy and age. Main results indicate that individuals associate themselves with friends of their friends but many differences exist between the three groups. To our knowledge, this is the first study that uses a stochastic actor-oriented model to analyze such

dynamics on multiple and non-experimental groups. Indeed, another study (Ilany et al. 2015) already used such model, but focused on only one group of hyenas and the effects of ecological variables. RSiena package was also used to understand social information transmission in experimental groups of drosophila (Pasquaretta et al. 2016). Our results show the importance of observing multiple groups when we want to assess the effect of different social variables on the temporal evolution of a network structure.

2.5.1. Limited triadic closure and degree popularity effect

The analyses on triadic closure (which represents the likelihood of two individuals to be associated if they have a mutual third party associate) indicated that such effect was present in all three groups. According to some hypotheses, triadic closure might facilitate the evolution of cooperation (Banks and Carley 1996; Davidsen et al. 2002; Righi and Tacaks 2014). For example, someone might be more likely to become friend with and potentially help a friend of a friend. This suggests that vervet monkeys' social system met the conditions for the emergence of triadic closure (Lusseau et al. 2006). In animals, only one study focused on how the triadic associations influence a social network structure (Ilany et al. 2013). However, what remains unknown with such theory is if triadic closure is the evolutionary consequence or the prerequisite of cooperation. More studies are needed to understand whether triadic closure is a by-product of social network or relatedness or is a social strategy conducting to better cooperation between multiple partners. The degree popularity results, which represent the preferred association to highly central individuals, indicate that individuals try to bond with individuals that are central within a network, but this effect was found only in two groups. This pattern results in more centralized networks having great impact on information and disease transmission and several researches are done to understand whether and how natural selection might impact these social network properties (Pasquaretta et al. 2014; Duboscq et al. 2016; Romano et al. 2016). As multiple previous studies found a positive correlation between rank and/or matriline and centrality (Schino 2001; Kanngiesser et al. 2011; Sueur et al. 2011; Borgeaud et al. in prep), our results partially support the generality of Seyfarth's model (1977). This model also suggests that grooming can be exchanged against tolerance among food resources or coalitionary support, which seems to exist in vervet monkeys (Borgeaud and Bshary 2015). Central individuals are either high-ranking individuals, either close relatives or experienced individuals. In this way we can easily understand how preferred association to central individuals might be selected as a social strategy increasing fitness but still, we can observe that this effect is dependent on group composition. However, it should be noted that some

studies fail to provide evidence for degree popularity, including in vervet monkeys (Henzi et al. 2013), as we do for one of the study groups.

2.5.2. Homophily within relationships

We also tested if individuals associated preferably with individuals of similar attributes. After controlling for the differences in sex ratio (Female ratio: AK: 44%; BD: 56%; NH: 50%), our results surprisingly indicate that females form stronger bonds between themselves rather than with males only in the AK and NH groups. These results confirm that individuals of the philopatric sex which normally remain in their natal group throughout their lives form strong and long-lasting bonds with each other (Cheney and Seyfarth 1990; Silk et al. 2010). However, it remains challenging to explain the absence of significant results in the BD group. One explanation could rely on the presence of multiple adult males who, in contrary to the other groups were already present within the group at the beginning of the project in 2010 and remained within the group for a large part of the study. In this situation and at least on the time period of our study, females might have developed strong and long lasting relationships with these males. Similarly, our results suggest that members from the same matriline form stronger bonds than members of different matriline, but only in the BD and NH groups. The positive results fit predictions by kin selection (Hamilton, 1964), while it remains unclear why such an effect should be absent in the AK group. In contrary to these two groups, the AK group is generally more tolerant and females of distant ranks regularly groom each other (Borgeaud and Bshary 2015), which could reflect the results of this study. Tolerance between non kin was shown to be an advantage to decrease risk injuries, energy costs to maintain social relationships or increase food research efficiency (Sueur et al. 2011; Fushing et al. 2013; Pasquaretta et al. 2014). Preliminary results on genetics indicate that the average relatedness from the AK group members is 0.25 while both BD and NH are related at the level of 0.15 (Schneider et al. unpublished data). These results support previous results indicating that kin form stronger bonds than non kin individuals (Silk et al. 2010). We did not find any effect of hierarchy on bonds' strength. This suggests that individuals of close ranks either do not have stronger bonds than individuals of distant ranks or they have stronger bonds but this effect is undone by the more important effects of sex and matriline. As our analyses include both males and females, another explanation could be that high-ranking males may bond as much with high-ranking than with low-ranking females, cancelling a potential rank effect. . Finally, our lack of results about association between individuals of similar age is rather surprising as this difference cannot really be explained by a difference in age ratio (Adult age ratio: AK: 43%; BD: 31%; NH: 42%). Previous studies suggested the importance of bonds with individuals of similar age. For example

juveniles' play-fights allow the development of the social techniques necessary to acquire a central position in a society (Shimada and Sueur 2014). On the other hand it might simply reflect that, despite the age difference, bonds between a mother and her offspring are the strongest of all associations which has also been found in baboons (Silk et al. 2010). Another explanation could rely on the fact that our juvenile age category included one to four years olds and it is likely that they form stronger bonds within rather than across generations.

2.5.3. Among-group differences in relationships stability

Finally, when testing how quickly relationships are modified according to the individual attributes, we found no patterns that were consistent among our three groups. In both AK and BD groups, females' relationships are more prone to variation than the males' and in BD the relationships of individuals belonging to high-ranking matriline were also less stable. This supports the Seyfarth's model (1977) which implies a potential instability of higher ranking individuals' relationships due to social competition. The BD group was the only one where the high-ranking matriline had a significant influence on how quickly relationships were modified. Similarly, previous studies found differences between populations in their relationships management (Silk et al. 1999; Henzi et al. 2013). Finally, in the NH group, our results suggest that adults' relationships are more stable than those of juveniles. These results support previous studies in baboons (Silk et al. 2006 a, b, 2010, 2012) which indicate stable relationships within adult females. Female juveniles in vervet monkeys form strong and rather stable relationships with adult females while male juveniles' relationships are more prone to variation (Fairbanks 2002; juvenile vervet monkeys). However, the fact that such results are significant only in one group is rather puzzling but could be due to group differences in relationships management and group composition (Cronin et al. 2014a, b).

2.5.4. Methodological considerations

We based our evaluation of effect size entirely on the distinction 'significant effect' versus 'non-significant effect' and the size of the estimate. In the future, it would be interesting to test multiple groups simultaneously following the "multilevel" SAOM method that has been recently developed (Snijders et al. 2013). To our knowledge this is the first time that a study focuses on the social network dynamics of three different groups of monkeys. Interestingly, our results indicate substantial intergroup variation. This variation might be due to 1) real intergroup difference, 2) problem in methodology, 3) non powerful statistical analyses. However, we made considerable efforts to apply the same scoring methods on the three groups. Despite this effort, various p values were either non-

significant or so very small (< 0.001) and seems to indicate that groups differed indeed with respect to various variables. However, we currently cannot test how far intergroup variation could be due to differences in genetic relatedness. On the other hand, a purely ecological explanation seems unlikely as all three groups live in overlapping home ranges. In part, the differences could also be due to different individual strategies and/or personalities, which could have various impacts on the network variation depending of their position within this network (Cronin et al. 2014a, b). Such a cause of variation would indeed be interesting. In any case, our results suggest that studies on multiple groups are necessary to build up any hypothesis concerning network features and dynamics within a species.

2.6. CONCLUSION

Most primates live in closely related and bonded social groups in which individuals have to deal with many social challenges and opportunities (Humphrey 1976; Harcourt 1988). Famously, Humphrey (1976) proposed that large brains evolved in primates primarily to cope with the social environment as it is less predictable than the physical environment. This idea has been developed further in the Machiavellian intelligence and social brain hypotheses (Byrne & Whiten 1988; Whiten and Byrne 1997; Dunbar 1992). Therefore, the complexity of a species' social network may be a good indicator for the cognitive demands that individuals face and be reflected in the complexity of the species' brain. To be able to test this hypothesis, we first need to establish methods on how to measure different aspects of network complexity (Lehmann and Dunbar 2009). The methods we used rely on quantifying the dynamics of relationships patterns according to individual attributes while considering changes in group composition. These analyses could be applied to a variety of species. Ultimately such measures should allow a comparison between species to assess how network dynamics is correlated with brain complexity. In this context, the observed variation among group network structures may turn out to be an indicator of great social flexibility that demands a social brain.

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FIGURES AND TABLE

Table 1. Group Composition.

	Group		
	AK	BD	NH
Adult males	4-7	4-5	2-7
Adult females	6-8	11-14	11-12
Juveniles and subadults	12-19	19-33	11-25
Total	26-33	36-48	25-41

Table 2. Results summary. Results from the RSiena analyses for the three groups.

	AK					BD					NH							
	Estimate	Std error	t ratio	X2	DF	P value	Estimate	Std error	t ratio	X2	DF	P value	Estimate	Std error	t ratio	X2	DF	P value
Transitive triplets	0.08	0.04	0.11	4.794	1	0.029	0.24	0.05	0.08	21.573	1	<0.001	0.27	0.04	-0.02	53.561	1	<0.001
Degree popularity	-1.02	0.18	0.12	3.918	1	0.048	0.06	0.03	0.09	4.228	1	0.039				0.131	1	0.718
Same sex	-0.5	0.17	0.1	8.615	1	0.003				0.003	1	0.986	-1.84	0.4	-0.01	21.719	1	<0.001
<i>Ego sex effect</i>	1.06	0.28	0.01	14.514	1	<0.001				0.002	1	0.963	3.83	0.76	0.03	25.452	1	<0.001
Same matriline				28.608	1	<0.001	0.83	0.13	0.01	41.833	1	<0.001	0.98	0.12	0.03	71.463	1	0.004
<i>Ego matriline effect</i>				1.235	1	0.266	0.01	<0.001	0.05	7.045	1	0.008	0.02	0.01	<0.001	8.309	1	0.004
Same hierarchy				2.715	1	0.099				5.486	1	0.019				19.866	1	<0.001
<i>Ego hierarchy effect</i>				0.156	1	0.692				0.017	1	0.898				0.423	1	0.515
Same age				0.029	1	0.864				0.322	1	0.57				4.531	1	0.033
<i>Ego age effect</i>				0.003	1	0.957				0.206	1	0.65				1.762	1	0.184
Rate effect on sex on rate	0.66	0.22	-0.14	9.048	1	0.003	0.98	0.23	0.03	17.889	1	<0.001				0.406	1	0.524
Rate effect on matriline on rate				2.774	1	0.096	-0.1	0.03	0.08	12.276	1	<0.001				1.147	1	0.284
Rate effect on hierarchy on rate				0.716	1	0.397				0.53	1	0.466				0.741	1	0.389
Rate effect on age on rate				1.236	1	0.266				1.001	1	0.317	0.64	0.19	0.03	11.334	1	<0.001

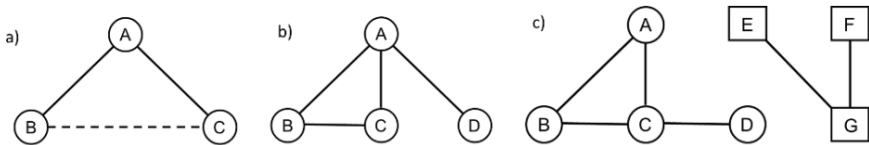


Figure 1. Representations of a) Triadic closure: If A and B are connected, the probability of B and C being connected is increased; b) Degree popularity: A being more connected has a higher degree popularity than B, C and D; c) Homophily: A, B, C and D are more connected to each other as they have the same attribute characteristics (i.e. rank, gender, age) than they are connected to E, F and G.

THIRD-PARTY RANKS KNOWLEDGE IN WILD VERVET MONKEYS (*CHLOROCEBUS AETHIOPS*)

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3.1. ABSTRACT

The Machiavellian/Social Intelligence Hypothesis proposes that a complex social environment selected for advanced cognitive abilities in vertebrates. In primates it has been proposed that sophisticated social strategies like obtaining suitable coalition partners are an important component of social intelligence. Knowing the rank relationships between group members is a basic requirement for the efficient use of coalitions and the anticipation of counter-coalitions. Experimental evidence for such knowledge currently exists in only few species. Here, we conducted rank reversal playback experiments on adult females belonging to three different groups of free-ranging vervet monkeys (*Chlorocebus aethiops pygerythrus*) to test their knowledge of the female hierarchy. Playbacks simulating rank reversals (subordinate aggressing a dominant) induced longer looking times than playbacks simulating a dominant aggressing a subordinate. Vervet monkey females therefore seem to compute the rank relationships between other females. Our results suggest that detailed social knowledge about rank relationships may be widespread in primates and potentially also in other species living in stable groups.

3.2. INTRODUCTION

There is enormous variation in both absolute and relative vertebrate brain size (Jerison 1973). The complexity of a species' social life has been identified as one important factor promoting the evolution of large brains (Cheney and Seyfarth 1990; Dunbar 1992), though exactly which aspects of social life require larger brains remains largely unknown. The most general hypotheses are the social brain

hypothesis (Dunbar 1992; Barton and Dunbar 1997) and the Machiavellian intelligence hypothesis (de Waal 1982; Byrne and Whiten 1988; Whiten and Byrne 1997), which in their generalist form include all possible aspects of social life. An important basic requirement for sophisticated social strategies is the knowledge not only of one's own relationships with all other group members but also of the relationships between other group members. In general, individuals of many species obtain such information through 'eavesdropping' on social interactions in a communication network (McGregor 1993). Evidence for this capacity has been provided in a variety of vertebrate taxa (McGregor 2005). However, subjects typically needed to remember few interactions of few individuals (Davis 1992; Bshary 2002; Paz-y-Miño et al. 2004; Grosenick et al. 2007). The existing evidence thus ignores the possibility that variation in brain size could at least in part reflect quantitative differences in knowledge/memory (Bshary et al. 2011). The knowledge that group living animals have about third-party relationships has been studied mainly in primates (Cheney and Seyfarth 1990; Cheney et al. 1995; Silk 1999; Bergman et al. 2003; Schino et al. 2006; Slocombe and Zuberbuehler 2007). Early experiments strongly suggest that primates recognise mother-offspring relationships (Bachman and Kummer 1980; Cheney and Seyfarth 1980). Furthermore, there is experimental evidence for more detailed social knowledge in baboons and in chimpanzees. Using playbacks simulating rank reversals Bergman et al. (2003) demonstrated that female baboons know the entire female hierarchy in their group. In chimpanzees, individuals exaggerate their screams when aggressed in the presence of a third-party that is dominant over their aggressor (Slocombe and Zuberbuehler 2007), suggesting both detailed knowledge about the group's hierarchy and strategic use of the information. Outside primates, evidence that individuals know the entire hierarchy within their group has been provided on pinyon jays (Paz-y-Miño et al. 2004). Thus, while current explicitly experimental evidence in primates is restricted to two particularly large brained species (Dunbar 1998; Deaner et al. 2007), observational evidence suggests that detailed knowledge about the relationships between other group members may well be widespread in primates (Silk 1999; Schino et al. 2006) and more generally in species living in large stable groups (Engh et al. 2005). Nevertheless, more explicit experimental studies seem warranted. Here, we studied vervet monkeys, which belong to the guenons (Xing et al. 2007), the most diverse old world monkeys' clade. Previous research indicates that vervets monkeys are not only able to group mother-offspring pairs and group membership of neighbours (Cheney and Seyfarth 1980; Cheney and Seyfarth 1990) but also that they may already use quite sophisticated social strategies, like forming coalitions that are affected by recent grooming interactions (Cheney and Seyfarth 1990), and adjusting the amount of grooming given to others in response to favours received (Fruteau et al. 2009). The social

structure of vervet monkeys closely resembles that of savannah baboons, with female philopatry and matrilineal ranks (Cheney and Seyfarth 1990). We therefore used an experimental design similar to the approach developed for baboons (Cheney et al. 1995; Bergman et al. 2003) to test whether vervet females know the rank relationships between other females. Previous studies found that subjects looked at speakers longer in response to incongruent playbacks mimicking conflicts out-of-line with the hierarchy than those that were congruent with the existing hierarchy (Cheney et al. 1995; Bergman et al. 2003). We predicted that if vervet monkey females know all rank relationships between other females they should also look longer at speakers if ranks are reversed.

3.3. MATERIAL AND METHODS

3.3.1. Study site and population

The study was conducted from October 2011 until April 2012 at the Inkawu Vervet Project, Mawana game reserve (S 28° 00.327; E 031° 12.348), Kwazulu Natal, South Africa. Subjects were adult females from three habituated groups of vervet monkeys. Ignoring infants, the Baie Dankie group included 37 individuals (4 males, 10 females and 23 subadults and juveniles), Noha 24 individuals (2 males, 10 females and 12 subadults and juveniles) and Ankhase 25 (3 males, 6 females and 16 subadults and juveniles).

3.3.2. Experimental design

Playback experiments mimicked the methodology of a previous study on baboons (Bergman et al. 2003) where a sequence of calls was played that simulated a conflict between two females. Sequences consisted of two aggression calls from the aggressor followed by one distress call from the victim. In the control sequence a dominant appears to aggress a subordinate while in the experimental sequence a subordinate appears to aggress a dominant. Calls were recorded during foraging experiments with a directional Sennheiser K6/ME 66 microphone and a Marantz PMD 660 recorder. Each call was played only once. The spacing between the two aggression calls (90 ms) as well as between the second aggression call and the distress call (40 ms) was kept constant (Audacity v. 1.3). Average length of the sequences was 2.3 seconds. The duration of distress calls was quite variable but for each subject the length was the same between the control and the experiment. The amplitude from each aggression call (65 dB) and distress call (78 dB) was normalised in Praat (v. 5.2.28) so that it was as similar as possible to a natural occurring conflict. We used calls from all 26 females to test 16 females (six from Noha, eight from Baie Dankie and two from Ankhase). Subjects invariably ranked two positions above or below the two dyads that were used as signallers for the two playback trials. Within the four individuals used for playbacks, the highest ranking

invariably aggressed a partner two ranks lower in the hierarchy, while the lowest ranking aggressed a partner two ranks higher in the hierarchy. For example, the alpha female was tested with female 3 against 5 as control and 6 against 4 on the rank reversal trial, while the 10th female was tested with 5 against 7 as control and 8 against 6 on the rank reversal trial. Each subject heard the two call sequences in trials separated by at least 24 h, with the order of control and experimental playbacks being counterbalanced between subjects. The subject and the two signallers were monitored by two or three observers who were in constant radio contact. Playbacks were only conducted when the two signallers were out of sight of the subject and at least 30 m away. Calls were played out of a Logitech S715i. Speakers were placed behind a bush or in the grass about 15 m away from the subject so that they were hidden from this one. From the subject's perspective the speakers were placed such that the playback came from the general direction in which the donors of the playback calls currently were. Playbacks were started when the subjects were resting or foraging and looking away from the speakers. Subjects were filmed 10 s prior the playbacks until 30 s after the end of the sequence.

3.3.3. Data and statistical analyses

Frame by frame (Virtualdub v. 1.6.19) analysis was used to score the duration the subject looked towards the speakers after the onset of the second signaller's call. Scoring stopped as soon as the individual moved its face away from the speakers' direction. Videos were analysed by the experimenter (CB) and by a naïve person (RB). Assessments matched within 2 frames (8/100 s) in 80% of videos, while 20% yielded quite differing results. It turned out that mismatches were likely if the subject had briefly looked away while the playback was still ongoing. We agreed that this should be dismissed as the complete information had not yet been available to the subject. With this in mind RB (still naïve) reanalysed the ambiguous videos to provide the values used for the statistics.

To compare each subject within both situations, we run a Wilcoxon signed rank test. The analyses were conducted using SPSS (v. 20).

3.3.4. Ethical note

The study was approved by the relevant local authority, Ezemvelo KZN Wildlife and by the University of Cape Town, South Africa. Our setup involved only playbacks of conflict vocalizations and video recordings. Playbacks were used only up to twice a day on different subjects, to avoid increase of stress or conflicts.

3.4. RESULTS

Individuals looked significantly longer towards the speakers during incongruent experimental sequences than during congruent control sequences (Mean time looking congruent = 2.612 (SE = 0.266), incongruent = 4.25 (SE= 0.872), N= 16, Wilcoxon Signed rank test: $Z = -22.068$, $p = 0.039$; figure 1). There was no correlation between the rank of the individual distressing and the time spent looking nor a correlation between the rank of the subject and the time spent looking (Spearman tests: N= 16, both $p < 0.2$).

3.5. DISCUSSION

3.5.1. *Females know the whole female hierarchy*

Our results demonstrate that female vervet monkeys distinguish between playbacks that suggest a female conflict congruent with the hierarchy and playbacks that suggest a rank reversal. Thus we could replicate the main result found in previous studies on baboons (Cheney et al. 1995; Bergman et al. 2003). The data suggest that similar evidence for baboons and chimpanzees can be generalized at least for old world monkeys and apes and potentially to species living in stable groups. Nevertheless, with respect to the quantitative arguments we have put forward in the introduction, we note that vervet monkeys live in smaller groups than either baboons or chimpanzees and hence our subjects needed to process less information than individuals in the latter two species. It would hence be interesting for the future to find an experimental design that explicitly tests whether individuals of different species have a maximal number of thirdparty relationships they can track that correlates with the species typical group size. Such experiments would bring us closer to actual testing of the social brain hypothesis, which proposes that brain size imposes a constraint on maximal group size due to an individual's limitation in the ability to track third-party relationships beyond that (Dunbar 1992; Lehmann et al. 2007).

3.5.2. *Methodological considerations and perspectives*

A potential criticism of the experimental design could be that subjects respond stronger to distress calls from more dominant individuals because they occur less frequently, and that this simple rule, rather than detailed knowledge about the hierarchy, may have caused the significant results. We consider this alternative explanation unlikely to be correct for two reasons. First, we did not find positive correlations between the apparently distressing individual's rank and the duration subjects looked at the speaker. Second, the three subjects that looked longer during control situations were exposed to distress calls from high ranking females during the experimental situation. According to the alternative Third-Party Ranks

Knowledge in Vervet Monkeys hypothesis, these trials should have evoked particularly long attention spans but they did not. Similarly, Cheney et al. (1995) controlled for the novelty of a sequence by showing that adding a third aggressive call from a female dominant to both (that could post hoc explain the previous sequence of calls) indeed yielded low attention by subjects. We also note that the rank of subjects was apparently not important for our results as there was no correlation between the rank of the subject and the time spent looking, and the three subjects that looked longer during the control situations did not occupy extremely high or low ranks. Thus, it appears that female vervet monkeys indeed know the entire female hierarchy of their group. Our study did not fully replicate the experiments by Bergman et al. (2003) on baboons as we did not have a third group of playbacks that involved rank reversals within matriline. We could not replicate these data on the vervet monkeys because in contrast to the study on baboons we did not have detailed information about the pedigree of subjects. Bergman et al. (2003) did not find any significant differences between subjects' responses to 'correct' rank interactions and reversals within matriline. While they interpreted this result as evidence for a nested representation of the hierarchy, Penn et al. (2008) argued that the very same data yield evidence for an absence of such a nested representation. In any case the non-significant result seems difficult to interpret as it could also mean that baboons do not track rank relationships within matriline. Thus, it appears that the third treatment group would not have yielded results that allow conclusions beyond knowledge about third-party rank relationships. As a final methodological remark, we note that due to the lack of information about the pedigree of subjects we cannot exclude that subjects sometimes reacted more strongly because one of the individuals involved in the playbacks was a full or half-sister. Also, the genetic relationships between the two individuals used for playbacks will have been variable. However, such uncontrolled effects should increase the variance in the data and hence favour the null hypothesis that vervet monkeys do not know the relative ranks of group members. Hence our approach was conservative, making the significant result robust. Furthermore an advantage of our study compared to Bergman et al. (2003) is that we kept the difference in rank between individuals used for playbacks constant. In the future, it would be interesting to test the females' knowledge about the males' hierarchy and vice versa, as well as investigating the juveniles' knowledge about third-party relationships. Most importantly, we can now start to expand on earlier research (Cheney and Seyfarth 1990) and study how vervet females use their detailed knowledge on relative ranks for strategic Machiavellian-like behaviour. Having stable coalition partners appears to be important for reproductive success (Silk et al. 2003) but it remains unclear how important social

competence (Oliveira 2009; Taborsky and Oliveira 2012) is in comparison to kinship to achieve a high fitness.

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FIGURE

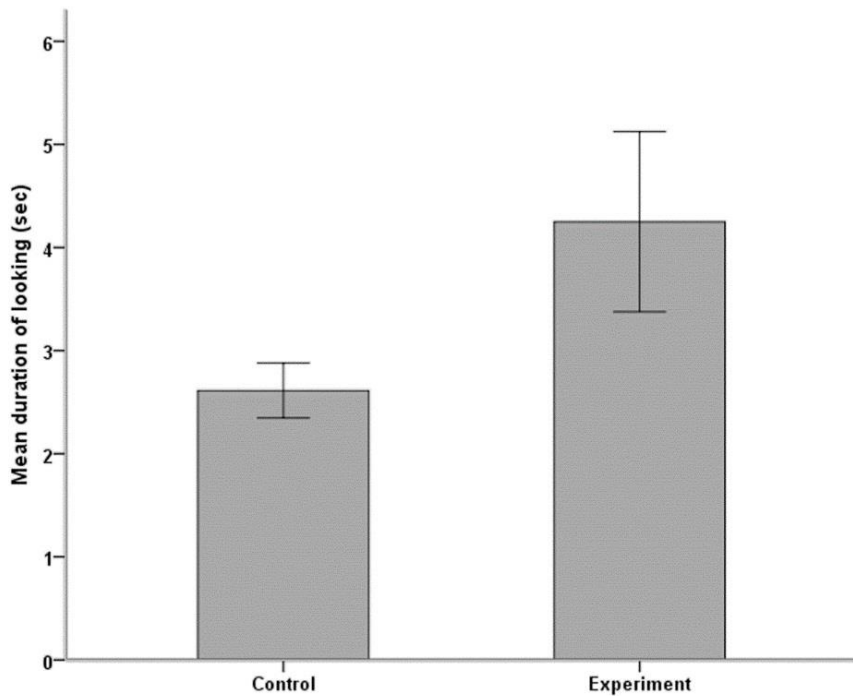


Figure 1. Duration of first look. Time in seconds that individuals looked towards the speakers during control (dominant aggresses subordinate) and experimental (subordinate aggresses dominant) playbacks. Histograms represent the mean duration of time spent looking while bars represent standard error.

**AGE/SEX DIFFERENCES IN THIRD-PARTY RANK
RELATIONSHIP KNOWLEDGE IN WILD VERVET
MONKEYS, *CHLOROCEBUS AETHIOPS***

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4.1. ABSTRACT

In mammals it has been proposed that complex social environments have selected for sophisticated social strategies. Third-party and more specifically third-party rank relationship knowledge is an important requirement for such strategies, especially in species with a strict hierarchy such as primates. Previous research has demonstrated that female vervet monkeys know the entire female hierarchy within their group, suggesting a detailed knowledge of their surrounding social world. What remains unclear, however, is the extent and detail of such social knowledge in other age/sex classes. We used the same experimental design to test whether females and males also keep track of each other's hierarchy and whether juveniles know about the female hierarchy. Our results suggest that females know about the male hierarchy but that males and juveniles seem to lack such knowledge regarding the female hierarchy. This indicates sex and developmental differences in the extent of social knowledge and especially third-party rank relationship knowledge in vervet monkeys. As a consequence, sophisticated social strategies may most likely be found in adult females in this species.

4.2. INTRODUCTION

Research on primates and other social species has focused on the extent to which an individual's need to cope with the complexity of decision making in a dynamic social world selects for increased cognitive abilities (Jolly, 1966; Humphrey, 1976). Compelling evidence for social complexity driving cognitive competence is based on comparative analyses that link brain size/structure with potential correlates of social complexity (Barton and Dunbar, 1997; Dunbar and Shultz, 2007). Such complexity has been mostly described under various theories, including the social or Machiavellian intelligence hypothesis (Byrne and Whiten, 1988; Whiten and Byrne, 1997). Numerous potential facets to social intelligence have been proposed and investigated empirically including improved social knowledge, discovery techniques, social problem solving, innovation, social expertise and mind reading, as well as social learning and traditions/culture (Byrne and Whiten, 1988; Whiten and van Schaik, 2007).

The strategic component of social intelligence concerns an individual's ability to form coalitions against third parties and to manipulate others, as well as the capacity to engage in tactical deception (Whiten and Byrne, 1997). For efficient strategic social behaviour, it is useful for an individual not only to possess knowledge of its own relationships with all other group members but also to have an understanding of the relationships that exist among other group members. Such third-party relationship knowledge yields various benefits. For example, it allows individuals to avoid soliciting support from a kin of their opponent and to pick partners that are sufficiently competitive to render the coalition successful. In chimpanzees, *Pan troglodytes*, and bonnet macaques, *Macaca radiata*, third-party rank relationship knowledge is also used to recruit help during conflicts through integrating the rank relationships between competitors and surrounding audience members into the recruitment decision-making process (Silk, 1999; Slocombe et al., 2010). Similarly, in an interspecific context, cleaner fish, *Labroides dimidiatus*, are likely to approach predatory client reef fish when chased by a nonpredatory client after having taken a bite of mucus, using the predator as a social tool to stop further chasing (Bshary et al., 2002).

While collecting knowledge about other individuals' social behaviour through eavesdropping is widespread throughout various vertebrate taxa (McGregor, 2005), evidence for third-party rank relationship knowledge is scarcer (primates: Dasser, 1988; Cheney and Seyfarth, 1990; Silk, 1999; Bergman et al., 2003; Slocombe and Zuberbühler, 2007; Borgeaud et al., 2013; pinyon jays, *Gymnorhinus cyanocephalus*: Paz-y-Mino et al., 2004; hyaenas, *Crocuta crocuta*: Engh et al., 2005; fishes, e.g. *Astatotilapia burtoni*: Grosenick et al., 2007). Furthermore, primates have been shown to recognize the kin relationships of others (Cheney and

Seyfarth, 1990; Tomasello and Call, 1997; Seyfarth and Cheney, 2000; Bergman et al., 2003; Schino et al., 2006) as well as each other's associative patterns or 'friendships' (Bachmann and Kummer, 1980; Cheney and Seyfarth, 1990; Tomasello and Call, 1997; Wittig and Boesch, 2010). However, studies providing evidence for third-party rank relationship knowledge in primates typically tested either female knowledge of female relationships (vervet monkeys: Borgeaud et al., 2013; baboons: Cheney et al., 1995; Bergman et al., 2003; hyaenas: Engh et al., 2005) or male knowledge of male relationships (bonnet macaques: Silk, 1999; chacma baboons, *Papio cynocephalus ursinus*: Kitchen et al., 2005; chimpanzees: Gilby et al., 2013). We are not aware of any study that has focused on third-party rank relationship knowledge between the sexes. Furthermore, exactly how such knowledge is acquired, ontogenetically, has not been investigated by using juveniles as subjects. There is evidence that primate juveniles learn early on who is above or below their mother's rank (Cheney and Seyfarth, 1990; Schino et al., 2007) but not about third-party rank relationships.

Here, we investigated these gaps in understanding of third-party relationships using wild vervet monkeys. In vervet monkeys, females are the philopatric sex and in principle remain in their natal group while males migrate several times throughout their lives (Cheney and Seyfarth, 1990; van de Waal et al., 2013). As a consequence the female hierarchy is very stable while the male hierarchy and group composition are highly variable. In this case, keeping track of the various relationships and rank relationships within a group should be complex and cognitively demanding. Vervets are a highly suitable species because it has already been shown that adults recognize kin relationships (Tomasello and Call, 1997; Seyfarth and Cheney, 2000; Bergman et al., 2003; Schino et al., 2006), and as they recognize each other's voices (Cheney & Seyfarth, 1990; Seyfarth and Cheney, 2010) they are well suited to playback studies to test for knowledge on third-party rank relationships. Rank reversal playbacks originally developed for baboons (Cheney et al., 1995; Bergman et al., 2003) have been successfully used to show that vervet monkey females know third-party rank relationships between other females within their group (Borgeaud et al., 2013, Chapter I): subjects looked significantly longer towards the speakers in response to an incongruent sequence, mimicking a conflict out of line with the current hierarchy, than to a congruent one. Here we used the same methodology to test whether females and males know each other's hierarchy. We predicted that female vervet monkeys should know the male hierarchy as there are fewer males within a group (Cheney and Seyfarth, 1990). Furthermore, it has been shown that females prefer mating with high-ranking males (Keddy, 1986; Andelman, 1987), and hence they would benefit from knowing the exact male hierarchy. As females are usually more numerous within a group and as

a male remains in a group for an average of 2 years (Cheney and Seyfarth, 1990), we predicted that male knowledge about female relationships may be a function of group membership duration. Furthermore, we tested whether juveniles already know the female hierarchy within their own group suggesting an early acquisition and monitoring of third-party social information. To rule out any bias from the novelty of a call sequence, we tested whether subjects paid more attention to a sequence in which a high-ranking individual was the victim (distress call). As high-ranking individuals are less often the victims of a conflict, an apparent distress call from them might elicit a stronger response from the subjects.

4.3. MATERIAL AND METHODS

4.3.1. Study site and population

The study was conducted from January 2013 to January 2014 at the Inkawu Vervet Project, Mawana Game Reserve, Kwazulu Natal, South Africa. Subjects were six adult females, 11 adult males and 18 juveniles from three habituated groups of vervet monkeys. In total, the first group, Ankhase, included 36 individuals (four adult males, nine adult females, 14 subadults and juveniles, and nine infants). The second group, Baie Dankie, included 49 individuals (four adult males, 11 adult females, 23 subadults and juveniles, and 11 infants) and the third, Noha, included 42 individuals (four adult males, 11 adult females, 20 subadults and juveniles, and seven infants).

4.3.2. Experimental design

Playback experiments were designed similarly to previous studies on baboons and vervet monkeys (Bergman et al., 2003; Borgeaud et al., 2013) in which a sequence of calls simulating a conflict between two individuals was played. Calls were recorded during naturally occurring conflicts and during unrelated foraging experiments with a directional Sennheiser K6/ME 66 microphone and a Marantz PMD 660 recorder. In a control, congruent, playback, the sequence mimicked a dominant individual threatening a subordinate individual, while in the experimental, incongruent playback, a subordinate appeared to threaten a dominant individual. Each subject heard one congruent and one incongruent sequence from the same pair of signallers. Each call was played only once. Each subject heard the two playback sequences in trials separated by at least 24 h, with the congruent and incongruent sequences being counterbalanced between subjects. Two playbacks could be run during the same day, separated by at least 1 h, but in this case the subject and both signallers of the first sequence were not involved in the second sequence. Furthermore, a maximum of one incongruent sequence was played per day to minimize potential habituation effects.

Playback experiments were conducted using an Apple iPod, an Anchor AN-mini speaker and a JVC Everio GZ-MG150 video camera. Subjects had to be at least 30 m from the signallers whose calls were used during the playback sequences, and about 15 m away from the speaker. To standardize the intensity of the different calls, aggression calls and grunts were set at 65 dB and distress calls were set at 78 dB using Praat (free software: www.fon.hum.uva.nl/praat, version 5.3.14). Subjects and signallers were followed by two or three observers, who were in constant radio contact. When the subject was in a favourable position for video recordings, the speaker was placed between the subject and the signallers such that the playbacks came from the current general direction of the signallers. A speaker was hidden behind trees or bushes so that it was out of sight of the subject. To investigate the subject's response, video recordings were initiated approximately 10 s before the onset of the playback sequence and stopped 30 s after the onset. The playback sequence was started by the experimenter when the subject looked away from the speaker.

4.3.3. Playbacks simulating conflicts between two males

Males' call sequences played to female subjects consisted of two aggression calls followed by four or five grunts and one distress call, which mimics how these calls are produced in naturally occurring conflicts. The average length of the sequences was 3.6 s. The average length of the aggression calls throughout the sequences was constant. The average length of the grunts and distress calls was variable but kept constant for each subject. In total, calls from five males were used to test six females from the Baie Dankie group. The two males involved in a playback sequence invariably differed by one rank within the hierarchy. Playbacks were run only during a period of stable hierarchy outside the mating season, where no fights between males had been observed during at least the last 2 months. Uncertainties about the exact male hierarchies in the other two groups prevented a larger sample size for females.

4.3.4. Playbacks simulating conflicts between two females

Females' call sequences played to male and juvenile subjects consisted of two aggression calls from the aggressor followed by one distress call from the victim. Such sequences are similar to naturally occurring conflicts. The spacing between the two aggression calls (0.9 s) of the aggressor and between the second aggression call and the victim's call (0.4 s) was kept constant throughout the sequences. The average length of the aggression call was constant throughout the sequences. The distress call's length was slightly variable but was kept constant between the congruent and incongruent sequences for each subject. The average length of the sequences was 2.15 s. The two females whose calls were used in a single playback

sequence invariably differed by two ranks in the adult dominance hierarchy. For adult male subjects (> 5 years, known to have migrated to their present group) the combination of females was chosen opportunistically, i.e. as a function of which of the possible combinations was absent. In contrast, for juvenile subjects we excluded their own mother and kept at least two ranks' difference (either higher or lower within the hierarchy) between the two signallers and the subjects to minimize the probability that the playbacks involved close relatives. In total, 16 females were used to test 11 male subjects. Respectively, this involved five females to test four males in the Ankhase group, five females to test three males in the Baie Dankie group and six females to test four males in the Noha group. Calls from 21 females (seven in Ankhase, eight in Baie Dankie and six in Noha) were used to test a total of 18 juveniles (six per group). In each group one male and one female of each generation (1, 2 and 3 years old) occupying different ranks in the hierarchy were chosen as subjects. As 1-year-old juveniles in the Baie Dankie group were only males, one low-ranking male and one high-ranking male were tested instead.

4.3.5. Data and statistical analyses

Frame by frame analysis, using Virtual Dub (free software: www.virtualdub.org, version 1.9.11), was used to score how long the subject looked towards the speaker. First, the duration of the first look was measured: the time spent looking towards the speaker was measured from the onset of the call of the second signaller, and stopped as soon as the subject looked away from the speaker after the playback sequence was finished (Borgeaud et al., 2013). As a second measure, we scored the total looking time within the first 10 s after the onset of the call of the second signaller (Cheney and Seyfarth, 1980; Cheney et al., 1995; Cheney and Seyfarth, 1999). All subjects looked towards the speakers after both control and experimental sequences.

The videos from adult males and juveniles were analysed by either both K.L. and C.B. or M.A. and C.B. independently. If, after the analyses, assessments of the looking times did not match within two frames (8/100 s), videos were reanalysed by both experimenters. If there was a new mismatch by both experimenters, the videos were analysed again by a naïve experimenter (K.L. or M.A.). The videos from adult females were analysed by C.B. and R.B. as a naïve person and, in this case, all the scores matched within two frames (8/100 s).

Data sets for each age/sex class were used for nonparametric two-tailed matched-pair comparisons with an exact *P* value. As the performance of males and juveniles might be a function of exposure to the female hierarchy, we additionally calculated correlations between performance and group membership duration (for males) or

age (juveniles). All tests were performed in SPSS version 22 (IBM, Armonk, NY, U.S.A.).

4.3.6. Ethical note

The study was approved by the relevant local authority, Ezemvelo KZN Wildlife, and by the University of Cape Town, South Africa. The subjects were habituated to human presence. Our set-up involved only playbacks of conflict vocalizations and video recordings. To avoid unnecessary stress or risk of inducing conflicts between group members, playbacks were restricted to a maximum of twice a day on different subjects. Subjects were typically isolated at the moment of playback in order to avoid disturbing bystanders. Individuals whose calls were used in a given playback were always out of hearing distance. Subjects typically continued with their prior activity (foraging or resting) after looking towards the speaker, suggesting that our manipulation was a minor disturbance.

4.4. RESULTS

4.4.1. Female knowledge about male hierarchy

Female subjects looked longer on their first look towards the speaker after an incongruent playback sequence than after a congruent one but this result only approached significance (mean time looking \pm SE: congruent = 1.946 ± 0.418 s, incongruent = 2.293 ± 0.765 s, $N = 6$; Wilcoxon signed-rank test: $Z = -1.992$, $P = 0.063$; Fig. 1a). When total looking time within the first 10 s after the onset of the second signaller was considered, females looked significantly longer after an incongruent sequence than after a congruent one (mean time looking \pm SE: congruent = 3.873 ± 0.552 s, incongruent = 4.353 ± 0.563 s, $N = 6$; Wilcoxon signed-rank test: $Z = -2.201$, $P = 0.031$; Fig. 1b).

There was no significant correlation between the rank of the distressed male in the playback sequence and the time spent looking by the female subjects for both first look and total look within 10 s (Spearman tests: $N = 6$, both $P > 0.2$).

4.4.2. Male knowledge about female hierarchy

Male subjects did not look significantly longer towards the speaker upon hearing an incongruent sequence than upon hearing a congruent sequence, whether we considered initial looking time (mean time looking \pm SE: congruent = 2.473 ± 0.550 s, incongruent = 3.623 ± 2.075 s, $N = 11$; Wilcoxon signed-rank test: $Z = -0.267$, $P = 0.831$; Fig. 2a) or total looking time within the first 10 s after the onset of the second signaller (mean time looking \pm SE: congruent = 3.429 ± 0.727 s, incongruent = 3.194 ± 0.798 s, $N = 11$; Wilcoxon signed-rank test: $Z = -0.133$, $P = 0.917$; Fig. 2b). Even when we considered only the nine subjects that had already spent more than 6 months in their current group we did not find any tendency for

incongruent playbacks to elicit longer looking times (first look: mean time looking \pm SE: congruent = 2.724 ± 0.646 s, incongruent = 3.898 ± 2.554 s, $N = 9$; Wilcoxon signed-rank test: $Z = -0.533$, $P = 0.652$; total looking time within 10 s: mean time spent looking \pm SE: congruent = 3.831 ± 0.834 s, incongruent = 3.329 ± 0.980 s, $N = 9$; Wilcoxon signed-rank test: $Z = -0.474$, $P = 0.668$). Consequently, there was no significant correlation between males' membership duration (tenure) and their performance (index of time spent looking during the experiment sequence minus control) in either first look or total looking time (Spearman tests: $N = 11$, both $P > 0.3$).

Overall, there was no significant correlation between the rank of the distressed female in the playback sequence and the time spent looking by the male subject for both first look and total look within 10 s (Spearman tests: $N = 11$, both $P > 0.05$).

4.4.3. Juvenile knowledge about female hierarchy

Like males, juvenile subjects did not look significantly longer towards the speaker upon hearing an incongruent sequence than upon hearing a congruent sequence, whether we considered initial looking time (mean time looking \pm SE: congruent = 2.049 ± 0.337 s, incongruent = 1.846 ± 0.484 s, $N = 18$; Wilcoxon signed-rank test: $Z = -0.588$, $P = 0.580$; Fig. 3a) or total time spent looking within 10 s after the onset of the second signaller (mean time looking \pm SE: congruent = 2.867 ± 0.370 s, incongruent = 2.449 ± 0.586 s, $N = 18$; Wilcoxon signed-rank test: $Z = -1.045$, $P = 0.309$; Fig. 3b). Furthermore, juveniles' sex and age did not significantly influence the time spent looking for either first look (Table 1) or within 10 s (Table 2). The analysis of variance of the index of the time spent looking during the experiment minus the control did not show any significant decrease for either first look or total looking time (Levene tests: $N = 18$, both $P > 0.3$; Fig. 4).

Furthermore, there was no significant correlation between the rank of the distressed female in the playback sequence and the time spent looking by the juvenile subjects for either first look or within 10 s (Spearman tests: $N = 18$, both $P > 0.5$).

4.5. DISCUSSION

In this study we investigated the extent to which vervet monkeys know about third-party rank relationships in other age/sex classes. Our results provide evidence that adult females know not only their own hierarchy (Borgeaud et al., 2013) but also that of the males. In contrast, our results suggest that both males and juveniles seem either to lack such knowledge or do not respond because the information regarding the female hierarchy is potentially irrelevant or of little interest to them. The observation that looking time was very similar between age/sex classes during the control situation may support the former explanation. Nevertheless, no final

conclusion can be drawn without further experiments. Sample sizes were generally small but much larger for males and juveniles (for which nonsignificant results were obtained) than for females. In this light the positive results for females indicate that knowledge about male rank relationships is of high value to them. To our knowledge this is the first study to focus on third-party rank knowledge between the sexes and one of the few that focuses on the juveniles' hierarchical knowledge (Range and Noë, 2005; Paxton et al., 2010). Exactly why we find these differences in social knowledge between ages and sexes, and whether there is a functional explanation, is open to interpretation.

4.5.1. Females know about the male hierarchy

As our results suggest, females seem to know the entire male hierarchy. Given that males migrate regularly and that their hierarchy is unstable over time (Cheney and Seyfarth, 1990), we propose such a capacity is probably very cognitively demanding. For females, it has been argued and documented in many species that mate choice is a key component of their fitness (Kappeler and van Schaik, 2002; Dixson, 2009; Kappeler, 2012). For vervet monkeys specifically, research suggests that females prefer mating with high-ranking males (Keddy, 1986) and actively reject copulation attempts (Andelman, 1987). As dominance may signal high-quality genes, increased access to resources or the ability to protect offspring, females should benefit from knowing the exact male hierarchy and subsequently employ this information to select high-quality partners. Weingrill et al. (2010) found that 76% of the juveniles of a vervet group were sired by the dominant male and that the rest of the juveniles were sired in accordance with the males' rank. This shows that dominance rank within males is positively correlated with mating success. As long as this result is due to female mate choice rather than dominant males monopolizing females, females would benefit from knowing the male hierarchy, as documented in the present study.

4.5.2. Males do not seem to know about the female hierarchy

In contrast to females, males' reproductive success is typically limited by the number of females they can access, at least in species with maternal care (review in van Noordwijk, 2012). Hence, it is conceivable that males gain little from knowing the female hierarchy. This might be particularly true for vervet monkeys as two studies failed to find a positive effect of a female's dominance rank on the survival of her infants (Whitten, 1983; Cheney and Seyfarth, 1990). Under such circumstances, a male should mate with as many females as possible and not limit copulation attempts to high-ranking individuals. The situation should be reversed for species in which a clear correlation between a female's rank and reproductive success exists (see review in Ellis, 1995 and van Noordwijk, 2012).

An additional explanation may be related to male group tenure and the relative number of females in vervet groups. Male vervet monkeys migrate from group to group throughout their lives and usually spend an average of 2 years in a group (Cheney and Seyfarth, 1990; Isbell et al., 2002) but even less at the Inkawu Vervet project where the study was conducted (long-term data). Furthermore, females are more numerous than males within a group. It may therefore be that, in comparison to females, males have limited time to acquire the necessary knowledge regarding an extensive female hierarchy. These results may therefore be important in helping us understand how long monkeys need to acquire the detailed social information specific to their group. Additional studies focusing on male social knowledge in subjects that have resided for long periods in groups may help disentangle these two functional explanations. Such findings suggesting an absence of female hierarchy knowledge in males are in line with le Roux and Bergman's (2012) study, which showed that male gelada baboons, *Theropithecus gelada*, did not possess any knowledge of third-party consort relationships within their group. However, it is also conceivable that males are aware of the female hierarchy but do not react to the playbacks because of a lack of interest regarding female rank relationships. Indeed, males rarely intervene in female–female conflicts whereas females often support a male in a male–male conflict (Cheney and Seyfarth, 1990; personal observation).

4.5.3. Juveniles do not seem to know about the female hierarchy

The negative results concerning the juveniles' lack of social hierarchy understanding are striking. Indeed, despite the small sample size, even the 3-year-old juveniles, which are nearing adulthood, did not seem to have any relative understanding of the female hierarchy. These results contrast with those of Paxton et al. (2010), showing that 3-year-old male rhesus macaques, *Macaca mulatta*, could quickly learn to recognize the third-party dominance rank relationships between unfamiliar individuals by the observation of behaviour alone, i.e. by eavesdropping, within only six laboratory training sessions. However, the individuals performed less well in situations in which they had to determine the third-party rank relationships between the same unfamiliar individuals in the absence of these dominance-related behaviours. This suggests that the limited amount of prior experience of these unfamiliar monkeys was not sufficient to reliably identify third-party rank relationships. Vervet monkeys have a low rate of agonistic interactions compared to other species such as rhesus macaques or baboons (Southwick, 1967; Ron et al., 1996; Isbell and Pruettz, 1998), which means that extracting the appropriate information from conflicts might be more complex and time consuming in vervet monkeys than in some other species. By looking at the index of the time spent looking during the experimental sequence minus the

control, we can see that the variance decreased slightly with age. This shows that older juveniles either pay more attention to their social environment or start forming a concept of third-party relationship knowledge. On the other hand, our study groups are regularly subjected to experiments involving clumped food which provides a perfect situation to observe third-party rank relationships as most monkeys eventually approach and compete for the food (van de Waal et al., 2010, 2012, 2013). There are potentially important additional differences between our experimental design and Paxton et al.'s (2010) given that they used visual cues to test for third-party rank relationship knowledge whereas we used only auditory cues. Nevertheless, it is possible that as rhesus macaques live in larger groups than vervet monkeys (Hasan et al., 2013) and have a higher rate of agonistic interactions (Southwick, 1967) they are capable of learning third-party rank relationships faster/earlier. In line with this idea and our present results, it appears that vervet monkeys use redirection during conflicts regularly only when older than 3 years (Cheney and Seyfarth, 1990). Previous behavioural research agrees with this prediction: in vervet monkeys third-party relationship knowledge benefits from redirection of aggression, with regard to both rank and kinship (Cheney and Seyfarth, 1990; Aureli et al., 1993). The authors' conclusion was that juvenile vervets develop third-party rank relationships more slowly and at a later age than the discrimination of simple relationships such as higher/lower in the hierarchy than one's self. Furthermore, Range and Noë (2005) also found that juvenile sooty mangabeys (*Cercocebus atys*) above 2.5 years old know their own status relative to other group members but are not necessarily aware of third-party rank relationships. However, similarly to the males, it is conceivable that juvenile vervets do not pay more attention to incongruent sequences because of a lack of interest. In meerkats, *Suricata suricatta*, for example, it has been shown that despite clear group-specific acoustic differences in close calls, receivers did not discriminate between them, potentially because there has been little selective pressure on receivers to extract group-specific information from the calls (Townsend et al., 2010). Although currently we cannot address this question with our data, future work could potentially begin to disentangle the contrasting explanations for male and juvenile responses.

4.5.4. Methodological considerations

When running our playback experiments we assumed that individuals would recognize each other vocally, which is a capacity present in many primate species (Tomasello and Call, 1997). However, whereas some studies found positive results (Bergman et al., 2003; Crockford et al., 2007; Slocombe and Zuberbühler, 2007; Slocombe et al., 2010), Bergman (2010) found limited vocal recognition in male gelada baboons. Furthermore, except for between-group recognition and mother–

juvenile pairs (Cheney and Seyfarth, 1990), no study has ever focused on males' or juveniles' vocal recognition ability in vervets. Playback experiments used to study the development of grunts and alarm calls of vervets indicate that the production of these vocalizations, as well as the response to the vocalizations of others, arises progressively during the first 4 years (Cheney and Seyfarth, 1990). Thus, it remains a possibility that both male and juvenile vervet monkeys have limited recognition of females by vocalizations alone but would perform better if the experiment was based on visual recognition. Thus, it would be interesting and important to additionally test males' and juveniles' capacity to discriminate group members from their vocalizations alone.

4.6. CONCLUSION

In conclusion, our results provide the first evidence of between-sex third-party rank relationship knowledge in monkeys. The asymmetric performance between females and males might be based on differences in the value of such knowledge or in the capacity for vocal recognition. The negative results for juveniles not knowing the female hierarchy is in line with previous studies that either found no influence (Range and Noë, 2005) or found that time and frequent exposure are necessary to extract the relevant information from agonistic interactions (Paxton et al., 2010). In this case, this suggests that such knowledge is cognitively demanding and requires a lot of time to be processed, which is in line with one of the aspects of the Machiavellian intelligence hypothesis (de Waal, 1982; Byrne and Whiten, 1988). Thus, our results indicate sex and developmental differences in the extent of social knowledge and especially extensive third-party rank relationship knowledge in vervet monkeys. The results may help to explain various results on social-learning strategies, where females are generally preferred models (van de Waal et al., 2010) but group members' exact choices may be affected by kinship but not by a female's rank position (van de Waal et al., 2012, 2014; Renevey et al., 2013). Given that extensive social knowledge is a prerequisite for complex social strategies, it would be interesting to collect similar data on various other social species to get a better idea of how far selection on social cognition is age/sex specific.

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FIGURES AND TABLES

Table 1. Summary table for juveniles' first look duration. Wilcoxon signed-rank tests according to three age and two sex categories.

Variable	Modality	<i>Z</i>	<i>P</i>	<i>N</i>
Age (years)	1	-0.314	0.844	6
	2	-0.943	0.438	6
	3	-0.105	1.000	6
Sex	Females	-0.280	0.844	8
	Males	-0.561	0.625	10

Table 2. Summary table for juveniles' look duration within 10s. Wilcoxon signed-rank tests according to three age and two sex categories.

Variable	Modality	<i>Z</i>	<i>P</i>	<i>N</i>
Age (years)	1	-0.105	1.000	6
	2	-0.943	0.438	6
	3	-0.943	0.438	6
Sex	Females	-1.120	0.313	8
	Males	-0.510	0.646	10

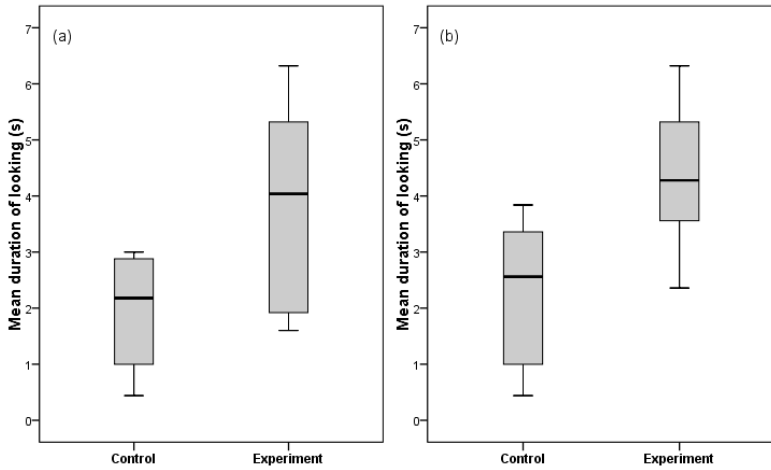


Figure 1. Mean time that females spent looking towards the speaker at (a) first look and (b) total look within 10s. Thick horizontal lines show medians, boxes show quartiles and the whiskers represent the highest and lowest values that are not outliers.

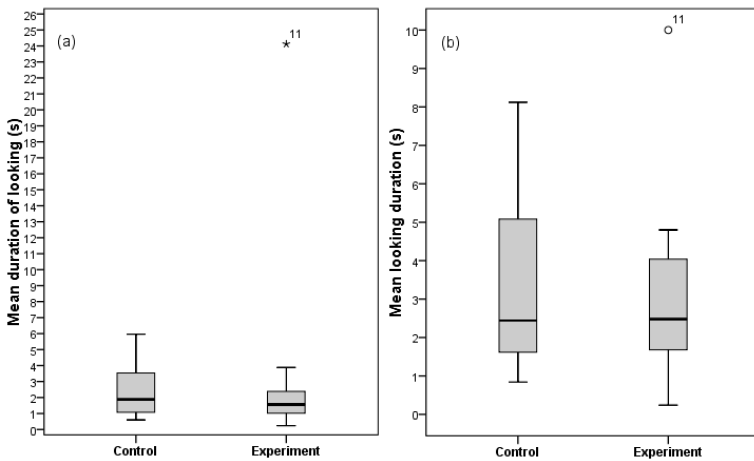


Figure 2. Mean time that males spent looking towards the speaker at (a) first look and (b) total look within 10s. Thick horizontal lines show medians, boxes show quartiles and the whiskers represent the highest and lowest values that are not outliers. Outliers are represented by a circle beyond the whiskers while extreme values are represented by an asterisk.

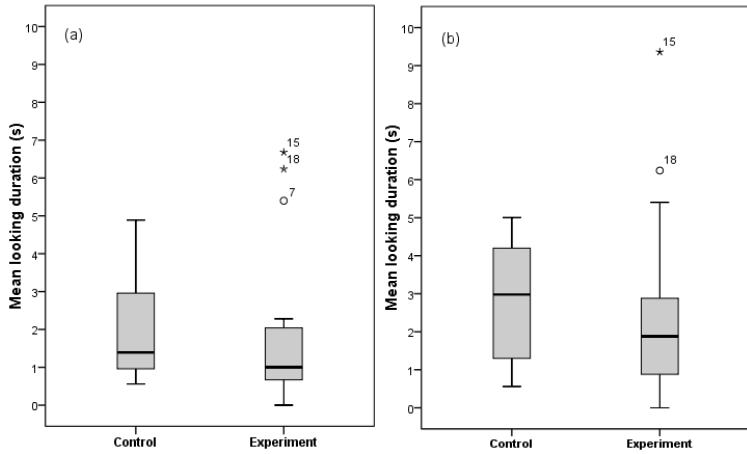


Figure 3. Mean time that juveniles spent looking towards the speaker at (a) first look and (b) total look within 10s. Thick horizontal lines show medians, boxes show quartiles and the whiskers represent the highest and lowest values that are not outliers. Outliers are represented by circles beyond the whiskers while extreme values are represented by asterisks.

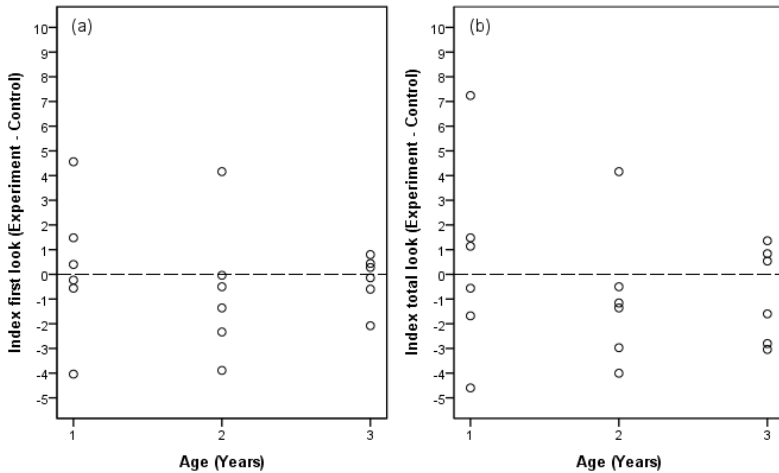


Figure 4. Difference of time juveniles spent looking between experiment and control. The index represents the duration of time spent looking during the experimental sequence minus the control sequence according to the subject's age, at (a) first look and (b) total look within 10s. The horizontal dashed line represent the 0 value.

WILD VERVET MONKEYS TRADE TOLERANCE AND SPECIFIC COALITIONARY SUPPORT FOR GROOMING IN EXPERIMENTALLY INDUCED CONFLICTS

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CB collected the data and run the analyses and both CB and RB contributed to the writing.

5.1. ABSTRACT

Grooming is a key social behavior in many primate species. Research has focused on three important aspects: the short- and long-term trading patterns of grooming for itself and/or for other commodities like tolerance or coalitionary support (Seyfarth 1977; Seyfarth and Cheney 1984), the issue of whether exchanges are a convincing example for reciprocity (Schino and Aureli 2010; Raihani and Bshary 2011), and what decision rules underlie trading (Axelrod and Hamilton 1981; Schino 2007). These issues remain largely unresolved due to the correlative nature of observational studies and the rarity of experimental studies (Seyfarth and Cheney 1984; Hemelrijk 1994; Fruteau et al. 2009; Cheney et al. 2010; Molesti and Majolo 2015). Here, we present a new experimental paradigm to address these questions in wild vervet monkeys (*Chlorocebus aethiops*). Adult females were first trained to approach a personal box, identifiable by unique color patterns, to access high quality food. During the experiments, two boxes were placed next to each other to induce conflict through forced proximity. We found that while dominants were generally more tolerant towards bonded individuals, recent grooming increased tolerance independently of relationship quality. The latter result shows that vervet monkeys traded grooming for short-term tolerance, where dominants used a direct reciprocity decision rule. In contrast, females invariably supported the higher ranking opponent in a conflict, independently of who was the recent grooming partner. Nevertheless, recent grooming increased the probability that a female supported the partner during conflicts with a low-ranking third party. Thus, females' decisions about coalitionary support seem to integrate information about

the current social hierarchy with recent grooming events. In conclusion, decision rules underlying trading of grooming for other commodities involve a variety of time scales and factors.

5.2. INTRODUCTION

Reciprocity – cooperation based on mutual investments – is probably rare in non-human species compared to other forms of cooperation (Raihani and Bshary 2011; Hammerstein 2003; Stevens and Hauser 2004; Leimar and Hammerstein 2010; André 2014). Nevertheless, reciprocity has seen a recent revival for at least four reasons. First, there are by now a few convincing experimental studies on contingent investments, i.e. in rats (Rutte and Taborsky 2008), flycatchers (Krams et al. 2008), vampire bats (Carter and Wilkinson 2013; Wilkinson 1984) and baboons (Cheney et al. 2010). Second, several empirical studies yielded intriguing cases of high levels of coordination based on alternating helping, like hunting strikes in lionfish (Lönnstedt and McCormick 2013), watchman behavior in rabbitfish pairs (Brandl and Bellwood 2014) and leadership during migration flights in ibis (Voelkl et al. 2015). However, none of these correlational studies demonstrated reciprocity by showing that individual contributions are contingent on the partners' contributions. A further boost for reciprocity research was the suggestion that generalized investments - help who needs help as long as you received help when needed (Rutte and Taborsky 2007) – may promote the establishment of direct reciprocity (Barta et al. 2011). Finally, various authors argued that reciprocal investments can readily be found in nature but not based on so-called 'counting' strategies like tit-for-tat, where the focal individual's behavioral choice matches the partner's previous choice: cooperate if the partner cooperated, defect if the partner defected (Axelrod and Hamilton 1981). Instead, primatologists in particular have argued that primates make decisions based on emotional states rather than on precise book-keeping of previous events. In this scenario, helping may lead to return helping either due to a short-term increase in positive emotions ('attitudinal reciprocity';(de Waal 2000)), or because long-term bonds lead to increased helping due to general positive emotions ('emotional book-keeping'; (Schino 2007)).

In primates, previous correlational evidence suggests that grooming may be traded against grooming but also against other commodities, including sex (Hemelrijk et al. 1992; Gumert 2007; Norscia et al. 2009), food (de Waal 1997) , tolerance (Henzi and Barrett 1999; Tiddi et al. 2011; Ventura et al. 2006; Port et al. 2009) and coalitional support during agonistic encounters (Seyfarth 1977, Seyfarth and Cheney 1984; Watts 2002; Koyama et al. 2006). However, few experiments have been conducted to test for conditional helping rules. A recent study (Molesti and

Majolo 2015) did not find evidence for short-term contingency between grooming and food sharing based on tolerance in Barbary macaques (*Macaca sylvanus*). Hemelrijk (1994) observed such support contingencies in captive macaques but lacked controls that would allow distinguishing between direct and generalized reciprocity. A classic field experiment reported that vervet monkeys stared at loudspeakers for longer (Seyfarth and Cheney 1984) and a recent similar study demonstrated that baboons were more likely to approach the speakers when a playback simulating an aggressive encounter involved a recent grooming partner (Cheney et al. 2010). A suitable extension of these studies would be to test for increased probability of support when there is a real conflict. In the recent study (Cheney et al. 2010) is also intriguing that non-bonded grooming partners elicited a stronger response than related grooming partners.

Here, we present a novel experimental design to test for reciprocal exchange of grooming for tolerance (i.e. total absence of conflict) and/or coalitionary support in three groups of wild vervet monkeys. Females were first trained to approach their personal box (identifiable by a unique color pattern) filled with high quality food, opened by the experimenter with remote control only if the box owner touched it (see also Figure S1 and S2). For experiments, two boxes were placed next to each other to induce a conflict through forced proximity, allowing us to test for any short-term direct or generalized effects of grooming. During the training phase, we observed that some pairs were more tolerant than others. For each pair, the maximum distance between boxes that consistently generated a conflict was considered as the reference distance. During experiments, for each pair, the distance between boxes corresponded to this reference distance. While running experiments, we sometimes had the opportunity to observe the formation of a coalition. By knowing the grooming history of the different individuals involved, we could test for the contingency of support after grooming. Assessment of the long-term quality of the relationships (i.e. bondedness) between subjects following the methodology of Fedurek et al. (Fedurek et al. 2013), which takes into account grooming and proximity data, enabled us to investigate how far relationship quality rather than recent interactions predicts levels of tolerance and/or coalitionary support (see supplemental information for detailed experimental procedure).

5.3. MATERIAL AND METHODS

For more detailed descriptions we refer to the supplemental information.

5.3.1. Training

Individuals were trained to recognize a personal box from which they could get a high quality reward (see Figure S1). In total 17 females from three wild groups of vervet monkeys, in Kwazulu Natal, South Africa, were successfully trained. A total

of 40 different pairs were tested, however it was not possible to test each of them in each situation as some females were never seen grooming each other. For the support data we analyzed coalitions occurring during experimental trials. These coalitions could involve also untrained females. Data on coalitions comprised a total of 12 females.

5.3.2. Data collection

Based on focal sampling of trained individuals, we set up experiments opportunistically, i.e. as a function of the documented presence/absence of recent grooming interactions and the presence of trained third parties. As experiments progressed, an effort was made to obtain data on hitherto untested pairs in the different situations at the expense of increasing sample sizes of regularly tested pairs. Any form of aggression was scored as the dominant being intolerant in the first experiment, and as the bystander joining a conflict to form a coalition.

5.3.3. Data and statistical analyses

Total absence of aggressive behavior was scored as tolerance or as not joining a conflict. We considered each conflict or tolerance as binary variables. A trial was only considered if both individuals were present at the boxes together. To test the effect of bondedness we distinguished between bonded and non-bonded pairs (see supplemental information for calculation of relationships quality). We had 20 pairs of bonded and 20 pairs of non-bonded females.

Statistics were performed in R (v.3.0.1). First each model was compared to a null model, confirming the robustness of all our models, which are presented in Table 1. For tolerance analyses we considered for each pair the outcome of each interaction as tolerance or conflict (dependent variable and binomial data) over all trials. The “Situation” (PG, DG, NoG), “Bondedness” and “Group identity” were all considered as fixed effects within the model. To account for pseudoreplication, as individuals were tested within different pairs multiple times across situations (sessions) and sometimes multiple times a day, we introduced the random factors for couples and session inside each couple as well as the number of interactions the dominant individual (i.e. making the decision) experienced per day. To analyze the probability of conflict across the three different grooming situations, we ran a GLMM with an analysis of deviance (Type II) using the function “glmer” of the R package “car” and “lme4”. We ran a post hoc test of Linear Hypothesis to compare each situation with each other using the function “ghlt” of the package “multcomp”. For the bond effect on distance between boxes (dependent variable), we ran a LMM with an analysis of variance (Type 3) using the function “lmer” of the R package “lme4”. “Bondedness” and “Group identity” were both considered as fixed effects while the identity of each subject and adversary was considered as

random effects. For the support analyses we considered the proportion of support over non-support data (dependent variable). Here, each data point was independent. Pairs were compared in situations of grooming and no grooming. “Situation”, “Bondedness”, “Group identity” were considered as fixed effects while the identity of each couple and each experiment session were considered as random effect. To analyze the probability of support after a grooming bout, we ran a GLMM with an analysis of deviance (Type II) using the function “glmer” of the R package “car” and “lme4”

5.4. RESULTS AND DISCUSSION

5.4.1. *Effect of grooming on tolerance*

Focal animal sampling enabled us to test pairs in three different situations: ‘partner grooming’ (PG) in cases where the subordinate had groomed the dominant within the last 60 min, ‘no grooming’ (NoG) in cases where the dominant had not been groomed at all during the previous 60 min and ‘dominant grooming’ (DG) in cases where a third party groomed the dominant. A testing episode could involve up to three trials, i.e. three times reloading the boxes with food. Multiple experiments involving the same subject could be run per day if this individual got involved in a grooming bout with other individuals or had not been involved in a grooming bout for at least 60min. A total of 40 pairs were tested, 28 of which in all three situations. All results are summarized in Table 1.

We found that for all three groups, tolerance varied across the grooming situations (GLMM: Situation: $\chi^2=35.79$; Df=2; $P<0.001$; Group identity: $\chi^2=1.84$; Df=2; $P=0.39$). When analyzing in detail the differences between situations within a single post hoc test, we found that grooming generally increased tolerance towards the partner (Fig. 1; Linear Hypothesis test: comparison no grooming against partner grooming: $Z=-3.86$; $P<0.001$). Furthermore, grooming per se did not make dominants more tolerant towards any group member but selectively more tolerant towards recent grooming partners (comparison partner grooming against dominant groomed by third party: $Z=-4.77$; $P<0.001$, Fig. 1). Finally, dominants were not more tolerant after being groomed by a third-party compared to trials in which they had not experienced any grooming for 60min (comparison dominant groomed by third party against no grooming: $Z=-1.52$; $P=0.27$, Fig. 1)

As expected from our definition of bondedness, we found that subordinates experienced an overall higher level of tolerance if they had a strong bond with the dominant partner (GLMM: $\chi^2=7.34$; Df=1; $P=0.006$). That result is even more strengthened by the fact that bonded pairs were tested on average with smaller distances between boxes than non-bonded individuals were, with an additional significant variation between groups as the AK group was generally more tolerant

and therefore tested on shorter distances (LMM; mean distance bonded pairs: 2.4 m; mean distance non-bonded pairs: 3.2 m; $F_{1,36}=27.1$; $P<0.001$; Group identity effect: $F_{2,10}=5.2$; $P=0.02$). Finally, there was no interaction effect between the situation and bondedness (GLMM: $\chi^2=4.25$; $Df=2$; $P=0.11$); the effect of short-term grooming was as strong in non-bonded individuals than in bonded ones (Fig. 1)

The results demonstrate experimentally that grooming can be directly exchanged against tolerance in a reciprocal way, which is in line with previous studies analyzing correlational data (Tiddi et al. 2011; Ventura et al. 2006; Port et al. 2009; Fairbanks 1980; Silk 1982; Schino and Aureli 2008). In addition, we did not find any evidence that dominants increase their level of tolerance towards any group member after being groomed as expected by the generalized reciprocity theory (Pfeiffer et al. 2005; Hamilton and Taborsky 2005)

The fact that subjects are regularly more tolerant towards some individuals suggests that tolerance at a foraging site is not only based on short-term effects but also on long-term ones. As we do not have genetic data on relatedness, we can currently not distinguish between the relative importance of kinship versus long-term emotional book-keeping of relationship quality. However, our results suggest that non-bonded individuals gain as much tolerance with grooming as bonded individuals do.

A methodological shortcoming of our data collection was that we do not have information about the subjects' involvement in recent aggressive interactions. Aggressive interactions may affect subsequent behavior (Cheney et al. 2010; Engh et al. 2006). Thus, we likely have some unexplained variance in our data due to this lack of information. We note, however, that such unexplained variance is most likely to support the null hypothesis that recent grooming and/or bonding does not affect the dominants' tolerance levels. Hence, our positive results appear to be robust.

5.4.2. Effect of grooming on coalitionary support

We asked two questions: First, whether a female joining a conflict is more likely to support a recent grooming partner than the third party; second, whether a female is more likely to join in the first place if a recent grooming partner is involved. With respect to the first question, we had 18 cases out of 42 conflicts that involved a total of eight joiners with seven recent grooming partners (Figure 2; see also Table S1). The resulting interdependence between data points largely prevented statistical analyses (see supplemental information). However, one main effect emerged: joiners ($n=8$) invariably supported the higher ranking individual in a conflict, yielding an overall significant effect based on six independent pairs of individuals

($n=6$, $x=0$, $p=0.031$). Pooled data do not provide any evidence that joiners formed coalitions with the recent grooming partner rather than with the third party (12/18 coalitions with grooming partner). Furthermore, preliminary evidence suggests that rank considerations also overrule bonds: in the only two cases in which the joiner had to choose between a bonded partner and higher ranking individual she supported the latter.

Given that joiners support the higher ranking individual in a conflict, we asked whether joiners are more likely to form a coalition if the conflict involves a bonded individual and/or a recent grooming partner against a lower ranking third party. In all three groups, the proportion of support was significantly higher after pairs had groomed each other compared to situations where they had not groomed each other (Fig. 2; Table 1: GLMM: Situation: $\chi^2=8.04$; Df=1; $P=0.004$; Group identity effect: $\chi^2=0.57$; Df=2; $P=0.44$). However, there was no bondeness effect ($\chi^2=0.31$; Df=1; $P=0.58$) nor any interaction effect between the grooming situation and bondedness ($\chi^2=0.004$; Df=1; $P=0.94$).

The results reveal that decisions about coalitionary support are rather complex in the sense that vervet monkeys consider various variables in their decision making process. The first general rule is that *if* individuals join a conflict they support the higher ranking against the lower ranking opponent rather than considering recent grooming events or bondedness. This appears to be a rather opportunistic strategy that has been proposed to minimize the risk of own injury (Cheney and Seyfarth 1990) and is widespread in primate species such as chimpanzees, baboons and macaques (Watts 2002; Bernstein and Ehardt 1985; Chapai et al. 1991; Wittig et al. 2007) and hyenas (Engh et al. 2005). Similar results have already been documented in vervet monkeys (Seyfarth 1980; Cheney 1983). Interestingly, the decision whether to join a conflict in the first place is best explained by short-term reciprocity, i.e. trading support for recent grooming, independently of bondedness. While small sample size provides a potential explanation for this negative result, we note that the recent grooming caused significantly higher rates of support indicator (approach) for non-bonded partners than for kin in baboons (Cheney et al. 2010). The results of the two studies present an interesting puzzle for kin selection theory and should be investigated in the future. In summary, our results indicate that vervet monkeys exchange grooming against coalitionary support but only if both grooming partners outrank the target of the coalition.

5.5. GENERAL CONCLUSIONS

The main conclusion from our experiments is that dominant vervets give both tolerance and selective support during agonistic encounters in direct exchange for recent subordinates' grooming while there is no evidence for generalized

reciprocity. These effects apply to both non-bonded and bonded pairs. The results thus demonstrate the general importance of short-term direct reciprocity (de Waal 2000). The results imply that short-term reciprocity occurs even between relatives; while we currently lack data on genetic relatedness in our monkeys, it is clear from other studies that bonded individuals are often also close relatives (Silk et al. 2006) and this applies particularly to our vervet females as they are the philopatric sex (Cheney and Seyfarth 1990; van de Waal et al. 2012). The positive effect of bondedness, i.e. long-term grooming and proximity scores (Fedurek et al. 2013), on levels of tolerance in our foraging context is in line with the concept of emotional book-keeping (Schino and Aureli 2008; Schino and Aureli 2009). Note, however, that these latter results do not demonstrate contingent helping based on reciprocity. This is because the fitness of bonded individuals is likely to be interdependent, i.e. disease or death of one partner will cause lower future fitness in the other (Roberts 2005). Such interdependency may hence lead to rather self-serving support (pseudoreciprocity; (Connor 1986) rather than to conditional support.

Another important conclusion from the data is that the dominants' decision rules regarding the trading of tolerance for grooming differ from the decision rules regarding the trading of coalitionary support for grooming. We propose that some observed differences make intuitive sense. The dominants' decisions about tolerance concern dyadic interactions, and hence tolerance can be given in exchange for received services like grooming without additional effects on the group social network. In contrast, supporting an individual also involves the decision to go against another group member. If dominants changed their support frequently based on recently received services, the social life would become highly unpredictable, and is not clear to us how dominants would benefit from that. Typically, high social instability is correlated with elevated stress levels in all individuals, including dominants (Creel et al. 2013; Engh et al. 2006). Some other results are more difficult to interpret. For example, we need to understand how supporting high-ranking rather than bonded individuals in a conflict fits recent evidence that stable social relationships are crucial for an individual's life time fitness (Silk et al. 2009; Silk et al. 2010; Seyfarth and Cheney 2012). Linked to this issue, it is not clear why bondedness had a significant effect on tolerance but not on support. A potential explanation for the latter result is that our index for bonding is based on scan data (Fedurek et al. 2013), which do not give appropriate estimates of rare events like aggressive interactions. Therefore, our bondedness score might hence been foremost a tolerance score.

As pointed out before, observational studies on social interactions cannot control for spatial proximity and for current needs (Puga-Gonzalez et al. 2015; Spinelli et

al. 2009). Our experiments controlled these two variables. We also believe that the experimental design is easily applicable to a variety of other species. We predict that similar experiments will not only provide further evidence for reciprocity but more importantly a diversity of decision rules, depending on the specifics of the social organization of the species tested: kin structure, bondedness, group stability as well as steepness of the social dominance hierarchy may all interact in producing differences between species. To advance our understanding of reciprocity, a future generation of reciprocity models needs to incorporate such new empirical evidence for a more realistic strategy set that explores the mechanisms and constraints involved in decision making (Raihani and Bshary 2011). Only the incorporation of mechanisms and constraints will allow us to understand differences between species as well as within species with respect to their cooperative performance.

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FIGURES

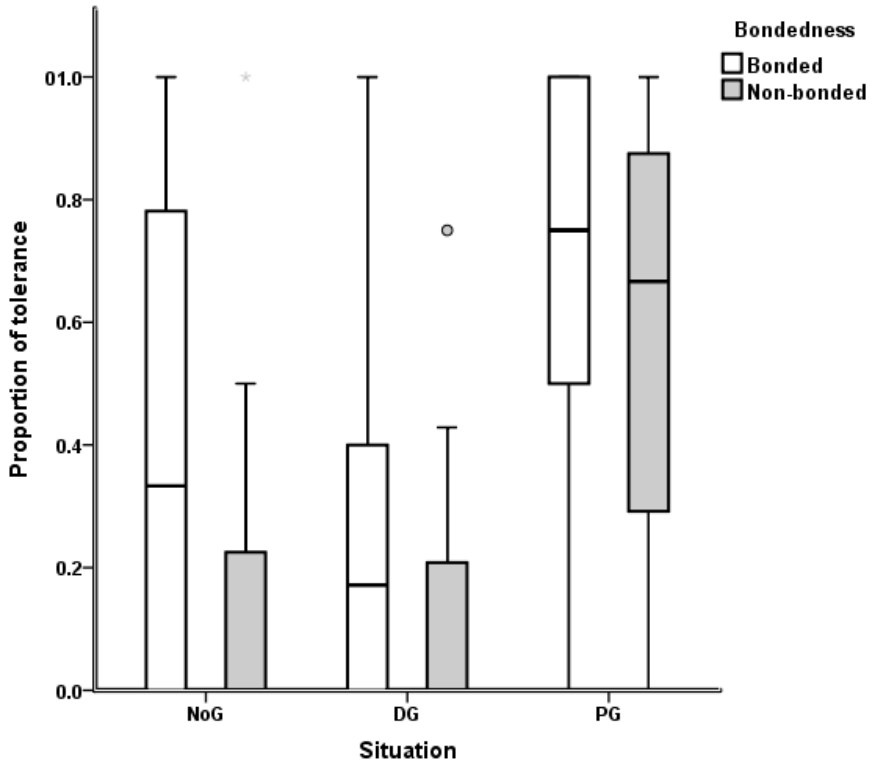


Figure 1. Dominants trade short-term tolerance for grooming. Representation of bondedness in all three grooming situation where, the dominant did not experience any grooming in the last 60min (NoG), the dominant have been groomed by a third party (DG) and the partner has groomed the dominant (PG). Thick horizontal lines show medians, boxes show quartiles, the whiskers represent the highest and lowest values that are not outliers. Outliers are represented by circles beyond the whiskers while extreme values are represented by stars.

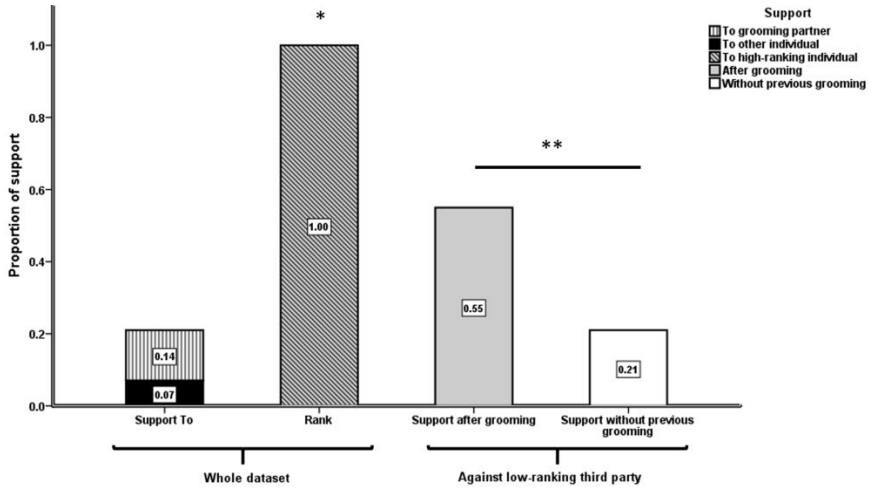


Figure 2. Coalitionary support. Proportion of support toward individuals according to recent grooming events and rank. We made the distinction between the whole dataset and the dataset that involved coalitionary support against lower ranking third party. Note that these are raw data with interdependencies due to repeated observations of individuals and pairs.

5.8. SUPPLEMENTAL EXPERIMENTAL PROCEDURES

5.8.1. Study site and group composition

Experiments were run from December 2012 until December 2014 at the Inkawu Vervet Project, Mawana Game Reserve, Kwazulu Natal, South Africa. Subjects were 17 adult females from three habituated groups of vervet monkeys. In 2014, not counting infants, the first group, Ankhase, included 27 individuals (4 adult males, 9 adult females, 14 sub adults and juveniles). The second group, Baie Dankie, included 38 individuals (4 adult males, 11 adult females, 23 sub adults and juveniles) and the third one, Noha, included 35 individuals (4 adult males, 11 adult females, 20 sub adults and juveniles).

5.8.2. Training

Individuals were trained to approach and obtain a small reward (piece of apple) by touching a wooden box that could be opened from a distance with the help of a remote control by the experimenter (an extension of the experimental design by Fruteau et al. [S1]). Boxes were covered with a variety of color and shape coded covers (Fig. S1). Each cover was attributed to one particular female, so that the experimenter would only open the box if a female touched the matching box. A female was considered as trained to her box when she consistently chose the box with her cover over other alternative boxes for at least the last 50 trials which could be spread throughout multiple training sessions. Successful training usually required a minimum of about 100 trials, depending on the individual. Not all females participated in the training. As a result, we had six females trained in the Ankhase group, four females in the Baie Dankie group and seven females in the Noha group. Usually the training took few months as multiple individuals were trained simultaneously.

5.8.3. Experimental design

During the experiments, two boxes were brought within 5 meters of each other (Fig. S2). Within such distance and in such food related situations, vervet monkeys are particularly intolerant towards each other (van de Waal unpublished observations). By choosing specific combinations of boxes, we could therefore create potential conflicts selectively between two individuals. The distance between boxes varied from 1 to 5 meters between pairs as some individuals were more tolerant than others. However, the distance was kept constant within each pair of individuals throughout the trials. The adequate distance between the boxes was assessed during the training phase for each pair of individuals. For each experiments, we recorded the distance between the two boxes, which individual arrived first at the box, and if the second individual approached the boxes we recorded the outcome of the interaction as either tolerance or conflict. A conflict

was recorded independently of its intensity, i.e. the higher ranking individual could just stare at the lower ranking one, displace, vocalize, attack, chase, and in most cases independently of whether or not the aggression prevented the subordinate from getting the reward. However, if a dominant just approached the subordinate, such behavior was considered as an aggression only in the case where the dominant voluntarily prevented the subordinate to access the apple (i.e. by trying to get the apple from the subordinate's box) or stole it from her. If during a conflict a third party intervened and showed any form of aggression as cited above we recorded its identity and the identity of the supported individual. If the individuals remained in the vicinity we reloaded the boxes up to a maximum of three trials. If the second individual did not approach, we reloaded the first box once again after 120s. Trials in which only one individual came to her box were excluded in the present analyses. Experiments took place from 5:00 until 12:00 in the morning.

5.8.4. Assessment of relationships quality

To test if the identity of a grooming partner had an influence on the subsequent behavior of dominant individuals, we assessed the quality of a relationship by analyzing natural scan data as our long term database is based on scan data and not focal data. As relatedness between females remain to be determined by genetic analyses, we integrated all group members within the analyses in order to assess the validity of our methodology. Indeed, our knowledge about kinship is limited to mother/juveniles and few pairs of sisters. If our analyses capture key features of close social relationships, we predicted based on other studies [S2] that these genetically related pairs should be classified as bonded. This was indeed the case. According to the Fedurek et al. [S3] methodology, we integrated the grooming, 1m and 5m proximity networks to determine bonded individuals using data collected over 24 months. For each index (i.e. grooming, 1m, 5m) a pair (A and B) was classified as "associated" if the value was one-third of standard deviation larger than the average of both A and B with all other group members. Pairs of individuals were then scored as bonded if they were "associated" for at least two out of three different indexes. All other pairs were scored as non-bonded. Observations took place from 5 until 18 in summer and from 7 until 17 in winter. At least one whole day of scan was collected per week and per group, conducting standard scan sampling [S4] every 30 min. The activity and the neighbors' identity within 1m and 5m of all visible animals was recorded during a 10 minutes scan window. To avoid collecting the most conspicuous behavior, once an individual was spotted, the behavior was recorded only after a 3 seconds delay. As data were collected by multiple observers, inter-observer reliability tests were performed to ensure high consistency.

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SUPPLEMENTAL FIGURES AND TABLE

Table S1 related to Figure 2. **Number of supports after a grooming bout.** Number (n) of aggressive encounters (symbolized with “!”) between a recent grooming partner and a third party and responses by the focal individual (no joining, joining and helping partner, joining and helping other), distinguishing different rank relationships in these triadic interactions. Rank relationships are depicted with a letter code, where A>B>C>D>E represent dominance relationships. The starting point invariably was that a high-ranking individual (B) received grooming by a low-ranking one (D), and then either of them could be involved in a conflict with an opponent that either outranked both of them (A), or was of intermediate rank (C), or lower ranking than both of them (E).

D grooms B	A!B	A!D	B!C	C!D	B!E	D!E
total n	1	8	4	3	10	18
n no joining	1	2	4	1	9	7
n joiner helps partner	0	0	0	0	1	11
n joiner helps other	0	4	0	2	0	0



Figure S1 related to Figure 1. **Color coded box covers.** Representation of the different box covers. Some covers were used for two different females but not within the same group.



Figure S2 related to Figure 1. **Picture of monkeys at the boxes.** Two monkeys present simultaneously at their personal box. The dominant individual is on the right, while the subordinate is on the left.

EVIDENCE FOR FINE-TUNED DECISIONS ON TOLERANCE VERSUS CONFLICT IN WILD VERVET MONKEY FEMALES

Manuscript in preparation

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6.1. ABSTRACT

Group living promotes opportunities for both cooperation and competition. Selection on the ability to cope with such opposing social opportunities has been proposed to be a key for the evolution of large brains in primates and other social species. However, we still know little about how sophisticated social strategies in such social species really are. Here, we report quite advanced social strategies in wild vervet monkeys. Building on recent experimental evidence that subordinate females trade grooming against tolerance from higher ranking individuals during foraging activities, we show that also the composition of the audience affects tolerance levels. First, tolerance was lower if the audience contained individuals that outranked the potential target. Second, we found a significant interaction between previous grooming and relative rank of bystanders: high ranking individuals valued recent grooming by subordinates while intermediate ranked individuals valued the option to aggress subordinates in the presence of higher ranking audience. Aggressors were also more likely to emit coalition recruitment calls if the audience contained individuals that outranked the target. As joining bystanders invariably support the higher ranking individual, vervets apparently integrate recent grooming and knowledge about third party relationships between targets and audience members to trade-off tolerance with opportunities to reinforce rank relationships.

6.2. INTRODUCTION

In an evolutionary context, the social complexity of group living has been considered as one of the main factor selecting for cognitive capacities and

correspondingly increased brain size (Humphrey 1976; Barton and Dunbar 1997; Dunbar and Shultz 2007). Social complexity arises in stable groups due to high frequency of encounters between members, where the same pairs can be partners, neutral or competitors, and the outcome of each encounter depends on the independent decisions of both. In order to successfully manage their relationships and social challenges under such circumstances, individuals have to keep track of their own relationships with other group members. An additional level of complexity arises when interactions take place within a communication network, where bystanders can extract valuable information about the interaction for future use or decide to intervene according to their own interests. Communication networks are indeed a widespread phenomenon described for all major vertebrate clades and even in invertebrates (McGregor 2005). As a consequence of being observed, interaction partners should adjust decisions to the presence of bystanders, leading to so-called ‘audience effects’ (see Zuberbühler 2008). Again, there is widespread evidence for audience effects, in competitive contexts but also in cooperative ones (for competitive: Matos and McGregor 2002; Slocombe and Zuberbühler 2007; Townsend et al. 2008; for cooperative: Wedekind & Milinski 2000; Pinto et al. 2011).

While audience effects are widespread, it is important to realise that the complexity of underlying decision rules may vary between species and situation, and that complexity may be particularly high in species that live in stable groups for at least three reasons. First, in stable groups the same pairs may sometimes be competitors and sometimes co-operators. Second, as stable groups are characterised by a social relationship structure, decisions about helping/support may often be linked to either genetic relatedness (Hamilton 1964a,b) and/or friendship (Silk et al. 2010). Therefore, it may become important to adjust own audience effects to the presence of supportive kin/friends either to self or to the interaction partner. Finally, stable groups are often characterised by a stable hierarchy, where decisions about audience effects should incorporate not only own but also the interaction partner’s rank relationships with bystanders. The basis for the latter is known as third party relationship knowledge (Bergman et al. 2003; Paz-y-Mino 2004; Engh et al. 2005; Schino et al. 2006; Borgeaud et al. 2013). If it were shown that individuals in stable groups integrate all such information into the expression of audience effects in a self-serving way, the results would provide important support for the strategic aspects of the Machiavellian intelligence hypothesis (Byrne and Whiten 1988; Whiten and Byrne 1997). This hypothesis builds on previous suggestions that cognitive processes mainly evolved to allow individuals to cope with the challenges of the rather unpredictable social environment (Jolly 1966; Humphrey 1976). While it covers social behaviour and cognition very broadly, for example

by including also the scope for social learning and traditions, our study focusses on the earlier more specific use of the term ‘Machiavellian’ as aiming for power (de Waal 1982).

We studied the decisions of wild adult vervet monkey females about tolerating or aggressing lower ranking group members in a foraging situation that was experimentally induced. Before the experiments, each female had been trained to approach her personal wooden box, recognisable by a unique colour pattern, in order to obtain high quality food inside. Boxes were opened by remote control only when the owner touched the top. In the experiments, two boxes were placed in close distance from each other. As vervet monkeys have a strict linear hierarchy and limited tolerance around food sources (Cheney and Seyfarth 1990), the set up allowed testing for the existence of factors that might decrease or increase the likelihood that dominants individuals aggress subordinates. In a previous study, we showed that recent grooming caused a reduction of aggression selectively towards the grooming partner (Borgeaud and Bshary 2015). In those analyses, we did not take into consideration that our trials took place in the presence of an audience, which varied between trials in number and composition. Therefore, the aim of the current paper was to investigate in how far audience composition affects the higher ranked individual’s decision on aggression/tolerance. Various studies have shown that in vervet monkeys, third party interventions in a conflict typically involve high-ranking individuals and only occur to support the aggressor against the victim (Cheney and Seyfarth 1990; Borgeaud and Bshary 2015). As a consequence, high-ranking vervet monkey females 1) do not have to worry about the audience but 2) are more likely to receive coalitionary support in an aggression if the audience contains individuals that outrank the target. Coalitionary support increases the benefits of aggression in two ways. First, it increases a chance of victory while decreasing risk of injury (Cheney 1977). Second, it may help strengthening the bond with the coalition partner and thereby reinforce the existing hierarchy beyond the relative physical strength of individuals (Cheney and Seyfarth 1990). Thus, if vervet monkeys have some awareness of these benefits we predicted that high-ranking females should be more likely to aggress subordinates in the presence of suitable coalition partners. Suitable coalition partners may be identified via more or less sophisticated knowledge. Simple decision rules include “increase probability of aggression if the audience contains individuals that outrank self and/or closely bonded individuals/kin”. A more sophisticated decision rule would take advantage of third party relationship knowledge and hence “increase probability of aggression if the audience contains any individuals that outrank the target”. As vervet monkey females are known to possess such triadic awareness (Cheney and Seyfarth 1990; Borgeaud et al. 2013), we predicted that the presence of intermediate rank

individuals between potential aggressor and target would lead to increased probability of aggression independently of the genetic relatedness or relationship quality. Finally, we investigated in how far the effects of recent grooming interacted with audience composition. If recent grooming promotes tolerance and a high-ranking audience promotes aggression, do vervet monkeys subtract the effects from each other or is one factor more important? And does the way how these two factors are integrated depend on the relative rank constellation? For example, one could predict that dominants give more weight to recent grooming while individuals of intermediate rank give more weight to the opportunity of acquiring a more dominant coalition partner. In that case, we predicted an interaction between relative rank and recent grooming events as explanatory variable for probability of aggression during the experiments.

6.3. MATERIAL AND METHODS

6.3.1. Study site and population

Experiments were run from December 2012 until December 2014 at the Inkawu Vervet Project, Mawana Game Reserve, Kwazulu Natal, South Africa. Subjects were 17 adult females from three habituated groups of vervet monkeys. In 2014, without infants, the first group, Ankhase, included 27 individuals (4 adult males, 10 adult females, 13 sub adults and juveniles). The second group, Baie Dankie, included 38 individuals (4 adult males, 11 adult females, 23 sub adults and juveniles) and the third one, Noha, included 35 individuals (4 adult males, 11 adult females, 20 sub adults and juveniles).

6.3.2. Training

Females were trained to approach and get access to a reward in a wooden box that could be opened from a distance with a remote control by the experimenter (see Borgeaud and Bshary 2015 for more details about methodology). Each box was covered with a colour and shape coded cover so that a monkey could learn that only one box (decided by the experimenter) would give her access to the reward. In the Ankhase group, 6 females were trained, in the Baie Dankie group, 5 females and in the Noha group, 7 females. A total of 40 different pairs were tested. The audience could involve any individual that was older than one year. Juveniles' ranks were assessed according to their mother's hierarchy and based on the project long term data. Adult males were considered as a lower ranking audience as these ones rarely intervene in a female-female conflict (Cheney and Seyfarth 1990), which was the case during this study as we never had any adult male intervention.

6.3.3. Data collection

Two personal boxes were put next to each other in order to induce an interaction through forced proximity. A maximum of pairs was tested in the two different grooming situations: After the box partners had not groomed each other (NG) and after they had (PG). In order to increase the power of our analyses as we had many categories of grooming and audience situations, we decided to integrate the “dominant groomed” (DG) situation with the “no grooming” (NoG) situation as these ones were not different from each other (Borgeaud and Bshary 2015) to create our “no grooming” (NG) control situation. After a grooming session, a time window of maximum 60 minutes was considered to run a trial. The outcome of each interaction was recorded as conflict or tolerance. If the individuals remained around the experiment location, the boxes were reloaded maximum another two times to assess a potential change of behaviour. Multiple experiments involving the same subject could be run per day if this individual got involved in a grooming bout with other individuals or had not been involved in a grooming bout for at least 60min. For each experiment, we recorded who was within 10 m and in case of conflict, the exact behaviour of each box partner and this of the audience in case of intervention.

6.3.4. Data and statistical analyses

To test if audience effect had an effect on tolerance, we compared the number of conflicts/tolerance between a pair in the three audience situation (high, middle and low-ranking audience) in the two grooming situations. Furthermore, to increase the data set and prevent a lack of variance, we also decided to integrate the low-ranking audience with the no audience at all as these ones were not significant from each other ($Z=0.40$; $P=0.94$). To test if the audience had an effect on the probability of conflicts, we analysed all trials results. In order to test if the audience had an effect on the production of aggression calls we compared the number of vocal/non vocal conflicts between a pair in the three audience and two grooming situations. A maximum of pairs was tested in each situation although it was not possible to get a complete data set as, for example, some females were never seen grooming each other or it was not possible to have the pair and an appropriate audience together within the right time window of 60 min after grooming. The long-term quality of the relationships (i.e. bondedness) between subjects was assessed following the methodology of Fedurek et al. (2013). We integrated the grooming, 1m and 5m proximity networks to determine bonded individuals using scan data collected over 24 months. For each index (i.e. grooming, 1m, 5m) a pair (A and B) was classified as “associated” if the value was one-third of standard deviation larger than the average of both A and B with all other group members.

Pairs of individuals were then scored as bonded if they were “associated” for at least two out of three different indexes. All other pairs were scored as non-bonded.

Statistics were performed in R (v.3.0.1). First each model was compared to a null model, confirming the robustness of all our models and for each test we ran a GLMM with an analysis of deviance (Type II) using the function “glmer” of the R package “car” and “lme4”. For the conflict analyses we considered for each pair the outcome of each interaction as tolerance or conflict (dependent variable and binomial data) over all trials. The type of “audience” (H, M, L), “situation” (PG, NG) and “group identity” were all considered as fixed effects within the model. To account for pseudoreplication, as individuals were tested within different pairs multiple times across situations (sessions) and sometimes multiple times a day, we introduced the random factors for couples and session inside each couple as well as the number of interactions the dominant individual (i.e. making the decision) experienced per day. To analyze the differences of audience effect between the two situations, we ran a post hoc test of Linear Hypothesis. For the vocalizations analyses (dependent variable and binomial data), we run a GLMM with the type of “audience” (H, M, L), “situation” (PG, NG), “age” (i.e. younger or older dominant compared to the subordinate) and “group identity” as fixed effects. We also introduced a random factor for couples and session inside each couple. To analyse the differences between the three types of audience, we ran a post hoc test of Linear Hypothesis to compare each audience with each other using the function “ghlt” of the package “multcomp”. We run a separate GLMM to test the effect of the presence of bonded individuals within the audience with “bondedness” as a fixed effect and the same random factors as above. We could not integrate it to the main model because of the presence of too many fixed effects leading to a lack of variance.

6.4. RESULTS

6.4.1. Audience effect on tolerance

We found that individuals were less tolerant in the presence of a dominant audience across all situations (GLMM: $\chi^2=23.57$; Df=2; $P<0.001$; Fig. 1). This effect was similar in all three groups (Group identity: $\chi^2=0.85$; Df=2; $P=0.65$) However, there was an interaction between audience and the grooming situation ($\chi^2=11.86$; Df=2; $P=0.002$). When running a post hoc analysis to compare the audience effect between the two grooming situations, we found that there was significant difference between high and low-ranking ($Z=3.05$; $P=0.008$) as well as between high and middle-ranking audience ($Z=3.07$; $P=0.007$), the effect of a high-ranking audience being stronger within the PG situation, but there was no difference between middle and low-ranking audience ($Z=-0.36$; $P=0.97$).

Following this last result we found with a supplementary post hoc test that across situations there is a significant difference of conflicts between a middle and a low-ranking audience ($Z=3.68$; $P<0.001$).

6.4.2. Effect of bondedness and kinship

Interestingly, although this effect was not significant, the probability of conflict was higher in the presence of a non-bonded than in the presence of a bonded individual in the audience ($\chi^2=0.05$; $Df=1$; $P=0.82$; Fig. 2). While the presence of a bonded/kin might be more likely within a middle-ranking audience, the results presented in Figure 2 suggest that such presence does not influence the probability of conflict. To confirm these results, we looked at the influence of the presence of a potential aggressor's kin within the audience as, thanks to the long-term data of the project, we know with certainty some kin relationships. Within the data set with a middle-ranking audience, we found that with the presence of a kin the proportion of conflict was 0.81, while in the absence of it the proportion was 0.76.

6.4.3. Audience effect on emission of vocalisations during a conflict

When looking at the vocalizations produced during the conflicts, we found that the presence of an audience that outranked the target had a significant effect on the production of vocalizations from the aggressor ($\chi^2=11.72$; $Df=2$; $P=0.002$; Fig. 3). When running a post hoc test, we found that there was no difference between the presence of high or middle-ranking audience ($Z=-1.38$; $P=0.34$), while there was significant difference between the presence of high and low-ranking audience ($Z=-3.38$; $P=0.002$) as well as between a middle and low-ranking audience ($Z=-2.46$; $P=0.036$). Furthermore, there was no effect of grooming situation ($\chi^2=0.83$; $Df=1$; $P=0.35$), group identity ($\chi^2=3.14$; $Df=2$; $P=0.20$) nor age ($\chi^2=2.33$; $Df=1$; $P=0.12$).

6.4.4. Punishment from the audience?

Out of all the tolerance data points with audience of high rank ($n=30$), we had only one clear aggression from the audience towards a tolerant individual at the boxes.

6.5. DISCUSSION

We had asked if vervet monkeys take the audience into account in their decision making to cooperate with or compete with their partner at a food experiment and how these audience effects interact with previous grooming effects. Results indicate that female vervets are more likely to aggress subordinates in the presence of an audience that outrank themselves but also the target, suggesting that they use strategically their third party rank relationship knowledge in order to assert their dominance. Conflicts were also more vocal in the presence of both high and middle-ranking audiences, suggesting that aggressors request support accordingly to the rank of the audience. We also found an interaction between audience and

previous grooming effects, suggesting that dominants give more weight to recent grooming while individuals of intermediate rank give more weight to the opportunity of acquiring a more dominant coalition partner. Taken together, these results suggest that vervet monkeys integrate in a rather strategic way knowledge about third party relationships and recent grooming in order to trade-off between cooperation and opportunities to reinforce rank relationships.

6.5.1. Audience effect on tolerance and vocalisations

Group living individuals face many social challenges which from a cognitive point of view require elaborated abilities and accordingly an increased brain flexibility/size. Amongst others, the major challenges involve choosing between cooperation and competition, remembering previous interactions with other group members and such complexity increases when interactions take place within a communication network, also known as audience effects. Our results indicate that, at least during competitive interactions, female vervet monkeys assess the audience composition and adjust their behaviour and calls, which serve in recruiting some help during a conflict (Cheney and Seyfarth 1990), in accordance with the presence/absence of a suitable coalition partner. We could however not find any evidence that younger and therefore smaller dominants were more likely to emit such calls when facing an older subordinate. Similarly to many other species (Chapais et al. 1991; Silk et al. 2004), vervet monkeys usually support the higher ranking individual during a conflict (Cheney and Seyfarth 1990; Borgeaud and Bshary 2015). This might be a rather opportunistic behaviour as this increases the probability of winning and minimizes the risk of injury (Cheney 1977) and allows the reinforcement of rank relationships. As individuals are more likely to aggress physically and vocally their box partner in the presence of an audience that outranks themselves but also the target, our results suggest that vervet monkeys are aware of the general rule “support the higher ranking” but also make use of their third party rank relationship knowledge (Borgeaud et al. 2013) during conflicts. While many studies suggest the presence of some knowledge about third party relationship (Bergman et al. 2003; Paz-y-Mino 2004; Engh et al. 2005; Schino et al. 2006; Borgeaud et al. 2013), only few studies focused on a potentially more sophisticated use of it. So called strategic triadic awareness has been demonstrated in chimpanzees where victims exaggerate their screams in the presence of an audience that outranks or equals the rank of the aggressors (Slocombe and Zuberbühler 2007). A study on capuchins (Perry et al. 2004) suggest similar awareness during the recruitment of an ally, although they could not rule between simpler explanations such as “Solicit an ally that outranks yourself” or “Solicit the highest ranking available individual”. Here we could rule out such simpler

explanation because a potential aggressor reacts in a similar way to the presence of an audience that outranks self, but also the target itself.

6.5.2. Interaction between grooming and audience effects

The interaction we found between audience and grooming effects reflects precisely the social challenge that individuals have to cope with when facing the choice to cooperate or compete with another group member. In this case high-ranking females at the boxes have to adjust their behaviour and choose between a potential aggression versus tolerance as a payback of grooming. While they still consider audience effects, dominants seem to give more importance to a recent grooming interaction. On the other hand, middle-ranking individuals seem to give more weight to the opportunity of strengthening their hierarchy rank by aggressing a subordinate in the presence of an audience that outranks the target. Such difference seems rather surprising but this underline the complexity that living in social group with a stable hierarchy causes.

6.5.3. Punishment or image scoring?

We also have asked if these results could be driven by the fear of a potential punishment from a dominant within the audience towards the high-ranking box partner if this one tolerated the subordinate. However, out of all the tolerance cases, we could find only one case where the audience actively aggressed the high-ranking individual which was tolerant with the subordinate box partner. It is possible that in species with a strict hierarchy such as vervet monkeys aggressing a subordinate in a presence of a dominant audience might enhance the reputation of the aggressor and helping to confirm its rank within the hierarchy. Such behaviour might resemble to some negative indirect reciprocity and might be evolutionary stable if the costs do not exceed the benefits (Johnstone 2001; Johnstone and Bshary 2004). This was probably the case in our study as conflicts mostly involved stares and vocalisations but very rarely costly aggression such as physical contact. Similarly to our results, fighting Siamese fish males are more aggressive in the presence of male audience (Dziweczynski et al. 2005) although this behaviour was also depending of the presence of nests within their territory.

6.6. CONCLUSION

Our results demonstrate that, in vervet monkeys, audience effect has an effect not only on the communication system but also on the behaviour itself. Such results are similar to previous studies that found that audience effect could induce a modification of calls production (Slocombe and Zuberbühler 2007; Townsend and Zuberbühler 2009) and also of a behaviour (Drea and Wallen 1999; Cartmill and Byrne 2007; Semple et al. 2009). However, it seems like vervets might combine

both modifications at the same time during conflicts. Taken together, our results suggest that vervet monkeys, similarly to chimpanzees (Slocombe and Zuberbühler 2007) and macaques (Silk 1999) use third party rank relationships knowledge in a strategic way by modifying their behaviour and vocalisations to gain support against an opponent, in our case a subordinate. This would suggest that conflict management in vervet monkeys implies some facets of the Machiavellian intelligence theory (Byrne and Whiten 1988; Whiten and Byrne 1997) and in particular the strategic component which gave the name to the hypothesis (de Waal 1982) and implies some sophisticated “manoeuvring” from an individual in order to increase its own benefit.

6.7. METHODOLOGICAL CONSIDERATIONS AND FUTURE PERSPECTIVES

Although we are still lacking genetics analyses, we are confident that the results presented would not vary even if we could control for kinship. However, to be able to discriminate with certainty if vervet monkeys are indeed using complex triadic knowledge and simpler rule of thumbs such as kinship, we would need to have complete genetic results. Therefore, further investigations are expected in the future order to establish the role of kinship in decision making during conflicts.

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FIGURES

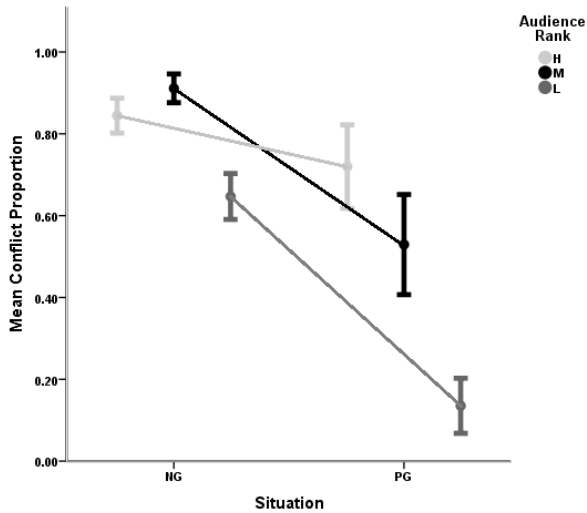


Figure 1. Influence of the audience on the tolerance. Proportion of conflicts within all trials with a high (H), middle (M) and low-ranking audience (L) in the two situations: partners groomed (PG), partners did not groom (NG). Bars represent +/- the standard error.

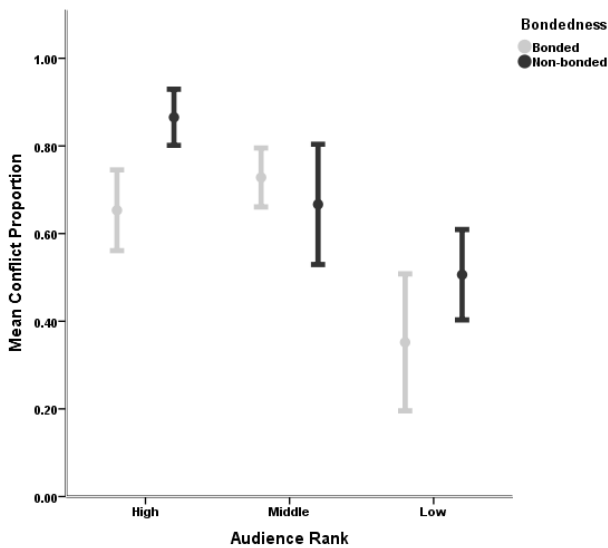


Figure 2. Influence of the presence of a bonded individual within the audience on tolerance. Proportion of conflicts within all trials with a high (H), middle (M) and low-ranking audience (L) and the distinction between the presence of bonded versus non-bonded individual within the audience. Bars represent +/- the standard error.

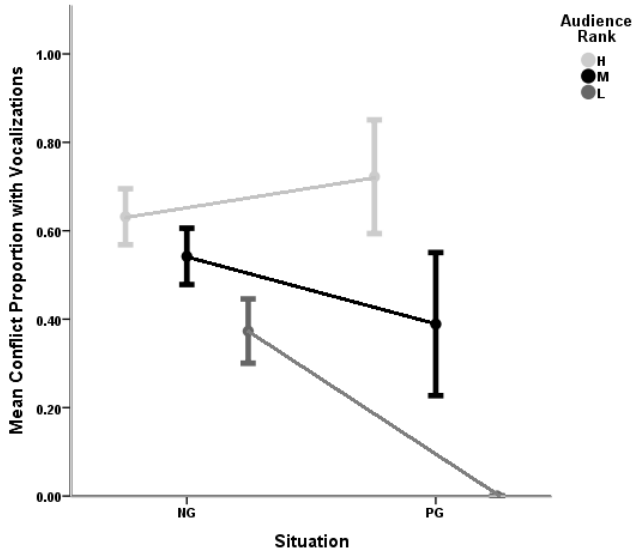


Figure 3. Influence of the audience on the production of aggression calls. Proportion of conflicts where vocalisations were produced within all trials with a high (H), middle (M) and low-ranking audience (L) in the two situations: partners groomed (PG), partners did not groomed (NG). Bars represent +/- the standard error.

TESTING FOR AWARENESS IN RECIPROCITY DECISION RULES: AN EXPERIMENTAL APPROACH IN WILD VERVET MONKEYS

Manuscript in preparation

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CB collected the data and run the analyses and both CB and RB contributed to the writing.

7.1. ABSTRACT

It has been suggested that social challenges in group living species caused the selection on advanced cognitive processes and correspondingly an increase of brain size. A key challenge for testing this hypothesis is to design experiments that allow the assessment of what animals know about each other and how they use the information to own advantage. Here, we present data on wild vervet monkeys using a paradigm we believe can be used on various other species. After training adult females to approach their personal box, identifiable by a unique color patterns, to access high quality food, we placed two boxes in close proximity to create potential for conflict. In a previous study, we found that high ranking wild vervet monkey females offer tolerance and coalitionary support in exchange for being groomed. Here, we therefore asked if lower ranking vervet female partners were aware of such decision rules by: 1) testing if subordinates were more likely to approach their box after they had groomed the high-ranking box partner and 2) to enter a conflict in the presence of their previous higher ranking grooming partner. While we found some effects of age and audience composition on decisions, we found no evidence for vervets being able to incorporate the effects of recent grooming in their decisions. However, we will discuss that if positive results were found in any species, they would imply an understanding on what affects decisions of other individuals. In the context of coalitionary support, positive results would suggest an understanding of how to use social tools against third parties.

7.2. INTRODUCTION

Living in social groups creates plenty of opportunities for cooperation but also for competition. Following pioneer work from Humphrey (1976), the Machiavellian intelligence hypothesis (Byrne and Whiten 1988; Whiten and Byrne 1997) proposes that the social complexity within a group promoted the evolution of specific advanced cognitive processes and correspondingly large brains. On the proximate side, it is hence a major task to identify the cognitive processes underlying social behaviour in a variety of species, in order to create a data base that allows testing for potential links between social cognition and brain (part) size/complexity.

Some subfields of social cognition have made substantial progress in the past 25 years. For example, there has been plenty of research on social learning (Heyes 1994; van de Waal et al. 2013; Aplin et al. 2014; see Galef and Heyes 2004 for a review). Also some basic requirements for sophisticated social strategies are relatively well documented, such as third party relationship knowledge. In primate species, chimpanzees (Slocombe and Zuberbühler 2007), baboons (Cheney et al. 1995; Bergman et al. 2003; Kitchen et al. 2005), macaques (Silk 1999), capuchin monkeys (Perry et al. 2004), mangabeys (Range and Noë 2005) and vervet monkeys (Borgeaud et al. 2013) recognise other individuals' ranks within their group. Such knowledge about third party relationships has also been shown in spotted hyenas (Engh et al. 2005), fish (Bshary et al. 2014) and birds (Paz-y-Miño et al. 2004), suggesting that it is widespread throughout various taxa. However, the ability to use social knowledge in a strategic way for its own advantage, as suggested by the Machiavellian intelligence hypothesis, has been largely anecdotal (Cheney and Seyfarth 1990; Byrne and Whiten 1988; Whiten and Byrne 1997) and successfully tested in only few studies (Wheeler 2009; Slocombe and Zuberbühler 2007). For example, victim chimpanzees modify their distress call during conflicts if there is a potential supporter that outranks the aggressor (Slocombe and Zuberbühler 2007).

The most enigmatic cognitive processes are linked to the question to what extent animals have a concept of others being agents with own goals, i.e. in how far animals have a theory of mind which is the capacity to attribute mental states such as beliefs and desires to oneself and others (Premack and Woodruff 1978; see Heyes 2015 for a review). A major conceptual advancement has been the recognition that theory of mind is an umbrella term for a diversity of cognitive processes (Tomasello et al. 2003). There is some evidence for experience projection (Emery & Clayton 2001) and perspective taking (primates: Tomasello et al. 1998; ravens: Bugnyar et al. 2004). Nevertheless, progress has been comparatively slow despite major research efforts (Povinelli and Eddy 1996; but

see also Povinelli and Vonk 2003). A recognised major hindrance is the lack of suitable, generally applicable experimental designs (Heyes 1998). For example, the food caching paradigm used by Emery and Clayton (2001) cannot be used on the vast majority of species that do not cache food. Other paradigms often cannot exclude behavioural cueing as a simpler explanation for correct behavioural choices (Hare et al 2000; Bungnyar and Heinrich 2005). The standard human developmental psychology test for theory of mind, the ‘Sally-Anne test’ (Wimmer and Perner 1983), involves several preparatory steps that make its application to animals extremely difficult. However, we must test for such processes in order to assess in how far social strategies such as coalition formation and forms of manipulation such as tactical deception are based on sophisticated social cognition. There is thus a clear need to develop experimental designs that can be used on a variety of species with relative ease, i.e. equivalents to artificial fruits in social learning research (Whiten et al. 1996) and playback techniques for third party relationship knowledge (Bergman et al 2003).

From a cognitive point of view, agonistic interactions are of particular interest for experimentation as they can reveal the social knowledge of the different parties involved and hence may help understanding the species’ cognitive capacities. Indeed, starting a conflict may have many behavioural consequences that can also involve third parties, such as coalition formation (Harcourt 1992; de Waal 1982; Cheney and Seyfarth 1990), redirection of aggression (Cheney and Seyfarth 1990; Aureli and van Schaik 1991) or consolation (de Waal and van Roosmalen 1979; Aureli et al. 2002). In primates, it is also known that conflicts are affected by grooming patterns. Grooming is not only used to reconcile with valuable partners after a conflict and hence reduces the risk of further aggression (Aureli and de Waal 2000) but it is also traded against other commodities like coalitionary support (Seyfarth 1977; Seyfarth and Cheney 1984; Hemelrijk 1994; Cheney et al. 2010; Borgeaud and Bshary 2015) and/or tolerance (Henzi and Barrett 1999; Watts 2002; Ventura et al. 2006; Port et al. 2009; Tiddi et al. 2011; Borgeaud and Bshary 2015). In conclusion, decisions and consequences of seeking conflicts involve many degrees of freedom. Therefore, it is conceivable that higher level cognitive processes may allow individuals to make superior evaluations of costs and benefits, by assessing a potential opponent’s intention, which in turn will depend on various factors like identity, rank, and relationships quality (Wittig and Boesch 2003). So far, correctional data suggest some form of awareness of grooming effect on tolerance in macaques (Ventura et al. 2006) and on future support in chimpanzees (Koyama et al. 2006). However, experimental evidence are still lacking.

Here, we provide an experimental paradigm we used to test in how far wild vervet monkey females are capable of anticipating how recent grooming interactions

affect the behavioural decisions of partners. In brief, females were first trained to recognise their personal box containing high quality food by unique colour patterns. Only if the owner touched the box, it would be opened with remote control by the experimenter (following Fruteau et al 2009). The following experiments involved placing two boxes at close distance, inducing the risk of conflict. In a previous paper, we used this paradigm to show that recent grooming affects the behaviour in two ways: the more dominant behaves selectively more tolerant when paired with the subordinate, and both are more likely to support the recent partner if around when she starts a conflict against a lower ranking third party with which she was matched in a box trial (chapter 5, Borgeaud & Bshary 2015). We could also document that tolerance is reduced if the audience (individuals within 10 m) contains individuals that outrank either both or the lower ranking partner (chapter 6, Borgeaud & Bshary unpublished). Reduced tolerance makes sense from a strategic point of view because in vervets, coalitionary support occurs and is given exclusively to the dominant individual (with the exception of mother infant pairs; Cheney & Seyfarth 1990, Borgeaud & Bshary 2015). This support pattern has been documented in other primate species (Chapais et al. 1991; Silk et al. 2004; Wittig et al. 2007), with chimpanzees being a notable exception (de Waal 1982; de Waal and Luttrell 1988). Now that we know how recent grooming and audience composition affects the decisions of dominants about tolerance and coalitionary support, we can ask whether subordinates know about these effects. If this was the case, such knowledge should become visible as an adjustment of their own decisions. First, with respect to tolerance, subordinates should be more likely to dare approaching their own box after recent grooming of the dominant partner as the benefit-cost ratio of taking the risk is positively affected. In addition, subordinates should assess the audience: as the presence of higher ranking third parties has a negative effect on tolerance, their presence should reduce the likelihood of subordinates approaching their own box. Second, with respect to coalitionary support, individuals should be more likely to aggress a lower ranking female at a neighbouring box if the audience contains the recent grooming partner as long as she also outranks the target. This is because the increased probability of receiving coalitionary support will make the aggression on average more successful at lower risk of own injury (Cheney 1977) but should allow the reinforcement of rank relationships. Importantly, such behavioural adjustments cannot be based on behavioural cueing: the potential partner will not indicate its willingness to join a coalition before the conflict is already initiated. Positive results would therefore support the notion that vervet monkeys have some knowledge how recent grooming affect the decisions of higher ranking individuals and use this knowledge to gain access to high quality resources and to use dominants as social tool against third parties.

7.3. METHODS

7.3.1. Study site and species

Experiments were run from December 2012 until December 2014 at the Inkawu Vervet Project, Mawana Game Reserve, Kwazulu Natal, South Africa. Subjects were 16 adult females and 1 sub adult female from three habituated groups of vervet monkeys. In 2014, without infants, the first group, Ankhase, included 27 individuals (4 adult males, 9 adult females, 14 sub adults and juveniles). The second group, Baie Dankie, included 38 individuals (4 adult males, 11 adult females, 23 sub adults and juveniles) and the third one, Noha, included 35 individuals (4 adult males, 11 adult females, 20 sub adults and juveniles).

7.3.2. Training

Individuals were trained to approach and get access to a small reward (piece of apple) from a wooden box that could be opened from a distance with the help of a remote control by the experimenter. Boxes were covered with a colour and shape coded cover, so that each box looked different from the others. As many adult females as possible got trained to access only one box by simple trial and error, the experimenter opening the box whenever the right individual touched the right designated coloured box. An individual was considered as trained whenever its first choice between its own box and a simultaneously presented alternative box was always correct within a training session and throughout multiple training sessions. A considerable number of females either did not dare approaching the boxes or failed to learn. In the end, we had six subjects (including one subadult) in the Ankhase group, four in the Baie Dankie group and seven in the Noha group.

7.3.3. Data collection

During the experiments, two boxes were brought within 5 meters of each other. Within such distance and in such food related situations, vervet monkeys are particularly intolerant towards each other (van de Waal unpublished observations). By choosing specific combinations of boxes, we could therefore selectively create the potential for conflicts between two individuals, one of which would be more dominant. The distance between boxes varied from 1 to 5 meters between pairs as some individuals were more tolerant than others: dominants were more tolerant towards partners that were scored as bonded, and there was also a group effect in that females in the Ankase group were generally more tolerant towards each other than females of the other two groups were (Borgeaud & Bshary 2015). The distance was kept constant within each pair of individuals throughout the trials. During preliminary trials we assessed a suitable distance for each pair of individuals, i.e. the maximum distance between boxes that consistently generated a conflict in the absence of recent prior grooming. This criterion was set as it would

yield the greatest power to detect a positive effect of recent grooming on tolerance if it existed. For each trial, we recorded the distance between the two boxes, who approached her box and if both did also which individual arrived first at the box. If the second individual approached its personal box, we recorded the outcome of the interaction as tolerance (i.e. absence of any aggression) or conflict. A conflict could vary in intensity but was coded as such if the dominant individual at least stared, displaced or prevented the subordinate from getting the reward. If the individuals remained nearby we reloaded the boxes maximally another two times. This rule also applied to cases in which an individual did not come or approached but not all the way. We waited two minutes before reloading the boxes for another trial.

7.3.4. Data and statistical analyses

To test if vervets are aware of an increase of tolerance after grooming, we compared the frequency with which subordinate individuals dared approaching their box when the dominant individuals arrived first between trials in which they had recently groomed the dominant and trials in which they had not groomed the dominant. To test if vervets are aware that previous grooming partners are more likely to provide support against a lower ranking third party, we compared the frequency of conflicts in the presence versus absence of the dominant's previous grooming partner. Importantly, the grooming partner had to be within 10 m and she had to outrank either both boxes' partners or at least the subordinate.

Statistics were performed in R (v.3.0.1). First each model was compared to a null model, confirming the robustness of all our models. We ran GLMM's with an analysis of deviance (Type II) using the function "glmer" of the R package "car" and "lme4". For the awareness of increased tolerance analyses we considered for each pair if subordinates dared approaching or not (dependent variable and binomial data) over all first trials. The "situation" (PG, DG, NoG), "bondedness", "age" and "group identity" were all considered as fixed effects within the model. To account for pseudoreplication, as individuals were tested within different pairs multiple times across situations (sessions) and sometimes multiple times a day, we introduced the random factors for couples and session inside each couple. We then ran a post hoc test of Linear Hypothesis to compare each group with each other using the function "ghlt" of the package "multcomp". For the awareness of increased support, we considered for each pair if the dominant individual aggressed or tolerated the subordinate (dependent variable and binomial data) over all trials in the presence or absence of the previous grooming partner. In this case, "presence", "audience" and "group identity" were considered as fixed effects and we introduced the random factors for couples and session inside each couple as well as

the number of interactions the dominant individual (i.e. making the decision) experienced per day.

7.4. RESULTS

7.4.1. *Vervet monkeys do not seem to be aware of increased tolerance*

We found that subordinates did not dare approaching more often after they groomed the dominant box partner (Situation: $\chi^2=0.02$, Df=1, P=0.87; Fig. 1a). However, we found that there was a group identity effect ($\chi^2=8.49$, Df=2, P=0.014), the AK group generally daring approaching more often than the other groups. A post hoc test indicated that only the AK and BD significantly differed from each other (AK-BD: Z=-2.61, P=0.024; AK-NH: Z=-2.00, P=0.11; BD-NH: Z=0.84, P=0.67). As the presence of a dominant audience affects tolerance and hence might have influenced the subordinates' behaviour, we tested if they dared approaching more easily after they groomed the box partner and in the presence of a low audience (i.e. lower ranking than both box partners). Similarly to the previous results, we could not find any significant effect of grooming on daring approaching ($\chi^2=0.08$, Df=1, P=0.77). Furthermore, when considering the age of the box partners, we found that older subordinates dared approaching more often towards younger dominants at their box ($\chi^2=5.09$, Df=1, P=0.024; Fig. 1b).

7.4.2. *Awareness of coalitionary support or audience effect?*

We found that in the presence of their previous grooming partner high-ranking individuals were significantly more likely to enter a conflict than in the absence of it (Presence: $\chi^2=4.27$, Df=1, P=0.038; Fig. 3) and in this case, there was no difference between groups ($\chi^2=1.65$, Df=2, P=0.43). However, we also found that apart from the grooming partner the presence of an audience that outranked either both box' partners or the subordinate significantly increased the probability of conflict ($\chi^2=65.42$, Df=1, P=0.019; Fig. 2).

7.5. DISCUSSION

We had asked in how far female vervet monkeys can predict how recent grooming interactions affect decisions of partners and use this knowledge to own advantage. Addressing this question was possible because we had found in a previous experimental study that vervet monkeys subordinate individuals exchange grooming given to a dominant against tolerance and also coalitionary support but only against a lower ranking third party (Borgeaud and Bshary 2015). We therefore asked if vervet monkeys were aware of such decision rules in a reciprocity context. Our main result is that we failed to provide any positive evidence for such awareness. Several results show that vervet monkeys assess the situation and

respond in a flexible way: older subordinates were more daring in the presence of younger dominants, subordinates in the more tolerant Ankhase group were more likely to approach their boxes, and higher ranking individuals were more likely to initiate a conflict if the audience contained a suitable coalition partner (Borgeaud and Bshary unpublished, chapter 6). This latter scenario included the presence of a previous grooming partner but without evidence for an even higher probability of conflict. Below, we first discuss methodological issues of our study and then turn to the question what could have been concluded with respect to potential underlying cognitive processes if results had been significant.

7.5.1. Methodological considerations

The default explanation for our negative results is that vervet monkey females are not able to incorporate the effects of recent grooming on the behaviour of partners into own decisions regarding social challenges. Nevertheless, we note that there are some shortcomings in our study that further experiments are needed to re-evaluate their cognitive abilities in this context.

First of all, it is likely that our negative results might be due to our small sample size. When considering only cases where the dominant arrived first at the boxes we drastically reduced the statistical power in order to test the subordinates' awareness about increased tolerance. To test the awareness about coalitionary support the sample size was even smaller, especially when in order to discriminate grooming and audience effects, we considered only cases with both the presence of the previous grooming partner and a high-ranking audience (n=17). It is also possible that our experimental design might not have been appropriate to test our hypothesis. Indeed, the boxes were placed within a very short distance of each other (i.e. 1 to 5m) and the reward was of high quality and could also be monopolized. For example, a direct approach from a subordinate towards a dominant in this case might have been considered as a potential aggression and as vervet monkeys' hierarchy is very strict, subordinates usually rarely challenge a higher ranking individual (Cheney and Seyfarth 1990). Consequently, because of the general high level of aggression, especially in the presence of an audience that outranks the target, it was not possible to test the subordinates' awareness about dominants' decision rules in either tolerance or coalitionary support contexts. A follow-up study would need to take these parameters into consideration and a good solution would be to increase the distance between the boxes to reduce the default proportion of aggression. If such level is decreased, if possible below 50%, in a control situation (i.e. without recent grooming) and in the presence of a high-ranking audience, then the influence of previous grooming should be measurable as an adjustment of the subordinates' behaviour.

7.5.2. Implications of potential future positive results

Potential positive results in future studies would have to be analysed very precisely and discussed very cautiously in order to make sure that these are the consequence of a cognitive awareness rather than the capacity from the subordinates of reading behavioural/visual cues given by the dominants. When testing for the tolerance awareness, it would be important to assess if the dominant while approaching the boxes is less likely to look at the subordinate after a recent grooming than in a control situation. During the approach some aggression from the dominant, commonly stares, could happen and consequently provoking the subordinate to stop approaching. However, from our perspective such behaviour did not seem to vary across grooming situation and usually dominants focused on their box while approaching, which would suggest that no visual cue is given by the dominants. Our negative results would also support this latter hypothesis as animals are usually very good at interpreting behavioural cues of their conspecifics (Dall et al. 2005) and if they would exist it is likely that subordinates would be able to read them accurately and manipulate their behaviour in consequence. In the case of support, it is very unlikely that the audience would be able to give any visual cue to the dominant to indicate a potential willingness of support, so we are rather confident that positive results would indicate some kind of awareness.

Grooming behaviour is usually linked with the release of beta-endorphins which are responsible for a decrease of stress (Keverne 1989). In this case, one could imagine that after a grooming bout and especially in the presence of the previous grooming partner, individual are “more daring” or “more aggressive”. It would be therefore important to test such behaviour is not only the consequence of a physiological modification. An important control to test the subordinate awareness about tolerance and support would be to compare reciprocated versus non reciprocated grooming within the same pair. In this case, one could imagine that if the subordinate groomed the dominant or if the grooming is reciprocated, the subordinate should dare approaching/aggressing more easily than if only the dominant groomed the subordinate. To assess awareness of tolerance, it would be important to test if the subordinate that groomed the dominant would dare approaching more easily than if she groomed with a third party, which ideally would be around. If the presence of an audience has an influence on the probability of conflict, it would be important to always have a high-ranking audience when testing for awareness of support.

If simpler mechanisms such as behavioural cues and physiological positive enhancement can be ruled out, positive results would very likely indicate some capacity to anticipate the behaviour of interaction partners. Such sophisticated behaviour could be achieved through mental representation of the partner's

intention and would resemble a simpler form of theory-of-mind. This would correspond to what has been suggested in chimpanzees: the capacity of “knowing what others know” (Crockford et al. 2012; Schel et al. 2013). Such awareness could be used in a more strategic way for present or eventually future decision making, which has been suggested by various studies, including Seyfarth’s model (1977) and would perfectly fit the Machiavellian intelligence hypothesis (Byrne and Whiten 1988; Whiten and Byrne 1997). So far, correctional data suggest an appropriate assessment of tolerance after grooming in macaques (Ventura et al. 2006), some awareness of grooming effect on future support in chimpanzees (Koyama et al. 2006) but not in mandrills (Schino and Pellegrini 2010). Further experimental evidence is therefore still needed.

7.6. CONCLUSION

Our experimental design could be easily applied to other species in which dominant exchange tolerance and/or coalitionary support against grooming by a subordinate. If such trading appears to be positive within the studied species, one could think about testing for the subordinates’ awareness of dominants’ decision rules. While we used grooming as a currency, other social parameters could be tested such as proximity or sex. An important point would be to establish a standardised methodology across species that could allow to assess the panel of their cognitive abilities, which could ultimately linked with brain/neocortex size.

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FIGURES

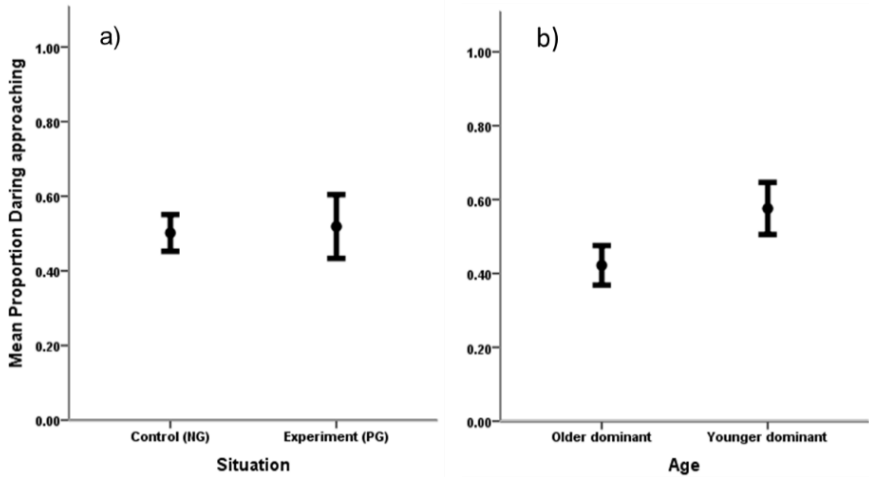


Figure 1. The effect of grooming and age on daring approaching from a subordinate. a) Mean proportion of daring approaching when the dominant is already at the boxes in the situations where the box partners did not have any previous grooming interaction (NG) and where the box partners did have a previous grooming interaction (PG) and b) when the dominant individual is either older or younger. Errors bars represent +/- 1 standard error.

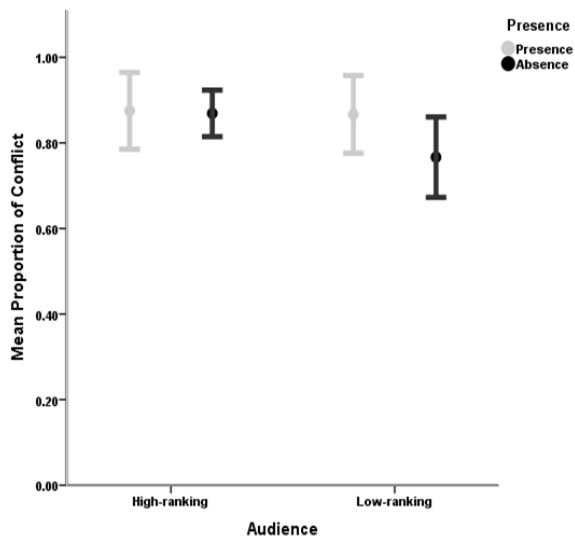


Figure 2. Influence of the presence of the grooming partner within the audience on tolerance. Mean proportion of coalitional support in the presence (P) or absence (A) of the previous grooming partner within 10m and with the presence of a high (H) or low-ranking (L) audience. Errors bars represent +/- 1 standard error.

GENERAL DISCUSSION

D.1. SUMMARY

In the first Chapter, I propose two new methods for analysing the stability of social networks by integrating the natural demographic variation of three vervet monkeys (*Chlorocebus aethiops*) groups. I suggest that such methods can be used to quantify social complexity. The results from method 1 (i.e. GLMM) suggest that demographic variation has a significant influence on both the individual centrality and the stability of dyadic relationships, particularly when individuals enter the group. The separate analyses between sexes suggest that females and juveniles had a stronger influence on the network stability than males, in particular within the grooming network. With the method 2 (RSiena), with respect to the social network structure, I found a triadic closure effect (i.e. the friend of a friend is a friend) in a single group, while degree of popularity (i.e. preference of association with well-connected individuals) was present in all three groups. Individuals prefer to bond with conspecifics of same sex and matriline but other results such as hierarchy and age were not consistent among groups. Similarly, I did not find among-group similarities with respect to relationship dynamics (i.e. how quickly relationships are formed or terminated according to sex, matriline, hierarchy and age). Interestingly, both methods indicate strong among-group variation, which is surprising given the overlapping home ranges of the three study groups. This suggests that individual differences or degree of relatedness might be causing this variation rather than environmental differences experienced by groups. Taken together, results from both methods suggest that natural demographic variation influences the stability of a social network through time and that such variability might represent an important cognitive challenge for group living species which must keep track of various types and ever-changing relationships. Such challenges might be the driver of more advanced cognitive adaptations as suggested by the Social Brain (Dunbar 1992) and Machiavellian intelligence hypotheses (Byrne and Whiten 1988; Whiten and Byrne 1997).

In Chapter II, I tested the social knowledge of vervet monkeys, specifically, their knowledge about third party rank relationships. Rank hierarchy knowledge has been successfully observed in wild baboons (*Papio hamadryas ursinus*) (Bergman et al. 2003) using rank reversal playbacks. I reproduced similar experiments on the same three groups of vervet monkeys as in Chapter I to assess whether vervets can also recognise rank relationships despite their smaller brain size. I also wanted to test if this capacity was common to all group members. Therefore, I tested 1) females' knowledge about the female hierarchy, 2) females' knowledge about male hierarchy, 3) males' knowledge about the female hierarchy and 4) juveniles of

different sex and age's knowledge about the female hierarchy. Rank reversal playback experiments showed that females looked longer towards the speakers after an incongruent (i.e. rank reversal) sequence than after a congruent one (i.e. in line with the hierarchy). These results suggest that females know both the female and male hierarchies within their group. Surprisingly, both males and juveniles seemed to lack knowledge about the female hierarchy. Males that did spend a relatively long time in a group (i.e. two years) did not perform better than males that had arrived 6 months before the experiments and there was no difference of age or sex within juveniles. These results suggest that some sex and developmental differences exist in third party rank relationship knowledge in vervet monkeys.

In Chapter III, I investigated whether vervet monkeys strategically use their social knowledge. Using a novel experimental design, I tested a) whether dominant female vervet monkeys exchange tolerance for grooming from a subordinate and b) if grooming is also exchanged for coalitionary support. Following the emotional bookkeeping theory (Schino 2007), I also tested how long-term relationships influence tolerance and coalitionary support by comparing bonded pairs with non-bonded ones. My results suggest that vervet monkeys do exchange grooming for tolerance and also coalitionary support, although only against a third party that is lower ranking than both allies. Data on bondedness suggests that bonded individuals are more tolerant towards each other, but this did not influence coalitionary support. I also did not find any evidence of generalised reciprocity (Pfeiffer et al. 2005; Rutte and Taborsky 2007). Results suggest that vervet monkeys use short-term reciprocity but also emotional bookkeeping when it comes to decision rules about reciprocal behaviour but they do so in accordance with the hierarchy.

While running the experiments mentioned above, I had the opportunity to assess the extent of variability in the outcome of an interaction (i.e. tolerance or conflict). Additional analyses revealed that the presence of an individual outranking the potential target (i.e. subordinate at the boxes) decreased the probability of tolerance even after the box partners had groomed each other. I also found an interaction between the relative audience rank and the grooming situation. Aggressors were also more likely to produce calls, which usually serve as recruitment for help. I consequently asked if the aggressive behaviour in the presence of a dominant audience is due to the fear of being punished by the dominant if the individual is tolerant towards its box partner. However, such explanation seems rather unlikely as I observed only one case of aggression from a dominant towards a tolerant individual. This suggests that 1) individuals take into account the audience and adjust their behaviour consequently, 2) individuals are aware of the general rule "support the higher ranking", 3) dominant individuals' decisions rely mostly on

recent grooming interactions, while 4) a middle-ranking individual has to weigh the costs and benefits of aggression versus tolerance. Taken together, these results suggest that female vervet monkeys use their third party rank relationship knowledge strategically to reinforce their dominance rank over lower ranking subordinates.

D.2. THE BIG PICTURE

D.2.1. AN EXPERIMENTAL APPROACH TO COGNITION AND COOPERATION

Results from this thesis have broad implications for studying social cognition and cooperation. Both the Social brain (SBH) and Machiavellian intelligence (MIH) hypotheses propose that selective pressure imposed by the social environment, such as competition and cooperation, selected for respectively larger brains and advanced cognitive processes. While previous correlational studies provide some evidence of a link between social complexity, cognitive processes and, ultimately, brain complexity, we still lack a clear picture of why some species differ in their cognitive abilities. Importantly, the lack of a coherent framework and methodology for measuring social complexity and intelligence hinder comparative studies and progress in the field. Although many abilities described by the Machiavellian intelligence hypothesis seem to be present in a variety of species/taxa, it is important to distinguish between processes based on associative learning from those that require more elaborate cognitive capacities. For example, an interesting experimental study found that highly social pinyon jays (*Gymnorhinus cyanocephalus*) outperform less social western scrub-jays (*Aphelocoma californica*) on tests of transitive inference (Bond et al. 2003) emphasising the importance of comparative studies between species. The general aim of this thesis was to develop and apply an experimental design that can be applied to a variety of species and allows the quantification of different cognitive abilities within an experimental design. If, ultimately, different experimental approaches are combined into a comprehensive framework, it may be possible to correlate quantitative measures with brain complexity and explicitly link findings to predictions of the Social brain hypothesis (Dunbar 1992, 1998; Barton and Dunbar 1997).

My results provide a valuable contribution to a growing body of evidence suggesting that, despite their relative small brain size (Stephan et al. 1981), vervet monkeys have well developed social knowledge and sophisticated cognitive abilities. Previous studies provide evidence for individual, kin and vocal recognition (Cheney and Seyfarth 1990) and transmission of knowledge through social learning (van de Waal et al. 2010, 2012, 2013). Females' rank hierarchy is

usually very stable while males' is more prone to variation because of the constant migration (Cheney and Seyfarth 1990). Playback experiments also showed that vervets understand the rank of third parties in relation to themselves (Cheney and Seyfarth 1982). As the mother usually support her youngest offspring, juveniles of the same matriline have an inverted rank compared to their age (Cheney and Seyfarth 1990). My results confirm that female vervet monkeys have complete knowledge of both female and male hierarchies. While it might be limited to the phylopatric sex, such knowledge is necessary for the development of strategic social behaviours, especially in despotic societies such as vervet monkeys. In a competitive context, vervets form coalitions against a third party and usually support is given to the higher ranking individual, which might serve as a rank reinforcement or decrease the risk of own injury (Cheney and Seyfarth 1990). The results presented in this thesis indicate that females, indeed, use the audience and their third party rank relationship knowledge to assert dominance over subordinates. In a cooperative context, vervets exchange grooming for other commodities varying the exchange rate, following the "biological market" theory (Fruteau et al. 2009). Previous playback experiments suggested that grooming is exchanged for coalitionary support (Seyfarth and Cheney 1984), although this finding was based on the time spent looking towards the speakers without any real intervention from the potential supporter. My results confirm such an exchange, and also indicate the presence of trading of grooming for tolerance from a dominant. This exchange can be considered as an example of direct reciprocity, but may also rely on long-term bondedness (i.e. emotional bookkeeping) as bonded individuals are more tolerant towards each other. I did not find evidence that individuals are aware of the dominant's decision rules, which would have corresponded to some attribution of mental state (Premack and Woodruff 1978; Call and Tomasello 2008). However, within a competition context, the cognitive processes that females use perfectly fit the Machiavellian intelligence hypothesis in its stricter sense, which implies that strategic social behaviours were developed in order to increase one's own benefits (de Waal 1982; Byrne and Whiten 1997). What remains unexplored is how these abilities correlate with brain complexity and, consequently, how the results of this thesis are linked with the Social brain hypothesis (Dunbar 1992, 1998).

D.2.2. DYNAMIC SOCIAL NETWORK ANALYSES: A NEW WAY OF QUANTIFYING SOCIAL COMPLEXITY?

Keeping track of the various relationships that exist among the different group members is necessary to be socially competitive and, ultimately, survive and reproduce. In despotic societies, this includes not only being able to assess the type of relationship (i.e. kinship, bondedness, rank relationship) between two

individuals, but also to what extent these relationships change through time as a consequence of the natural demographic variations. Although group size is often used as a proxy of social complexity (Dunbar 1992, 1995), it fails to precisely qualify and quantify the complexity of the various group relationships. The lack of correlation between group size and the frequency of social learning is a good example of this shortcoming (Reader and Laland 2002). Alternatively, bondedness, based on the type of mating system or the formation of close bonds in primates (Shultz and Dunbar 2007; Dunbar and Shultz 2010), correlates positively with neocortex size. However, describing, quantifying and classifying such relationships is challenging as it partially relies on assessing an individual's emotional state. A more recent study suggested using the number of differentiated relationships of an individual, in other words, the number of relationships that can be distinguished (Bergman and Beehner 2015). While this method still needs to be tested, it might be applicable in various taxa and similar suggestions for the measurement of social complexity are needed (Kudo and Dunbar 2001; Lehmann and Dunbar 2009; Stanley and Dunbar 2003).

Social network analysis offers a new, potent tool for investigating the evolution of complex social systems. Previous encouraging work has found a positive correlation between grooming clique size based on social network analyses and neocortex size (Kudo and Dunbar 2001). However, this approach limits analyses and comparisons of social complexity to social species that engage in grooming behaviour. While many studies have focused on the analysis of static networks, a growing body of studies have tried to integrate a dynamic approach, which is more biologically realistic as the composition of a social group changes regularly in nature (Connor et al. 2001; Henzi et al. 2009; Ramos-Fernandez et al. 2009; de Silva et al. 2011; Barret et al. 2012; Holekamp et al. 2012; Hobson et al. 2013; reviewed in Pinter-Wollman et al. 2013). Dynamic social network analyses seem to be an appropriate tool to quantify the quality of social relationships and consequently social complexity. Additionally, these methods are more easily applicable to a diversity of taxa, including less social species since proximity or other bondedness measurements could be considered either as independent or combined parameters. Although these methods are promising, we lack an adequate way of measuring effect sizes, which would allow comparative analyses both within and, potentially, across species. Correlations between time periods as presented in method 1 of the first Chapter could eventually be used as an effect size and therefore be a good starting point for comparative studies. Results from Chapter I generally indicate a strong influence of demographic variation on network stability, suggesting that relationships vary throughout time. This supports the idea that an individual's social environment is, indeed, complex and may

promote the evolution of both strategic social behaviours (Byrne and Whiten 1988; Whiten and Byrne 1997) and brain complexity (Dunbar 1992, 1998). Interestingly, all three methods used in Chapter I (Glm, correlations and RSiena) indicate notable among-group differences. This suggests that establishing species-specific or even population-specific characteristics of social networks is challenging but could be tackled by integrating multiple groups. However, while such variation might result from differences in degree of relatedness, individual strategies, group size or sex ratio, it nonetheless suggests that individuals, especially those from the migrating sex, must show high levels of cognitive flexibility to adapt successfully to their social group. Quantifying such among-group variation could be a way of measuring cognitive flexibility. On the other hand, pair-bonding in vertebrates and stable relationships in primates positively correlates with neocortex size (Shultz and Dunbar 2007). While these findings seem contradictory with the results presented here, it might actually reflect the high complexity of a social environment. My results indeed suggest that some relationships are stable while some might vary in quality according to the individuals' identity, rank or sex. Similarly, another study indicated that, depending on group size and kin, female baboons form more stable bonds with preferred partners while relationships with other partners were more ephemeral (Silk et al. 2012). However, having to remember relationships of different stability and quality is very likely to be cognitively challenging which would still fit with the argument a social environment is complex. It is however important to mention that first correlations between network dynamics and brain features will be highly exploratory as both stability and instability might simultaneously select for a higher brain complexity. Thus, it is clear that consistent data collection and measurement of bondedness is needed across species/taxa to understand the complexity linked to social relationships quality. Furthermore, while social network analyses seem to be a promising tool, it might be challenging to correlate such structure with advanced cognitive processes such as those described by the Machiavellian intelligence theory. One would have to think about a potential combined measurement with group size or number of differentiated relationships for example.

D.2.3. KNOWLEDGE ABOUT THIRD PARTY RANK RELATIONSHIPS MIGHT BE SEX AND AGE DEPENDANT

An important basic requirement for sophisticated social strategies is the knowledge of not only one's own relationships with all group members, but also those among other group members. In species with a rank hierarchy (i.e. despotic societies), recognising the relative rank of other individuals, also known as third party rank relationships, could be of a great individual benefit. For example, during conflicts, this knowledge might help in recruiting the most appropriate supporter. Obtaining

such information through eavesdropping (McGregor 2005) would be enhanced through the ability to use transitive inference and such capacity is present in various taxa (Seyfarth and Cheney 2015).

The results of the playback experiments in Chapter II indicate that females know both the female and male hierarchies. As females normally spend their whole life within their natal group, it is logical that they know the whole female hierarchy as it is usually maternally inherited and therefore very stable (Cheney and Seyfarth 1990). In contrary to some other species (Kappeler and van Schaik 2002), female vervets choose their mating partners (Keddy 1986; Andelman 1987) and therefore, knowledge of the male hierarchy may allow them to select males with high quality genes. In contrast, I did not find any evidence of female hierarchy knowledge in either adult males or juveniles. Given the number of females generally present in a group (i.e. up to 12), acquiring knowledge of the whole female hierarchy may take up too much time for it to be beneficial to males. Similarly learning the vocal identity of the different group members might also require too great time investment for males. However, a simpler explanation may be that males and juveniles do, in fact, know about the female hierarchy, but do not show any interest during the playbacks. For example, males usually refrain from intervening in female-female conflicts. On the other hand, females might intervene in male-male conflicts in order to support one of the opponents (Cheney and Seyfarth 1990). It is, therefore, important to develop experiments that allow us to discriminate between “not knowing” and “not caring” to test the extent to which knowledge about the hierarchy is actually sex/age dependent, and at what age such information is acquired. Although such experiments might be limited to captive individuals, using visual rather than vocal cues might be an interesting option that has been successfully used in macaques (Paxton et al. 2010).

Chapter II provides the first evidence for third party rank relationships knowledge between sexes and one of the few that focused on juveniles’ knowledge (Range and Noë 2005; Paxton et al. 2010). Our results demonstrate that playback experiments can be successfully performed in the wild and that female vervet monkeys not only vocally recognise different group members but also know about the two main linear hierarchies within their group. Such knowledge is cognitively complex and fits with the processes described within the Machiavellian intelligence hypothesis. In many primate species, it is assumed that individuals, especially the matriarchal sex, have knowledge of their group’s hierarchy. However, while these results suggest that knowledge of the hierarchy might be well developed in Old World monkeys, more similar experiments are needed to test how well spread this knowledge is across other primate taxa.

D.2.4. EVIDENCE FOR STRATEGIC SOCIAL BEHAVIOUR IN VERVET MONKEYS

D.2.4.1. Evidence for direct reciprocity

While strategic social behaviours described by the Machiavellian intelligence hypothesis might be more easily selected within a competition context, cooperative behaviour is not incompatible with the hypothesis as it also involves individual recognition and memory of previous interactions. In humans, both antagonistic cognitive processes that are cooperation and competition are processed in different brain areas (Lissek et al. 2008), suggesting that both might select for larger brain but in different ways. Cooperation has been extensively studied across taxa using a combination of natural observations, experiments in captivity and, most recently, experiments in the wild. However, showing the contingency of reciprocal events has been challenging and only conclusively demonstrated in a handful of studies (Seyfarth and Cheney 1984; Helmerijk 1994; Krams et al. 2008; Carter and Wilkinson 2013). Consequently, it has been suggested that cooperation in primates is mostly driven by positive emotions, in either the short- (i.e. attitudinal) (de Waal 2000) or long-term (i.e. emotional bookkeeping) (Schino 2007). Another recent hypothesis suggests that cooperation might have evolved through generalised reciprocity (Rutte and Taborsky 2007), which involves helping a random partner if if you yourself are helped by a random one. Except for humans, positive examples of generalised reciprocity have only been observed in rats (*Rattus norvegicus*) (Rutte and Taborsky 2007) and, more recently, capuchins (*Cebus appella*) and chimpanzees (*Pan troglodytes*) (Leimgruber et al. 2014; Claidière et al. 2015). In primates, a broad range of behaviours are considered to be cooperative such as coalition formations (see Bisonnette et al. 2015 for a review), cooperative hunting (Boesch 1994) and trading of grooming (Hemelrijk 1994; de Waal 1997; Watts 2002; Koyama 2006; Ventura et al. 2006; Schino 2007; Port et al. 2009; Tiddi et al. 2011).

Data provided by the new experiments outlined in my thesis indicate that vervet monkeys exchange grooming and coalitionary support in a contingent way, but that bonded individuals are also generally more tolerant towards each other, supporting the emotional bookkeeping theory (Schino 2007). However, the lack of a positive effect of bondedness on coalitionary support is rather surprising. Although this result could be due to the small sample size, it nonetheless corroborates evidence in baboons whereby a simulated fight between a random individual and a previous grooming partner provoked a stronger reaction (i.e. approach) from non-bonded individuals than from kin (Cheney et al. 2010). Such results represent an interesting challenge for the kin selection theory. However, as genetic results are still not available, I could unfortunately not control for such effect in this thesis. I

also did not find any evidence of generalised reciprocity, suggesting that the development of such helping behaviour might be restricted to very particular conditions.

These findings offer support for two different theories about cooperation: direct reciprocity (Trivers 1971) and emotional bookkeeping (Schino 2007), which rely on short-term or long-term helping behaviour. Most importantly, short-term reciprocity also occurs between related individuals. Although I lack genetic data, my index of bondedness likely encompasses most kin relationships. This experimental design is applicable to a variety of species and is likely to provide further evidence for reciprocity. However, I predict that evidence for reciprocity in other systems might depend on specific details of the social organisation, such as steepness of the hierarchy, kin structure or bondedness. This might bring about new insights into differences between species, especially with respect to cooperative behaviour.

D.2.4.2. Evidence for audience effect

As mentioned above, a great cognitive challenge facing group living individuals is when to cooperate or compete against other group members. While these two antagonistic forces seem to be a prerequisite for the evolution of brain size, an additional level of complexity is added when interactions occur within a communication network (McGregor 2005). As a consequence, individuals have to adjust their behaviour according to the presence of bystanders, which is known as the audience effect (Matos and Schlupp 2005; reviewed in Zuberbühler 2008). Many studies have focused on the influence of the audience on the production of food or alarm calls (Marler et al. 1986; Cheney and Seyfarth 1990) and copulation calls (Townsend and Zuberbühler 2009). However, few have examined audience effects on the manipulation of an individual's own behaviour in a competition context (Dziewieczynski et al. 2005). For example, victim chimpanzees are known to exaggerate their scream in the presence of an audience that outranks or equals the rank of the aggressor in order to solicit help (Slocombe and Zuberbühler 2007). More studies are needed across a range of taxa to assess how strategically third party and third party rank knowledge is used and most importantly one should try to quantify positive results.

With the individualised box experiments in Chapter III, I demonstrated that, like chimpanzees, vervet monkeys take into account the presence of an audience and can integrate audience and rank relationships in an competitive context. This suggests that individuals are aware that support should be generally given to the high-ranking individual, which could result purely from associative learning. However, they also strategically use their third party rank relationship knowledge

to assert their dominance on lower ranking individuals, which perfectly fits with the Machiavellian intelligence theory (Byrne and Whiten 1988; Whiten and Byrne 1997). This indicates that despite their rather small brain size, vervet monkeys are capable of behaviours that are considered as highly cognitive.

D.2.4.3. No evidence for awareness about decision rules

Despite being mostly correlational, evidence suggests that trading of grooming is well spread in primates. In despotic species, one could imagine that if subordinates were aware of positive effect of grooming given to a dominant, they could manipulate their behaviour accordingly to increase their own benefits. For example, a subordinate could groom a dominant to foresee or plan a future aggressive interaction. The extent to which this type of behavioural manipulation exists in primates is unclear: correlational data suggests such a capacity exists in chimpanzees (Koyama et al. 2006), but not in mandrills (*Mandrillus sphinx*) (Schino and Pellegrini 2010). My experimental design presented in Chapter III allowed me to test the knowledge that subordinates possess about the dominants' decision rules. In cases where the dominant arrived first at the boxes and if subordinates would be aware of an increase of tolerance after grooming, I expected that subordinates would dare to approach the boxes more often after they had groomed the dominant than if they had not. Similarly, a female should be more likely to enter a conflict in the presence of its previous grooming partner, if this partner outranks the subordinate (i.e. coalitionary support). Positive results would correspond to some form of theory of mind (Premack and Woodruff 1978), which is the capacity to attribute a mental state to another individual (but see below for discussion). In primates, except for humans, such capacity has only been shown in chimpanzees (Call and Tomasello 2008; Heyes 2014 for a review). My results, however, suggest that vervet monkeys do not incorporate recent grooming events in their decisions for tolerance nor support. However, I found that older subordinates were more daring when approaching younger dominants. I also found a negative effect of the audience rank (i.e. independently of the grooming partner) on tolerance during these interactions. Unfortunately, I was unable to discriminate between the relative importance of the presence of the previous grooming partner compared to the audience. To do so, distances between the feeding boxes should be appropriately adapted to decrease the baseline conflict rate. One could argue that my experimental design is appropriate to test the trading of grooming for tolerance between partners, but other commodities such as proximity or sex could be tested. I am also confident that such experiments could be performed in multiple species and results might reveal some variation across species. However, one would have to be careful with the interpretation of the results. To be indicative of awareness, the subordinate's behaviour should only be due to her awareness rather than visual

cues given by the dominants or a relaxed state from the subordinate after being involved in a grooming bout.

Taken together, results from Chapter III indicate that, as a social species, vervet monkeys have to find the right balance between cooperation and competition. However, my findings suggest that competition might be more likely to select for strategic social behaviours than cooperation as I could not find any sign of strategic behaviour within a cooperation context. Such results might be expected in despotic societies such as vervet monkeys where individuals have to cope with a rather steep and stable hierarchy. As the experimental design could be applied to many different species, it would be interesting to run comparative studies to test to what extent populations, species and potentially a range of taxa differ in their competitive and cooperative behaviours. One could expect that in more egalitarian societies, strategic behaviours might be more related to cooperation than to competition.

D.3. METHODOLOGICAL CONSIDERATIONS

Although this project began in 2010, we are still missing information about genetic relatedness among individuals. Such information would have allowed me to test not only both the long and short-term influence of kinship on tolerance and coalitional support, but also whether the rank of the audience influences the behaviour independently of kinship or not. For example, if the audience effect found in Chapter III is the consequence of the presence of a kin, results about strategic use of third party rank knowledge would have to be reassessed as support from a kin might rely on a simple rule of thumbs. Since tested females were of relatively different social ranks, I believe that the presented results would be similar while controlling for kinship. Nonetheless, this knowledge would have strengthened the confidence in my results.

An important improvement to the experimental design would be to create boxes with an automated release of food to reduce the need of manual reloading. This would enable the first individual to remain at its box while the box partner approaches. Unfortunately, the engineers at the University of Neuchâtel failed to develop a mechanism small enough to be carried in the field while powerful enough to ensure seamless food distribution.

The process of learning a personal box was relatively slow in my vervet populations. Indeed, some females, especially subordinates who had a limited access to the boxes, never really managed to learn the features of their personal box. Future studies in this or other species should allow sufficient time to train individuals and assess their visual acuity before beginning experimentation.

D.4. FUTURE RESEARCH

This work conclusively demonstrates the feasibility of conducting experiments on multiple groups in a natural habitat. It also highlights the extent of among-group variation that can exist within a population, suggesting that future studies should focus on multiple groups in order to assess the generality of a particular phenomenon. For the results presented in this thesis, it is very unlikely that an ecological factor promoted these differences as all three groups live in overlapping home ranges. Unfortunately, I cannot completely exclude an effect of kinship. However, the possibility that individuals have different strategies to cope with their complex social environment is an interesting avenue to explore. For example, in chimpanzees, tolerance within dyadic relationships ultimately has an impact at the group level (Cronin et al. 2014). Such tolerance might be transmitted through social learning. As experiments on social learning have been conducted successfully in many species, it could be possible to test whether personal strategies are, indeed, transmitted across generations or if they develop independently.

I presented two rather new methods that could be used to measure social complexity in various species and to some extent taxa. My hope is that similar methods will be commonly used in the future, although this remains to be seen. Nonetheless, it emphasises the fact that new methodologies for studying cooperation in the wild are needed, as are pilot studies to test their feasibility, efficiency and accuracy. Further work by statisticians and mathematicians is also needed in order to develop quantitative ways of comparing results between groups of the same species and ultimately between species.

Last but not least, I provide a new experimental design which can be used to test 1) reciprocity/trading of commodities among individuals, 2) audience effect and potentially 3) individual awareness of decisions rules underlying such trading. Although I only considered grooming behaviour, the trading of other commodities could also be tested using this design. Presently, a master student from the University of Neuchâtel is testing the reversed effect: i.e. if tolerance from a dominant is rewarded by grooming from a subordinate. While I could not test the level of awareness about decisions rules, I propose that increasing the distance between boxes to decrease the basal threshold of aggression might help testing this hypothesis with a minimal bias. Ideally, to distinguish between grooming and audience effect, experiments on coalitinary support would be run only in the presence of a high-ranking audience, independently of the grooming partner. However, such experimental conditions would be needed only in species where, similarly to vervets, audience has an effect on tolerance. Testing more individuals and possibly more groups would increase statistical power and also allow

observing whether different strategies exist across groups or populations. Studying the exchange of commodities between sexes would also be interesting. However, males might monopolise the boxes, thus preventing females from coming. Such experiments could easily be applied to different species in captivity and in the wild, but only to the condition that individuals can be fed. Comparative studies with similar social network analyses and box experiments would be interesting to assess how social factors such as kin structure, bondedness, dominance hierarchy, matriarchal system or group stability influence strategic social behaviours. Most importantly, experiments should consider how advanced cognitive abilities correlate with brain size or part of the brain. The role of social learning in Machiavellian intelligence has been well demonstrated in wild vervet monkeys (van de Waal et al. 2010, 2012, 2013). This research provides additional information about the general cognitive capacities of vervet monkeys. Future research should strive to correlate these and previous results with brain size, or parts of the brain responsible for the related cognitive processes. However, many social learning experiments also involve food, and, as a consequence, might be restricted to captivity or private reserves. Ultimately, it is necessary to understand how brain size evolution is linked to cognitive processes in a qualitative but most importantly in a quantitative way.

To conclude, our different experiments and social network analyses suggest that because of the natural demographic variation, vervet monkeys face cognitively demanding social challenges. However, they can generally cope with these challenges successfully by assessing third party relationships. Although vervets seem to develop strategic behaviours, including trading commodities and using the audience to assert their dominance, their awareness and anticipation of decision rules appears somewhat limited. Comparative studies on multiple species are needed to test the extent to which these results are good indicators of social complexity and the capacity of strategic social behaviour, such that between-species variation in performance may be predicted by differences in brain size and/or brain part size.

D.5. REFERENCES

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IVP monkeys 2012-2014

