INTERGROUP CONFLICT AND THE DEVELOPMENT OF COOPERATION IN JUVENILE VERVET MONKEYS

MADISON AVERY CLARKE
Bachelor of Science, University of Lethbridge, 2022

A thesis submitted
in partial fulfilment of the requirements for the degree of

MASTER OF SCIENCE

in

PSYCHOLOGY

Department of Psychology
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

INTERGROUP CONFLICT AND THE DEVELOPMENT OF COOPERATION IN JUVENILE VERVET MONKEYS

MADISON A. CLARKE

Date of Defence: July 12th, 2024

Dr. S.P. Henzi	Professor	Ph.D.
Thesis Supervisor		
Dr. L. Barrett	Professor	Ph.D.
Thesis Examination Committee Member		
Dr. T. Bonnell	Associate Professor	Ph.D.
Thesis Examination Committee Member		
Dr. C. Vilette	Postdoctorate	Ph.D.
Thesis Examination Committee Member		
Dr. D. Logue	Associate Professor	Ph.D.
Chair, Thesis Examination Committee Member		

DEDICATION

For my Nana, Judy, who showed me how to embrace my inner witch, taught me to never take anything too seriously, and always reminded me to breathe, go for a walk, and have a laugh.

For my Papa, Jim, who nurtured my love of the natural world by helping me find frogs, minnows, and grasshoppers because I wanted to see them up close, setting up a hummingbird feeder so I could watch them when they flew by for a snack, and helping me build the most luxurious birdhouses.

ABSTRACT

Little is known of the mechanisms that maintain risky cooperative behaviours in the absence of linguistically acquired cultural and social norms. This is especially the case when considering non-adult individuals who are theoretically assumed to be risk-averse, yet still incur the risks associated with cooperation. Using observational data from three troops of habituated wild vervet monkeys (*Chlorocebus pygerythrus*) and multilevel Bayesian models, I tested three explanations of how non-adult individuals in a non-linguistic species come to cooperate by participating in intergroup conflict. I first explored how individual attributes, social network position, and situational factors influence the likelihood and intensity of participation. I also tested how participation in intergroup conflict predicts whether non-adults will be groomed and if they will be groomed by their mothers. Thirdly, I investigated how similarities in intragroup social network and intergroup conflict participation network structures vary between the sexes across time. Overall, I found that non-adult participation in intergroup conflict is regulated by a myriad of individual, social, and situational factors.

CONTRIBUTIONS OF AUTHORS

This thesis includes collaborative work.

Chapter 3. This data chapter has been submitted for publication under the title "Social Induction and the Developmental Trajectory of Participation in Intergroup Conflict by Vervet Monkeys." The authorship list for the submitted version is as below. Dr. Henzi, Dr. Barret and I conceived the ideas. Dr. Bonnell, Dr. Vilette, Dr. Nord, Dr. Blersch, Dr. Young, and I contributed to the methodology. Dr. Bonnell and I conducted the formal analyses. Dr. Bonnell, Dr. Vilette, Dr. Nord, Dr. Blersch, Dr. Young, Dr. Henzi, Dr. Barrett, and I wrote and reviewed the manuscript. Dr. Henzi and Dr. Barrett contributed to funding acquisition and supervision of the project. All authors approved the final version of the manuscript.

M. Clarke[1,2], T.R. Bonnell[2,3], R. Blersch[2,4], C. Nord[2,4], C. Vilette[1,2], C. Young[2,5], S.P. Henzi[1,2] & L. Barrett[1,2]

[1]Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada

[2]Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, Pretoria, South Africa

[3]Department of Computer Science, University of Calgary, Calgary, AB, Canada

[4]Neuroscience and Behavior Unit, California National Primate Research Center, Davis, CA, USA

[5]Department of Psychology, Nottingham Trent University, Nottingham, UK

ACKNOWLEDGMENTS

When I joined the Banzi lab in 2019, I was a second-year undergraduate student who dreamed of studying wild animals but had no research experience and was terrified of anything to do with numbers, especially statistics. Thanks to the support from my amazing network of colleagues, family, and friends, I have managed to overcome my fear of numbers, get research experience, and work with wild animals. This thesis would not have been possible without them.

I am incredibly thankful to my supervisors, Peter Henzi and Louise Barrett, for accepting me into the lab, sending me to the field, for all of their expertise, and for trusting me with this project. Peter, thank you for your patience while we worked through the analyses, and most importantly, for teaching me how to braai. Louise, I truly appreciate our book exchanges and follow-up discussions. You have shown me that no reading is a wrong one and that sometimes the best conversations come from the worst books.

Christina Nord, Tyler Bonnell, and Chloé Vilette were patient with me every time I messaged them in a frenzy because my code would not work. Christina, none of this would have been possible if you had not hired me as your research assistant. You taught me many invaluable skills and challenged me to step out of my comfort zone. Thank you for taking a chance on me and for all of your guidance in the years that followed. Tyler, you showed me that modelling and coding can be fun and that it is okay when things go wrong. You are always ready with encouraging smiles when models go awry and excitement when they work as planned. Thank you for your patience and all of your help as I worked through my analyses. Thank you, Chloé, for introducing me to the magic of

the for loop and for guiding me through my analyses. I always felt much better after meeting with you.

David Logue, you provided me with spaces to present my work and take on leadership positions. Thank you for pushing me to take opportunities that I would have refrained from taking otherwise.

I have many people both in the Banzi lab and outside of it who have been there for me through the good and the bad. There are many members who are or have been in the lab during my research and I could probably write an entire book thanking each of them for all of their help and support. Writing my thesis would have been much harder without the members of my master's cohort, Dylan LaValley, Sam Booth, and Anna Quinn, who reminded me to take breaks and listened to my rants when code would not work. Anne Jones and Mabel spent many weekends in Waterton with me so I could train for the field and try to recreate the feeling of following baboons around. Leila Armstrong, Josie Mills, Christa Avram, and Lou, thank you for forming our coven and for all of our discussions on folklore and fairytales.

Thank you to Rhiannon Batstone, Sydney Chertoff, Tori Keeping, Casey Arnestad, and Caleb Bunselmeyer for getting me out of the house, providing moral support, and for all of the laughs. I am especially grateful to Sydney who got me through many things including long workdays by reminding me that if I can survive the field, I can write a thesis.

Thank you to everyone at Swebeswebe. The baboons reminded me every day why I wanted to become a scientist. I spent a lot of time trying to figure out the who, what,

why, and how of the baboons. I am grateful for the time I had with them. Thank you to Rich McFarland who allowed me to go to the site to see monkeys in the wild. Thank you, Jamie Flynn, for everything you did for me while I was in the field and after. Your banter kept me on my toes and taught me to always be prepared to justify my ideas. Wayne, Messiah, Betroth, Hedley, and Bernice, thank you for welcoming me into your family. Thank you to Andre and Nadea for keeping me safe during my field season and for showing me the amazing wildlife on the reserve.

Grandma and Grandpa, you supported me with your excitement for my work and by making sure I had everything I could possibly need for the field, including 180+ Band-Aids "just in case."

Rhonda Stuckey, you have supported me in many ways during both of my degrees. Thank you for your support, encouragement, and friendship.

Chelsea Woolf, you have been with me through it all. Thank you for being my person and for bringing so much light into my life.

To my pets, Oliver, Arlo, Tibbles, and Wallace. They were the best audience when I needed to talk through my ideas or practice a presentation. They made sure I took breaks to go for a walk, play fetch, or even just lay on the couch in a dog pile.

Finally, I am grateful to my parents who nurtured my love for animals and reading for as long as I can remember. Thank you for giving me the space to become my most authentic self.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

CI	Credible Interval
IGC	Intergroup Conflict
ESS	Effective Sample Size
EC	Eigenvector Centrality
RST	River Side Troop
PT	Picnic Troop
RBM	River Bend Mob

CHAPTER 1: GENERAL INTRODUCTION

1.1 Aims

Individuals in many species of primates live in groups that include both relatives and non-relatives. Wrangham (1980) argued that group living evolved to allow individuals to cooperate and so outcompete other individuals or groups for access to feeding patches. However, cooperation is vulnerable to exploitation by individuals who do not cooperate yet reap the benefits earned by those who do. There is a need to understand how cooperation persists despite the risks of exploitation by defectors especially in the absence of language and cultural norms. Previous research has primarily investigated the mechanisms that regulate adult participation in intergroup conflict (Arseneau-Robar et al., 2016; Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017), but non-adults have also been observed to participate (Heinsohn, Packer, & Pusey, 1996; Cords, 2007). My aims in this thesis, therefore, are to understand how cooperation develops in the absence of linguistically-imposed cultural norms. I propose to investigate the individual, social, and situational factors that lead to non-adult participation in intergroup conflict using long-term data from a population of wild vervet monkeys (*Chlorocebus pygerythrus*). What follows is an overview of relevant topics.

1.2 Defining Cooperation

Altruistic behaviour can be defined as an act that benefits an unrelated individual while imposing fitness consequences on the actor (Trivers, 1971). Here, fitness refers to one's ability to survive and reproduce, thereby contributing one's genes to future generations. Cooperation is inherently altruistic as it occurs when an individual incurs a cost (time or resources) for the benefit of other individuals, with no guarantee of a

commensurate return (Henrich & Henrich, 2006; Nunn & Deaner, 2004). We see examples of cooperation, such as cooperative breeding (Lukas & Clutton-Brock, 2017), reciprocal grooming (Silk & Boyd, 2010), and territory defence (Heinsohn, Packer, & Pusey, 1996; Bossema & Benus, 1985; Nunn & Deaner, 2004) in both primates and other mammals. Some forms of cooperation, such as territory defence, can be further defined as collective action where multiple individuals work together in pursuit of a common goal or public good.

1.3 The Problem(s) with Collective Action

The maintenance of cooperation creates an evolutionary conundrum as there are sometimes high risks and costs, such as fitness consequences, injury, or death, that are vulnerable to exploitation by other group members (Rand & Nowak, 2013). Collective action is particularly vulnerable to exploitation by "free-riders" who choose not to cooperate yet reap the benefits earned by those who do (Nunn & Deaner, 2004). The existence of free-riders creates a collective action problem where individuals must choose to cooperate and incur the associated risks in order to benefit the group or defect and protect their individual fitness while still receiving the benefits sought out by the cooperators.

1.4 Explanations for Cooperation

1.4.1 *Kinship*

Hamilton (1964) argued that genetic relatedness can explain the emergence and persistence of apparently altruistic traits, wherein natural selection favours or rejects altruistic behaviour in relation to the interaction between relatedness and fitness outcomes. In what is now known as Hamilton's rule (Hamilton, 1964a; Hamilton,

1964b), he identified a relationship between selection and altruistic behaviours—$rb > c$—where selection will favour altruism if the relatedness between the actor and recipient (r) multiplied by the genetic benefit to the recipient (b) is greater than the cost imposed on the actor (c) (Hamilton, 1964a; Hamilton, 1964b). In developing this rule, Hamilton introduced inclusive fitness theory where an individual's total genetic contribution to the next generation is a summation of their own reproductive success as well as the reproductive success of relatives that is due to their altruistic help (Hamilton, 1963; Hamilton, 1964a; Hamilton, 1964b). Despite Hamilton's (1964) suggestion that altruistic behaviours will only be favoured when expressed between kin, altruistic behaviours, including cooperation, between unrelated individuals can be explained as a consequence of mechanisms such as reciprocal altruism (Trivers, 1971; Clutton-Brock, 2009).

1.4.2 Reciprocal Altruism

Trivers (1971) introduced the term 'reciprocal altruism' to define instances where individuals will act altruistically to others with the expectation that the recipient will behave similarly at a later time. He argued that altruistic genes will be favoured by selection if individuals direct prosocial behaviours toward other altruistic actors or cooperators (Trivers, 1971). He explained this by reference to 'the Prisoner's Dilemma' game, where two players must choose to either cooperate or defect in return for one of four pay-offs. He classifies the pay-offs as either: rewards for each player if neither cheats (R), the temptation to cheat (T), the pay-off an altruist will receive if they are cheated (S), and the punishment both players receive if neither are altruistic (P) and defines a relationship where $T > R > P > S$. Given the value of the pay-offs, the greatest benefit as an actor is to defect if the partner cooperates, and the lowest pay-off comes

when the actor cooperates and partner defects (known as the 'sucker's pay-off). The general solution to the one-shot version of this game is always to defect because it guarantees the least damaging outcome for both parties compared to the case where one player cooperates while the other does not (Trivers, 1971; Dugatkin, 2002).

Axelrod and Hamilton (1981) proposed an alternative solution to the Prisoner's Dilemma: the tit-for-tat (TFT) strategy. TFT relies on a probability of encountering one's partner again in the future (Axelrod & Hamilton, 1981). Axelrod (1984) showed that, in order for cooperation to emerge with TFT, there must be an indefinite or unknown number of moves or encounters with the same partner. Additionally, he explained that the success of TFT depends on three characteristics: the nice strategy, retaliation, and forgiveness. The nice strategy requires that TFT is never the first to defect. Retaliation means TFT immediately defects on a defecting partner. Finally, forgiveness means that the TFT strategy only remembers the previous move (Axelrod, 2001; Dugatkin, 2002).

Wilkinson (1988) suggested five criteria for a behaviour to be considered reciprocal altruism. (1) The behaviour must reduce the actor's fitness. (2) The fitness of the recipient must increase in comparison to non-recipients. (3) The behaviour cannot occur if it depends on immediate benefit. (4) There must be a mechanism for recognizing individuals who receive the benefits without paying altruistic costs. (5) There must be an indefinite number of opportunities for partners to exchange aid in each of their lifetimes (Wilkinson, 1988).

Reciprocal altruism was once a widespread evolutionary explanation for cooperation. There is some evidence showing that reciprocal altruism may be possible in non-human animals. For example, Packer (1977) showed that coalition formation in male

olive baboons (*Papio anubis*) meets the criteria to be considered reciprocal altruism (Packer, 1977). However, this was based on a very small sample size. Otherwise, reciprocal altruism is rarely seen in non-human animals, rendering it a controversial explanation for cooperation across species (Carter, 2014). Additionally, most studies that find support for reciprocal altruism in non-human animals have been conducted on captive or provisioned populations. Evidence for reciprocal altruism in wild or natural populations is scarce (Henzi & Barrett, 1999; Clutton-Brock, 2009).

1.4.3 *Social Norms and Language*

Humans are known for being hyper-cooperators (Burkart et al., 2014) due to the variability of how we cooperate and with whom we do it (Henrich & Henrich, 2006). The maintenance of cooperation in humans is often explained by cultural and social norms that are instilled early in life (Fehr, 2004; Tomasello, 2009; Willer, 2009). Fehr (2004) defines norms as enforced behavioural standards. Axelrod (1986) lists three types of norm definitions: expectations, values, and behaviours (Axelrod, 1986). When trying to explain human cooperation, all three types of norms play a role. Tomasello (2009) suggests social institutions as an explanation for why we cooperate. He defines social institutions as organized ways of interacting that include consequences for non-cooperators (Tomasello, 2009). In other words, social institutions create expectations for how we should behave. Henrich and Henrich (2006) state that people will often reply with, “It’s the right thing to do” (p. 221) when asked why they cooperate showing that humans value helping each other.

A key component in norm creation and maintenance is language (Smith, 2010), which is unique to humans. While non-human animals are able to communicate in other

ways, they do not have the capacity for language (Cheney & Seyfarth, 1998). Smith (2010) explored how language facilitates large-scale cooperation and collective action efforts in humans. He suggests that language can help overcome some of the limitations associated with current explanations of human cooperation including reciprocity and kin selection. Smith (2010) argues that language is a tool that can solve collective action problems by lowering the costs associated with detecting and punishing free riders as it can be used to establish norms and gossip can help to establish past patterns of behaviour. Further, he suggests that the hyper-cooperation seen in humans may be a result of language amplifying existing forces on the evolution of cooperation while also creating new opportunities for cooperative behaviours (Smith, 2010). Language facilitates the cultural and social norms that regulate cooperation and its local expression in humans.

1.4.4 Reward and Punishment

Cooperation in both humans and non-human animals may be acquired and maintained through the rewarding of cooperators and the punishment of defectors (Fehr & Gächter, 2002; Sigmund, 2007; Arseneau-Robar et al., 2016). Fehr and Gächter (2002) demonstrated that humans were likely to use altruistic punishment to limit free-riders in cooperative games. Altruistic punishment means that individuals will incur a cost with no material benefit to punish defectors for not cooperating. The authors claim that current explanations for cooperation, including kin selection and reciprocal altruism, neglect altruistic punishment as a mechanism for maintaining cooperative behaviours (Fehr & Gächter, 2002). Arseneau-Robar and her colleagues (2016) have shown that adult female vervet monkeys use directed grooming to reward adult males for participating in intergroup conflict (IGC) while also using aggression to punish male defectors. While

Arseneau-Robar et al. (2016) found support for the use of reward and punishment in wild non-human primates, most studies investigating the use of reward and punishment in non-human animals have been conducted in laboratories and therefore do not reflect natural behaviours (Raihani, Thornton, & Bshary, 2012).

1.5 Intergroup Conflict

Intergroup conflict (IGC) results from intergroup competition where groups must compete for access to resources and territories (De Dreu & Triki, 2022). IGC can typically be classified as parochial altruism where individuals will behave altruistically towards their own group members while simultaneously showing hostility to out-group members (Abbink, Brandts, Herrmann, & Orzen, 2012). IGC occurs in humans through warfare (Kissel & Kim, 2019; Bowles, 2009) and raiding parties (Glowacki et al., 2016). While non-human animals do not have warfare in the human sense, IGC occurs in many species of group-living animals (banded mongooses, *Mungos mungo*, (Thompson, Marshall, Vitikainen, & Cant, 2017); meerkats, *Suricata suricatta*, (Dyble, Houslay, Manser, & Clutton-Brock, 2019), chimpanzees, *Pan troglodytes*, (Boesch et al., 2008); white-faced capuchins monkeys, *Cebus capucinus*, (Crofoot, 2013); vervet monkeys, *Chlorocebus pygerythrus*, (Arseneau-Robar et al., 2017); termites, *Zootermopsis angusticollis*, (Thompson et al., 2020); spotted hyenas, *Crocuta crocuta*, (Montgomery et al., 2023)).

IGC provides an excellent means to study the bases of cooperation because it poses a collective action problem. Participation in IGC carries high risks including injury and, potentially, death. Additionally, all members of a winning group are able to share resources, though not always equally (Isbell, Pruetz, Lewis, & Young, 1999; Foerster,

Cords, & Monfort, 2011), which means defectors will reap the benefits despite their unwillingness to cooperate. Previous studies have shown that there is both intra and inter-individual variation in the rates at which group members will participate in IGC (Nunn & Deaner, 2004; Kitchen & Beehner, 2007; Cords, 2007; Garber & Kowalewski, 2011; Koch, Signer, Kappeler, & Fichtel, 2016; Arseneau-Robar et al., 2017). Previous studies have shown that participation varies based on individual attributes, such as sex and rank (Cords, 2007; Koch, Signer, Kappeler, & Fichtel, 2016b; Arseneau-Robar et al., 2017), situational factors such as the presence of infants (Cords, 2007; Arseneau-Robar et al., 2017) and the numbers of contestants (Lewis, Sandel, Hilty, & Barnett, 2020; Koch et al., 2016), and social factors such as social network position (Chakraborty et al., 2023). Investigating why individuals vary in their rates of participation allows us to determine possible explanations for cooperation.

1.6 The Development of Cooperation

Joining collective action efforts is riskier for young individuals relative to adults because juveniles are vulnerable to injury from adult opponents (Silk, Samuels, & Rodman, 1981). Given the assumption that juveniles should be risk-averse (Janson, 1993), it is theoretically unlikely that juveniles will participate in collective action. However, it has been shown that juveniles do, in fact, participate in collective action at increasing rates with age (Cords, 2007; Heinsohn et al., 1996).

While there is evidence that shows that non-adults cooperate and participate in collective action, we still do not have a clear understanding of the mechanisms underlying their cooperation. Tomasello (2009) suggests that cooperation comes naturally for human children. Ideas of how we should behave are reinforced as we age which leads

to an internalization of the cultural and social norms surrounding cooperation (Tomasello, 2009). Lazić, Purić, and Krstić (2021) showed that parochialism develops before adulthood by demonstrating that young humans show a preference for their own group when incurring personal costs for cooperation. These explanations function when explaining juvenile cooperation in humans but, as previously mentioned, cultural norms acquired through language cannot explain how cooperation develops in non-human animal groups.

1.7 Thesis Outline

In this thesis, I investigate how cooperation develops in the absence of linguistically acquired cultural norms, using observational data collected on three troops of wild, habituated vervet monkeys (*Chlorocebus pygerythrus*; hereafter, vervets). I investigated how non-adult individuals come to cooperate by examining the factors that influence their participation in IGC. Vervets are an excellent study species as they are known for having high rates of intergroup conflict, and there is good evidence for the structure of adult participatory dynamics (Cheney, 1981; Arseneau-Robar et al., 2017; García, de Guinea, Bshary, & van de Waal, 2022).

To gain a better understanding of how cooperation develops, I tested three hypotheses. First, that there are certain individual and social attributes that influence non-adults' likelihood to participate in IGC. Second, that non-adults learn to participate in IGC through the use of directed grooming as a reward. I predict that if nonadults learn to participate, they will be more likely to be groomed if they have participated in IGC. The third hypothesis is that participation in IGC is socially facilitated. Social facilitation implies that individual behaviours are more likely given the presence of other individuals

(Stamm, 1961). If participation is socially facilitated, I predict that there will be structural similarities between non-adults' grooming, spatial association, and IGC participation networks.

Following this general introduction, Chapter 2 provides an overview of my study species and population as well as the general methods used in my study (more detailed methods are provided in the specific chapters where they occur). In Chapter 3, I present findings from four Bayesian multilevel models. I tested how individual attributes (personality, age, rank, and sex) and social factors (social network position, troop size, the numbers of participants, and maternal participation) influence non-adults' likelihood to participate and likelihood to participate more aggressively in IGCs. Additionally, I investigated how being groomed during IGCs may be related to participation.

In Chapter 4, I present findings from an analysis in which I compare three types of networks to determine if nonadult social networks are similar to their IGC co-participation networks. I constructed dynamic ego networks for three types of social networks: grooming, spatial association, and IGC for all of the non-adults in my study groups. I then compared them using cosine similarity which captures the structural similarity between the types of networks. Using multilevel models within a Bayesian framework, I was able to test how non-adult social networks compare throughout development.

Finally, Chapter 5 is a general discussion of my findings. I elaborate on how my results relate to the current discourse on the development of cooperation and possible mechanisms for the maintenance of cooperation in the absence of linguistically acquired

cultural norms. Further, I consider the limitations of my thesis as well as possible directions for future research.

CHAPTER 2: GENERAL METHODOLOGY

2.1 Samara Field Site

I conducted my analyses using long-term data from the Samara Private Game Reserve in South Africa (32°22'S, 24°52'E) (Pasternak et al., 2013). Sitting on 27 000 ha, the reserve contains mountains, nama-karoo grasslands, and semi-riparian woodland. The study population uses the Melk (Afrikaans) or Milk (English) River that flows through the reserve as its only source of water. The wet season occurs between October and March with a dry season between April and September. The site experiences a mean maximum temperature of 27°C and a mean minimum temperature of 10°C (Pasternak et al., 2013).

There are several other species residing on the reserve in addition to vervet monkeys. Other mammals include chacma baboons (*Papio ursinus*), buffaloes (*Syncerus caffer*), white rhinos (*Ceratotherium simum*), zebras (*Equus burchelli*), giraffes (*Giraffa camelopardalis*), kudus (*Tragelaphus strepsiceros*), gemsboks (*Oryx Gazella gazella*), red hartebeests (*Alcelaphus buselaphus*), duikers (*Sylvicapra grimmia*), springboks (*Antidorcas marsupialis*), elands (*Taurotragus oryx*), aardvarks (*Orycteropus afer*), warthogs (*Phacochoerus africanus*), cape porcupines (*Hystrix africaeasutralis*), scrub hares (*Lepus saxatilis*), and meerkats (*Suricata suricatta*) (Sashaw, 2012).

Predators known to prey on the vervets or elicit alarm calls include cheetahs (*Acinonyx jubatus*), caracals (*Caracal caracal*), black-backed jackals (*Canis mesomelas*), martial eagles (*Polemaetus bellicosus*), verreaux's eagles (*Aquila verreauxii*), and cape eagle owls (*Bubo capensis*). While there are no large constrictors on the reserve

(Pasternak et al., 2013), venomous snakes such as cape cobras (*Naja nivea*), boomslang (*Dispholidus typus*), and puff adders (*Bitis arietans*) are found and are known to be responsible for the deaths of vervet monkeys (Sashaw, 2012; Pasternak et al., 2013).

2.2 Study Species and Population

2.2.1 *Taxonomy and Distribution*

Savanna monkeys (genus *Chlorocebus*; generally referred to as vervet monkeys or green monkeys) are the most widely distributed species of the cercopithecines (Turner, Schmitt, & Cramer, 2019). My thesis will focus on vervet monkeys (*Chlorocebus pygerythrus*; hereafter "vervets"). Of the six species in the genus, *Ch. Pygerythrus* is the most studied in the wild and has the largest latitudinal distribution (Turner, Schmitt, & Cramer, 2019). Vervets are small, semi-arboreal old-world primates occupying regions of sub-Saharan Africa.

2.2.2 *Ecology*

Vervets are omnivorous and their diet consists of seeds, nuts, fruits, fungi, insects, and succulents (Pasternak et al., 2013). They live in multi-male, multi-female groups (Isbell, Cheney, & Seyfarth, 1991). Females are the philopatric sex, remaining in their natal troops throughout their life, while males will migrate between neighbouring troops once they have reached sexual maturity. Non-natal males in Samara remain in a troop for an average of 1.3 years (459 days) before emigrating (Young et al., 2019). Rank is inherited amongst the females with daughters inheriting the rank below their mother in reverse birth order (Mertz, Surreault, van de Waal, & Botting, 2019). Vervets are highly territorial and both males and females respond aggressively to the presence of individuals

from neighbouring troops. Pasternak et al. (Pasternak et al., 2013) argued that group fission is inhibited by the inability of the troops in our population to move away from the river and associated riverine woodland due to the lack of available resources. Consequently, local population density is high, and troops are uncharacteristically large, with discernable overlap between territories (Figure 2.1. See also Pasternak et al., 2013).

Our study population is comprised of three troops (RBM, RST, PT) with overlapping home ranges along the Melk River (Fig 2.1). All individuals in the population were identifiable using unique facial and body features. RST and RBM had been studied continuously since 2008. We began studying PT in 2012. Group size and composition varied throughout the study period (Figure 2.2). The research program ended in December 2018.

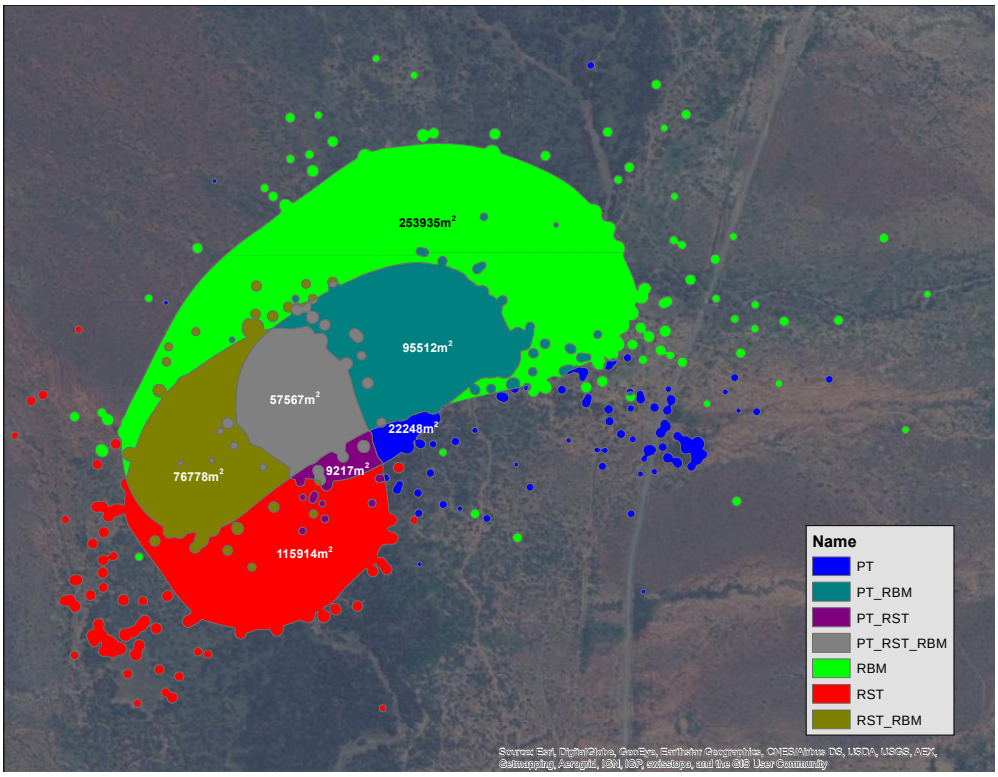


Figure 2.1 Figure shows the home ranges of the three troops as well as the overlap between troops (Marcus Dostie, 2023)

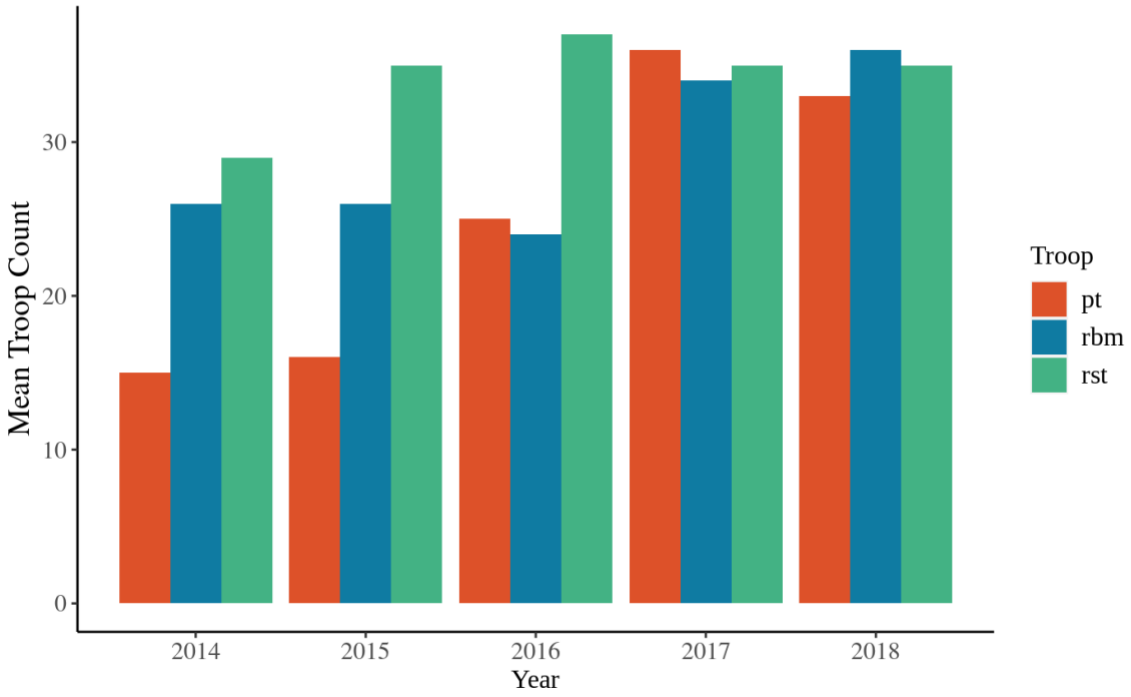


Figure 2.2 Bar plot of troop size with the year during the study period on the x-axis and the mean number of members in each troop on the y-axis. The colour of the bars represents each troop (red=PT, blue=RBM, and green=RST).

Similar to other populations, the vervets at Samara are seasonal breeders (Blersch et al., 2023). The mating season typically occurs in the austral fall, with births occurring in the Austral spring (Butynski, 1988). Vervet monkeys have a gestation period of ~163 days (Johnson, Valerio, & Thompson, 1973). Interbirth intervals are largely dependent upon whether or not offspring from the previous breeding season survived. Females give birth to a single infant approximately every 1 to 2 years (Sashaw, 2012). Infants in our population are expected to be fully weaned from their mother by the age of 7 months (Blersch et al., 2023; Sashaw, 2012). I used data from three sequential birth cohorts (2013-2015; Figure 2.3) as few members of the previous three cohorts (2010-2012) survived beyond their first year due to severe drought.

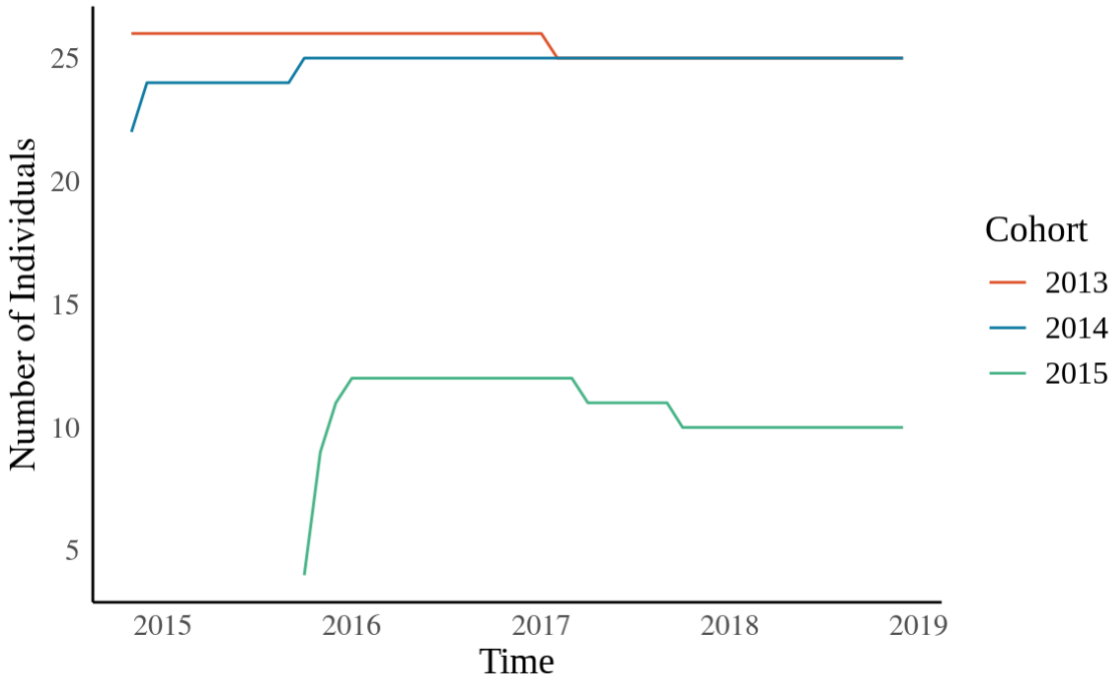


Figure 2.3 Line plot showing changes in cohort size across time. Time is shown on the x-axis and the number of individuals present on the y-axis. The colours of the lines represent each birth cohort (red=2013, blue=2014, and green=2015).

2.2.3 *Physical Characteristics*

Infants are born with a pink face and black coat but develop the adult colouring of a grey coat with a black face by ~3 months old (Lee, 1984). Male vervets reach sexual maturity around 5 years old whereas females reach maturity between 3.5 to 5 years old (Henzi et al., 2023). Adult males have brightly coloured genitalia, with a red penis and blue scrotum. Vervets are sexually dimorphic with females being smaller than males. Male vervets at Samara weighed 5.93 kg on average compared to females who weighed 3.3 kg. The juvenile cohort from 2013 weighed 1.10 kg more on average than individuals from the 2014 cohort (Jarrett et al., 2020).

2.3 Behavioural Data Collection

The vervets were followed 5 days a week for 10 hours each day. Given seasonal variation in daylight at this latitude, we balanced daily follows in the summer to allow for equal data collection in the morning and the evening. In this way, the number of days that began at dawn (0400 hours) and finished 10 hours later equalled the number of 10-hour days that ended at 1900 hours.

2.3.1 *Scan Sampling*

We used scan sampling (Altmann, 1974) to record activity and other relevant behavioural data. Scans were conducted every 30 minutes for a maximum of 10 minutes for each scan. For both the juvenile and adult scans, we recorded the identities of all individuals as well as their activity (foraging, resting, moving, grooming). We recorded the partner's identity for activities that required a partner (e.g., allo-grooming, play, aggression, and copulation). Additionally, we noted the nearest adult male, adult female, and juvenile to the individual and the distance between the individuals for the adult scans. For juvenile scans, we recorded all individuals within 3m of the focal individual as neighbours.

2.3.2 *Agonistic Interactions and Dominance Hierarchies*

We collected data on interindividual agonistic interactions ad libitum. Agonism was recorded when one individual (the aggressor) threatened another (the victim) using facial threats, vocal threats, charges, lunges, chases, and physical aggression, or if the aggressor displaced or supplanted the victim. We recorded the IDs of the aggressor, the victim, and any animals that supported either the aggressor or the victim. We also

recorded the outcome of the interaction from the perspective of the aggressor (win, lose, draw, or unknown).

Using the agonistic interaction data, I generated ranks using the "EloRating" method (Neumann & Kulik, 2020) and a burn-in period of 6 months in Rstudio software version 3.5.2(RStudio, 2018; Vilette, Bonnell, Henzi, & Barrett, 2020). EloRating allows users to calculate ranks sequentially rather than using interaction matrices (Neumann et al., 2011). In comparison to other rank methods, the EloRating method allowed me to update the ranks of the vervets through time which is important for our population as evidence has shown that our population's ranks are dynamic (Nord, Bonnell, Dostie, Henzi, & Barrett, 2021). I used agonistic interactions from all troop members in the calculation of the dominance hierarchies (Vilette et al., 2020).

2.3.3 *Intertroop Encounters*

I analyzed data from intertroop encounters (ITEs) from 2014-2018 (Table 2.1). We collected data on all observed ITEs. An ITE occurred when one or more members of one of the three troops encountered a neighbouring troop or lone individual (Figure 2.4). We collected data on both aggressive and non-aggressive ITEs. We recorded all individuals who participated in the ITE as well as the maximum level of aggression (ITE call, non-aggressive, stationary, active, physical) shown by each individual where applicable. Intergroup conflicts (IGC) could have bouts of aggression with breaks between the conflicts. We assigned an identity to each bout during the ITE for subsequent analyses. As grooming and play could occur during an ITE, we recorded the individuals involved in play or grooming during or after the ITE.

Table 2.1

Average numbers of intertroop encounters, intergroup conflicts, and participants across study periods

Troop	Number of ITEs per month	Number of participants in ITEs	Number of IGCs per month	Number of participants in IGCs
RST	39 ± 21	9 ± 9	24 ± 14	10 ± 8
RBM	56 ± 32	9 ± 9	36 ± 24	9 ± 8
PT	59 ± 39	11 ± 11	36 ± 28	12 ± 10

Figure 2.4 An ITE in progress (Photo, Chloé Vilette).

2.4 Study Species Suitability

Vervets are well known for their high rates of intergroup conflict (Cheney, 1981; Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017). Arseneau-Robar and colleagues (2017) have shown that IGC can be triggered by the defence of valuable resources such as food and water, there is variation in participation both within and between individuals, and the costs and benefits individuals will experience from

participation varies. Additionally, because vervets are a semi-terrestrial species and they occupy savannah habitats, we were able to collect more specific data from the habituated troops even during highly aggressive inter-troop encounters. Taken together, vervets make an excellent species to investigate the development of prosocial behaviours in non-humans.

2.5 Statistical Analyses

All of my analyses were conducted using multilevel models under a Bayesian framework in R 4.4.2 (R-Core-Team, 2022) on data collected between 2014 and 2018. I ran all of my models with weakly informative priors (normal (0, 1)) and scaled and mean-centred all continuous variables. I confirmed model convergence using $\hat{R}$s ($\hat{R}$s=1.00) and used the 'pp_check' function in 'bayesplot' (Gabry & Mahr, 2017) to assess model performance (see appendices). I set the credible intervals to 95% due to their interpretative familiarity and calculated probability of direction estimates (PD) from the 'bayestestR' package (Dominique, Mattan, Daniel, & Lüdecke, 2019) to evaluate the precision of the outcomes. All figures were generated using the 'ggplot2' (Wickham, 2009) and 'ggridges' (Wilke, 2018) packages.

CHAPTER 3: SOCIAL INDUCTION AND THE DEVELOPMENTAL TRAJECTORY OF PARTICIPATION IN INTERGROUP CONFLICT BY VERVET MONKEYS

This data chapter has been submitted for publication under the title "Social Induction and the Developmental Trajectory of Participation in Intergroup Conflict by Vervet Monkeys." The authorship list for the submitted version is as below. Dr. Henzi, Dr. Barret and I conceived the ideas. Dr. Bonnell, Dr. Vilette, Dr. Nord, Dr. Blersch, Dr. Young, and I contributed to the methodology. Dr. Bonnell and I conducted the formal analyses. Dr. Bonnell, Dr. Vilette, Dr. Nord, Dr. Blersch, Dr. Young, Dr. Henzi, Dr. Barrett, and I wrote and reviewed the manuscript. Dr. Henzi and Dr. Barrett contributed to funding acquisition and supervision of the project. All authors approved the final version of the manuscript.

M. Clarke[1,2], T.R. Bonnell[2,3], R. Blersch[2,4], C. Nord[2,4], C. Vilette[1,2], C. Young[2,5], S.P. Henzi[1,2] & L. Barrett[1,2]

[1]Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada

[2]Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, Pretoria, South Africa

[3]Department of Computer Science, University of Calgary, Calgary, AB, Canada

[4]Neuroscience and Behavior Unit, California National Primate Research Center, Davis, CA, USA

[5]Department of Psychology, Nottingham Trent University, Nottingham, UK

3.1 Abstract

We assess the proposition that the study of inter-group conflict (IGC) in non-human primates offers a useful comparison for studies of human IGC and its links to parochial altruism and prosociality. Specifically, among these non-linguistic animals, social network integration and maternal example likely promote non-adult engagement of valuable future allies and can serve as an analogue for the cultural processes that drive the emergence of human cooperation. We use longitudinal data from three cohorts of non-adult vervet monkeys (*Chlorocebus pygerythrus*) across three wild groups to describe the emergence of participation in intergroup conflict (IGC). Our results indicate that non-adults are sensitive to personal (age) and situational risk (participant numbers), and that the frequency and intensity of participation, while also modulated by rank and temperament, both mirrors concurrent maternal participation and reflects their centrality in the grooming network. The possibility of social induction is corroborated by the distribution of grooming during IGC, with non-adults being more likely to be groomed if they were participants and if they were female and higher-ranking. Mothers were more likely to groom younger offspring participants of either sex, while other adults targeted higher ranking female participants. While we caution against a facile alignment of these outcomes to human culturally mediated induction, we argue that there is merit in considering more closely how the embodied act of participation, and the resultant social give -and-take—which is shared with humans—might serve as the basis for a unified comparative investigation of prosociality.

3.2 Introduction

Human social groups are characterised by the sheer scale and diversity of the cooperative interactions of their members (Boyd & Richerson, 2009) that can extend well beyond ties of kinship and incorporate extreme altruism (Henrich & Henrich, 2006; Rand & Nowak, 2013). Choi and Bowles (2007; see also 2008), amongst others, have argued that human hyper-cooperation is essentially parochial, being restricted primarily to members of the same group and coupled to the distinctively non-cooperative violent conflict, principally warfare, that has historically characterised the interactions between groups.

It is the deep hominin roots of this coevolutionary linkage of in-group altruism and out-group aggression (Bowles, 2009) that links human cooperation to its equivalents in other obligate social species, most notably anthropoid primates (Crofoot & Wrangham, 2010). Intergroup conflict (IGC) across a wide range of such species generally involves two or more group members, is also aggressive, and can readily escalate into violent or lethal physical attack (Hausfater, 1972; Harrison, 1983; Crockett & Pope, 1988; Miller, 1998; Cords, 2002; Palombit, 1993; Wilson et al., 2014), with all the attendant risks that this carries for participants.

Where such goal-directed collective action constitutes a public good, such that benefits, but not costs, are shared by non-participants, one central question concerns the mechanisms that promote participation and the prevention of exploitation by 'free-riders' (Willems, Hellriegel, & van Schaik, 2013). Proximally, there are regulatory processes directed at rewarding participants and punishing defectors that, at least in broad relief, are shared by humans and non-humans, and which serve directly to promote the production of a public good (Glowacki & Wrangham, 2013; Mathew & Boyd, 2011; Arseneau-

Robar et al., 2016; Cheney & Seyfarth, 1987; Kowalewski & Garber, 2015; Raihani, Thornton, & Bshary, 2012; Gao, Wang, Pansini, Li, & Wang, 2015; Bshary, Richter, & van Schaik, 2022). More distally, however, human parochial altruism is buttressed by the developmental inculcation of prosocial norms that are fundamentally and distinctively rooted in cultural learning, norm psychology and the transformative effects of language (Richerson & Boyd, 2005; Chudek & Henrich, 2011; Smith, 2010).

While human infants have a biological predisposition to altruistic behaviour, not apparent in chimpanzees (*Pan troglodytes*, Warneken & Tomasello, 2009), they are also born into culture and internalise cultural 'rules' through the necessary mediation of enculturated others and their participation in cooperative cultural activity (Vygotsky, 1997; Moll & Tomasello, 2007). The consequences of these features of human life are that inequity aversion and altruistic sharing (egalitarianism) emerge prior to puberty, and in lockstep with parochialism (Fehr, Bernhard, & Rockenbach, 2008), constituting a fundamentally powerful force in overcoming the undermining of collective action by the defection of 'rational egotists' (Ostrom, 2000), and thereby providing a mechanistic basis for Bowles' arguments (Bowles, 2008).

Given good evidence for variability within and across individuals in participation during IGCs (Kitchen & Beehner, 2007; Cords, 2007; Crofoot & Gilby, 2012; Kowalewski & Garber, 2015), the comparative question that we wish to address is whether, in the absence of the powerful cultural forces available to humans, there are developmental trajectories in non-human animals that might underpin differential and variable participation. In the absence of both a cultural toolkit and a capacity for empathy (Vasconcelos, Hollis, Nowbahari, & Kacelnik, 2012), the principal possibility that

suggests itself is that participation in IGCs promoted through social network structure (Siegel, 2009; Crofoot, Rubenstein, Maiya, & Berger-Wolf, 2011; Glowacki et al., 2016) might serve as an analogue for the emergence of baseline prosociality in non-human societies.

At the same time, despite the potential severity of the consequences of physical aggression with adults (Silk et al., 1981), and the theoretical expectation that juveniles should be risk-averse (Janson, 1993), there is evidence that juvenile blue monkeys (*Cercopithecus mitis*), for example, participate in aggressive IGCs at rates that increase with age (Cords, 2007). This phased increase has also been observed in lions (*Panthera leo*), where the involvement of juvenile females is tied to the numbers of both defendants and intruders, and indicates the early development of an appropriate sensitivity to context and risk (Heinsohn et al., 1996). These examples make it clear that physical immaturity need not impede participation in risky ventures and confirm that a developmental approach to understanding the patterns of adult intergroup behaviour is likely to pay dividends.

Vervet monkeys (*Chlorocebus pygerythrus*) provide an excellent opportunity to investigate these issues. They are a widely distributed African group-living Old World monkey species with female philopatry and, like the closely related blue monkeys, have long been known for aggressive IGCs (Struhsaker, 1967; Cheney, 1981; Harrison, 1983) in the context of resource defence, and typified by considerable variation in adult participation that is tied to differential costs and benefits (Arseneau-Robar et al., 2016). Here we take advantage of longitudinal developmental data from three birth cohorts of vervet monkeys to consider four questions.

Principally, we wish to consider the proposition that the extent of social integration is positively linked to cooperation during IGC. In humans, altruistic cooperation is more likely where individuals are both strongly connected to a few other individuals but where such clusters are also connected to one another by bridging individuals (Burt, 2000). Juvenile vervets form distinctive and stable ego network structures (Vilette, Bonnell, Dostie, Henzi, & Barrett, 2022) that, while they do not mirror maternal networks (Jarrett, Bonnell, Young, Barrett, & Henzi, 2018), nevertheless have maternal bonds at their core (Vilette, Bonnell, Dostie, Henzi, & Barrett, 2023). Consequently, we use the extent of maternal participation in IGC, alongside a juvenile's eigenvector centrality (EC), which reflects the depths of the latter's penetration in the relevant network (Brush, Krakauer, & Flack, 2013), to predict participation rates.

Second, we expect juvenile participation to be modulated by intrinsic individual attributes such as sex, dominance rank and personality. We cannot specify a directional prediction *a priori* with respect to which sex is more likely to participate, as we have good reasons to predict participation in both sexes: juvenile males, because they are larger than their female age mates (Jarrett et al., 2020) and juvenile females, because they are philopatric (Heinsohn et al., 1996; Cords, 2007). Nevertheless, any differential outcome or encouragement may help clarify underlying processes or selection pressures.

Rank is important because, whether or not IGC delivers a public good, it is reasonable to expect a correlation between the extent of participation and the likelihood of the direct benefits afforded by high rank (Willems & van Schaik, 2015) that are evident in our population (Blersch et al., 2023). We therefore predict that higher ranking juveniles will participate more frequently than will lower-ranking ones (Cheney, 1981).

By the same token, higher ranking adult female blue monkeys, who do not benefit disproportionately from resource defence, are also more likely to participate in IGC (Cords, 2007). This raises the possibility that the underlying driver actually reflects differences in personality traits. We therefore predict that higher neophilia scores (indicative of greater boldness/exploratory tendencies) will underpin an increased likelihood of participation.

Third, in accordance with the perceived need to balance costs and manage risk, we expect participating non-adults to scale their involvement over time. Principally, we expect older, and therefore larger and more experienced, non-adults to participate more frequently and with greater intensity. Here again, however, involvement may be modulated by rank and personality, as well as by external considerations, such as the extent of concurrent participation by others. Both an increase in the overall numbers of participants from their own group (hereafter the focal group), or a numerical advantage over the opposing group, may reduce exposure to risk and encourage non-adult participation.

Finally, we expect that, while non-adults may not be punished for not participating in IGC, grooming will be used as an incentive to participate (Arseneau-Robar et al., 2016), especially by mothers (Vilette et al., 2023). We therefore predict a positive relationship between non-adults participating and being groomed during the IGC. As grooming may simultaneously encourage future collective action, we also consider whether grooming is preferentially directed at females, who will remain in the group for life, and to younger participants.

3.3 Methods

3.3.1 *Study Species and Population*

Data were collected from three adjacent groups (RST, RBM, and PT) of habituated vervet monkeys with overlapping home ranges on the Samara Private Game Reserve in South Africa (Pasternak et al., 2013). RST and RBM have been studied continuously since 2009. The third group (PT) was added in 2012. All individuals were identifiable using unique facial and body markings. Each group was followed by at least one observer for 10 hours each day, 5 days per week across the study period.

Vervets are seasonal breeders and this, at our study site, results in distinct juvenile cohorts (Blersch et al., 2023). Here we use data from the 2013-2015 cohorts (N=68 infants and juveniles, hereafter non-adults) and followed them until the end of the study in 2018. The subjects ranged in age from 1 day to ~5 years, with females reaching sexual maturity at between 3.5–4.5 years, and males likely to leave their natal groups at ~4.5 years of age (Henzi et al., 2023).

3.3.2 *Data Collection*

i. General methods. We used scan sampling (Altmann, 1974) to collect behavioural and activity data. To do so, we recorded the IDs of all visible individuals, their activity (foraging, resting, grooming, moving, playing), their social partners, and their nearest neighbours during a 10-min window every 30 min (N=754,641 individual data points from 2014 to 2018).

ii. Social networks. We used the scan data to generate annual grooming and spatial association networks with the ‘igraph’ package (Csardi & Nepusz, 2006) in R

4.4.2 (R-Core-Team, 2022). We extracted all occurrences of non-adults being groomed by, or grooming, another individual to generate directed and weighted grooming networks. Spatial association networks were constructed using dyads that included the identity of the target individual and each animal within 3m during the scan. We then extracted eigenvector centrality (EC) measures for non-adults from each network. Those with a higher EC score are connected to individuals who themselves are highly connected.

iii. Personality. We used data from a previous study where individuals were presented with novel food and tested on whether they would eat it (see Nord, 2021; Nord et al., 2022). We then used Bayesian mixed effects modelling to estimate novel food neophilia which served as an index for personality in our models.

iv. Agonism. Data on aggression were collected whenever observed. We recorded the identities of the aggressor, the victim, and the outcome from the perspective of the aggressor (win, loss, draw, or unknown; N=50,924 occurrences). These data were used to calculate ranks for the entire group using the 'EloRating' package (Neumann & Kulik, 2020), allowing us to estimate a non-adult's rank on the day of each observed intergroup encounter.

v. Intergroup encounters. We collected data on all observed intergroup encounters, which were scored when one or more members of one group directed their behaviour or moved towards individuals of another group. Not all encounters were aggressive and here we consider only data when intergroup conflict (IGC) was identified through the actions of one or more members of either group. In addition to recording group IDs and the number and IDs of participants, we scored the extent of participation,

with the highest level observed for each participant being recorded. In ascending order, participants were ‘non-aggressive’ (at the immediate site of the IGC but did not otherwise participate), ‘stationary’ (offered facial or vocal threats), ‘active’ (lunged, charged at, or chased opponents), or ‘physical’ (slapped, grabbed or bit opponents).

3.3.3 *Statistical Analyses*

We constructed three Bayesian multilevel models using the ‘brms’ package (Bürkner, 2017) in R 4.4.2 (R-Core-Team, 2022), and a fourth in ‘rstan’ (Carpenter et al., 2017).

i. Model 1: What factors influenced the likelihood of participation (yes/no)? For each IGC, we entered participant age (days), sex, rank, neophilia score, spatial and grooming EC, whether the non-adult’s mother was a participant, the total number of participants from the non-adult’s group, the total number of participants from the opposing group, and the total group sizes as fixed effects. We specified an interaction between the number of participants from the non-adult’s group and the opposing group. We included non-adult ID, nested in its group (hereafter focal group) ID and opposing group ID as crossed random intercepts. We specified a Bernoulli distribution and ran the model with four chains and 2500 iterations.

ii. Model 2: What factors influenced the level of aggression shown by those non-adults that did participate? We used the same model structure and entered the same predictors as Model 1 but replaced maternal participation with the level of maternal aggression as a monotonic predictor, using the ‘mo’ function in brms to specify that maternal participation is ordinal (Bürkner & Charpentier, 2020). Both non-adult and

maternal levels of aggression were ranked from least to most aggressive, using the maximum level of aggression recorded in the IGC dataset (0=non-participant, 1=non-aggressive, 2=stationary, 3=active, 4=physical). We specified an ordinal distribution and ran the model using 4 chains and 4000 iterations.

iii. Model 3: Was the receipt of grooming (yes/no) by non-adults at the time of the IGC related to their participation (yes/no)? We also included sex, age, rank, grooming and spatial EC, group size and IGC participant numbers as predictors. Non-adult ID, nested in focal group ID, was entered as a random intercept. We specified a Bernoulli distribution and ran the model with four chains and 3500 iterations.

iv. Model 4: What predicted whether non-adult participants were (i) groomed during the IGC and then, (ii) what predicted whether the groomer was their mother? To address this, we used the "rstan" package to construct a nested double-hurdle structure. Following the outcome of Model 3, we included sex, age and rank as predictors for both models. Non-adult ID, nested in maternal ID, nested in focal group ID was entered as a random intercept. We specified a Bernoulli distribution and ran the model using eight chains and 500 iterations.

All models were run with weakly informative priors (normal (0, 1)) and continuous variables were scaled and mean-centred. We used $\hat{R}$s to confirm convergence ($\hat{R}$=1.00) and evaluated model performance with the 'pp_check()' function from the "bayesplot" package (Gabry & Mahr, 2017) (see Appendix A.1-A.4). We set the credible intervals at 95% because of their interpretive familiarity and used these, backed by "probability of direction" (PD) estimates from the "bayestestR" package (Makowski,

Ben-Shachar, & Lüdecke, 2019), to evaluate the size and precision of model outcomes (see Henzi et al., 2021). We calculated conditional and marginal R^2 values for models 1-3 using the 'bayes_R2' function (Bürkner, 2017), recognising that specifying an ordinal distribution in Model 2 requires caution in their interpretation. As R^2 is an inefficient estimate of explained variance for Model 4, which predicts individual instances, we generated a receiver operating characteristic (ROC) curve for each of the sub-models and calculated the area under each curve (AUC).

All figures were created using the 'ggplot2' (Wickham, 2009) and 'ggridges' packages (Wilke, 2018).

3.4 Results

Non-adults participated in ~79% of the 3,350 observed IGCs. Most non-adult participation was non-aggressive (76.4%). They were, however, active participants in 13.4%, stationary participants in 8.9%, and physical participants in 1.4%. Mothers were co-participants in 41.5%. Participation was almost equal between the sexes (males: 50.4%; females: 49.6%). The average age of participants was 2.5 years, with the youngest being present as an inadvertent ventrally carried observer at 3 days of age, and the oldest being 5 yrs.

3.4.1 Predictors of non-adult participation in IGCs

We found that non-adults were more likely to participate as they got older, if their mother participated, and as the number of participants in their own group increased (Figure 3.1, Appendix A.5). We also found small, precise positive effects for rank, grooming EC, and the number of participants in the opposing group. We found small,

precise negative effects for focal group size, spatial EC, and the interaction between the number of participants in the contesting groups. Examination of the interaction indicates that it was driven largely by changes in the number of focal group participants (Appendix A.6), with declining numbers reducing the likelihood of non-adult involvement. We found no meaningful effects for sex and our estimate of personality. The full model accounted for 28.5% of the variance (Main effects: 24.2%).

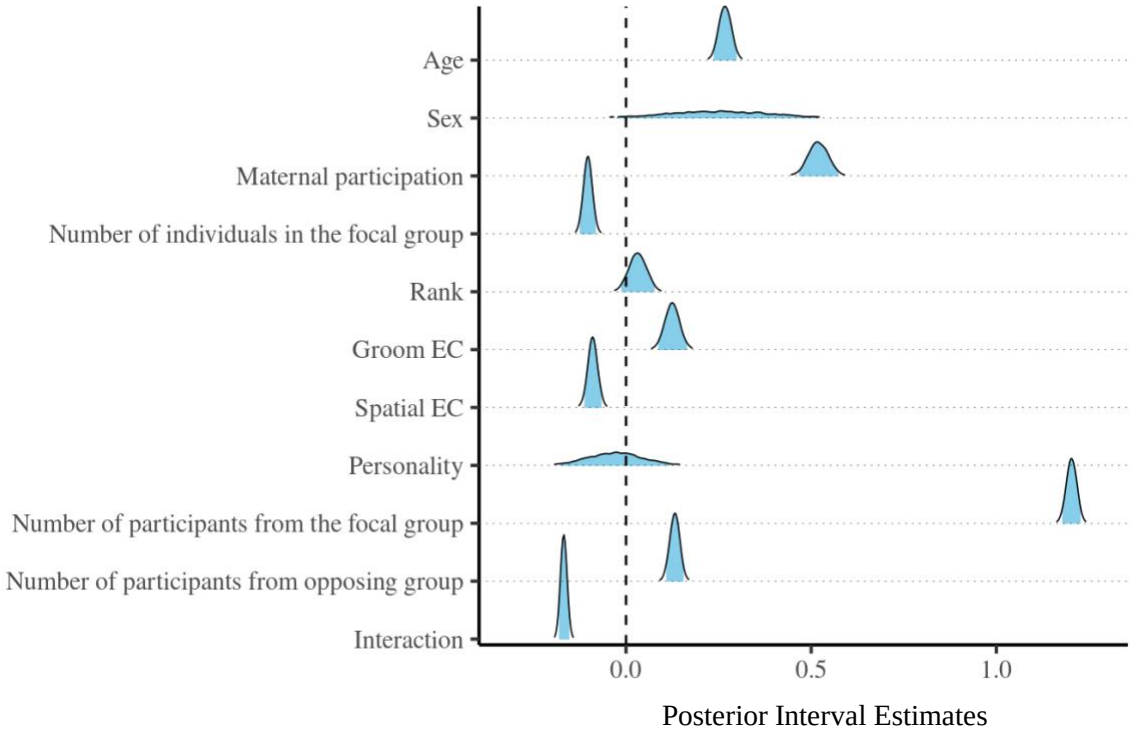


Figure 3.1. Posterior density estimates of the probability of participation (Y/N) in intergroup conflict in relation to age, sex (Ref: Female), maternal participation, the number of individuals in the troop, rank, grooming eigenvector centrality (EC), spatial EC, personality, the number of participants from the focal and opposing groups, together with their interaction. The blue fill is truncated to indicate the 95% credible intervals.

3.4.2 *Predictors of the level of aggression shown by non-adults during IGCs*

Our second model (Figure 3.2, Appendix A.7) showed that the likelihood of a non-adult being aggressive was positively associated with its age and the level of its mother's involvement, with its level of aggression tracking that of its mother, and the

effects being moderately strong and precise. There was reasonable evidence that neophilia was positively associated with levels of recorded aggression. We found the same contrast between grooming and spatial EC as in Model 1. Unlike the outcomes in Model 1, non-adults were less aggressive as focal group participant number increased, and more aggressive as the number of opposing group participants grew. We detected no interaction between these two variables. As in Model 1, we found no evidence of a sex difference. The full model accounted for 13.3% of the variance (Main effects: 7.7%).

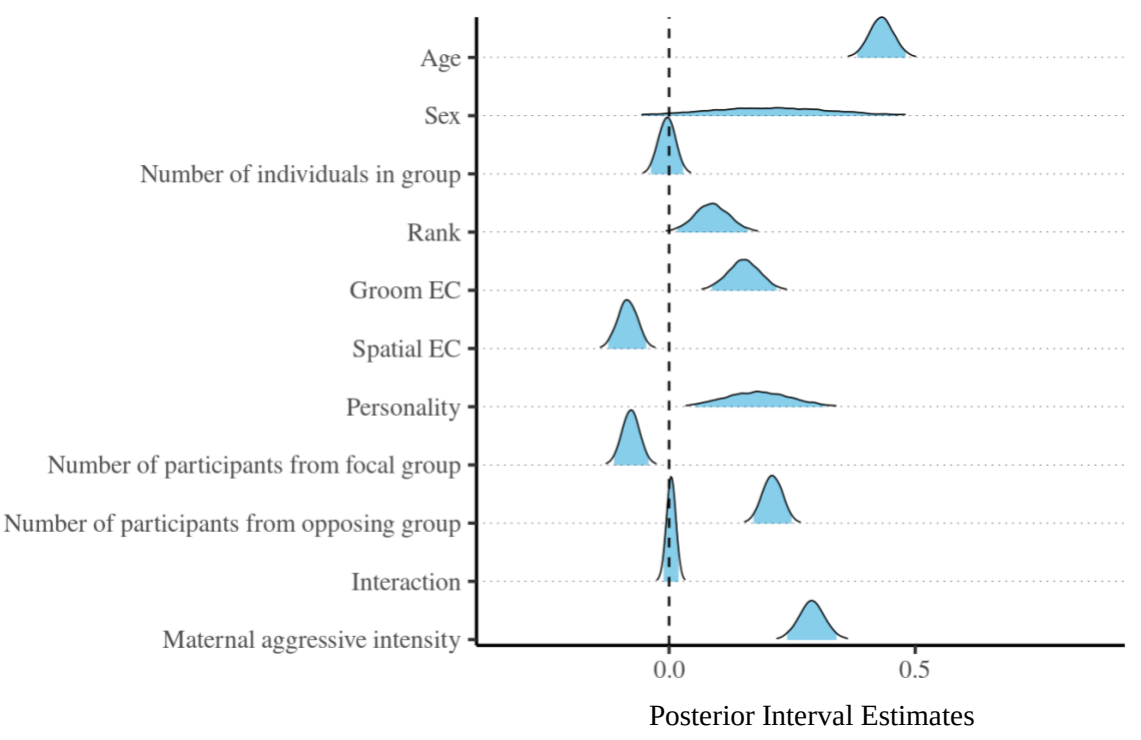


Figure 3.2. Posterior density estimates of changes in the level of aggressive intensity in relation to age, sex (Ref: Female), the number of individuals in the focal group, rank, grooming eigenvector centrality (EC), spatial eigenvector centrality, personality, the number of participants from the focal and opposing groups (and their interaction), and maternal aggressive intensity. The blue fill is truncated to indicate the 95% credible intervals.

3.4.3 *Grooming during the IGC and non-adult participation*

Model 3 (Figure 3.3, Appendix A.8) identified a strong and precise positive relationship between non-adult participation and the likelihood of being groomed, and

smaller but precise positive relationships between grooming and focal group size, as well as participant number in both the focal and opposing groups. There was moderate evidence for a positive relationship between rank and grooming and the same opposing relationship for grooming and spatial EC. Interestingly, there was less precise but moderately strong evidence that non-adult males were less likely to be groomed during IGCs. We detected little evidence of effects for age and personality. The full model accounted for 12.2% of the variance (Main effects: 9.3%).

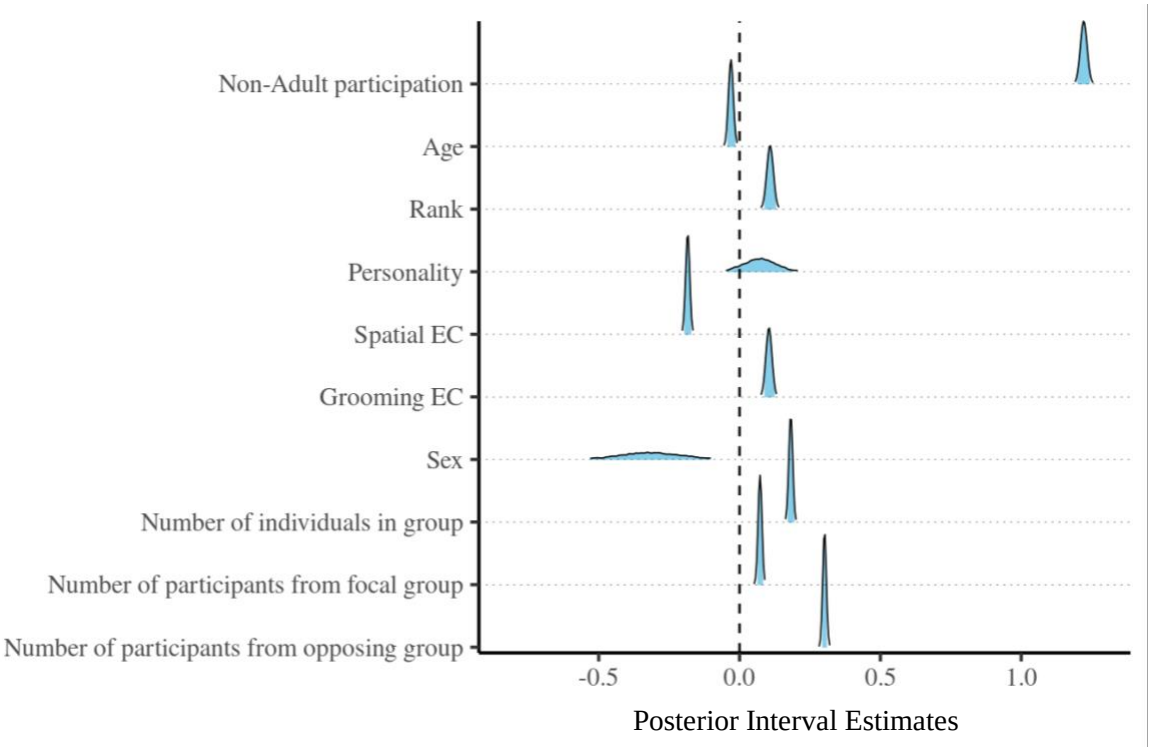


Figure 3.3. Posterior density estimates of the probability of grooming (Y/N) in relation to participation (Y/N), age, rank, personality, spatial eigenvector centrality, grooming eigenvector centrality, sex (Ref: Female), the number of individuals in the focal group, and the number of participants from the focal and opposing groups. The blue fill is truncated to indicate the 95% credible intervals.

3.4.4 *Grooming of non-adult participants and the role of the mother.*

Model 4 (Figure 3.4a, Appendix A.9 and A.10) indicates non-adult participants were more likely to be groomed if they were older, while there was strong, moderately

precise evidence that this was more likely to be by their mother if they were younger (Figure 3.4b). There was a small, precise effect for rank, with higher ranking participants more likely to be groomed although there was little evidence that mothers differentiated in this way. Similarly, while there was moderate, imprecise evidence that male participants were less likely to be groomed than females, there was little suggestion that mothers discriminated by offspring sex. AUC values for the first hurdle model were 0.62 and 0.54 for the full model and main effects respectively; those for the second hurdle model were 0.77 and 0.63.

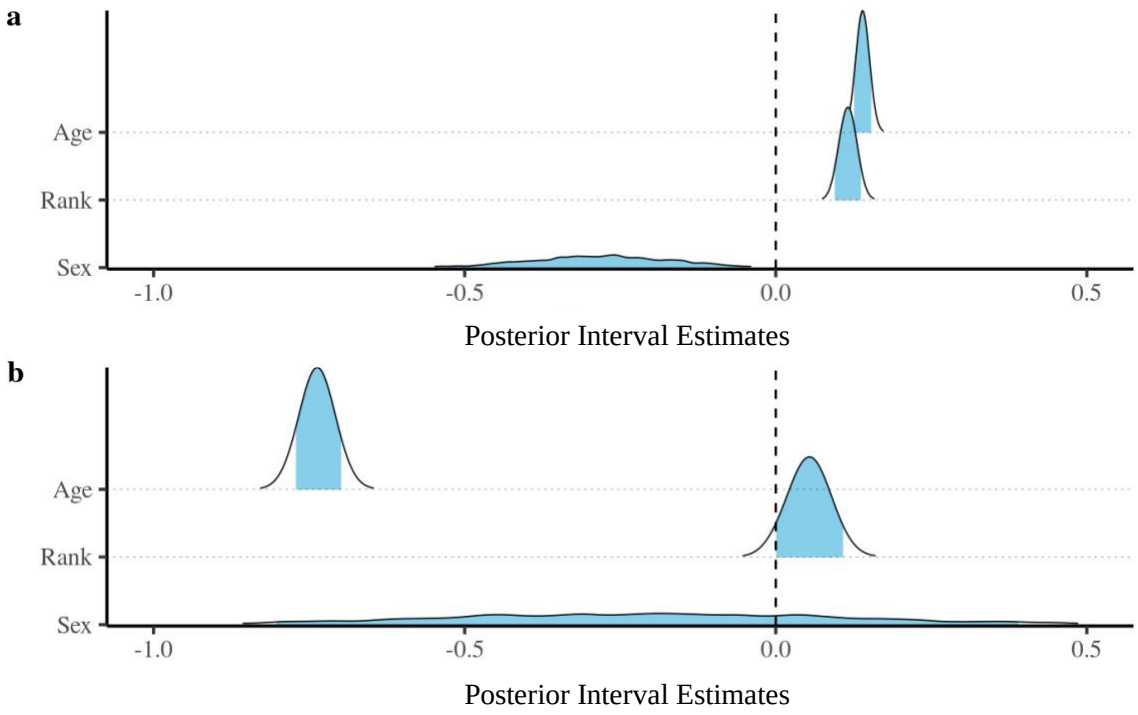


Figure 3.4. Posterior density estimates of the effects of sex, age and dominance rank on (a) the probability that nonadult participants would be groomed, and (b), if they were groomed, that it would be by their mothers. The blue fill is truncated to indicate the 95% credible intervals.

3.5 Discussion

Our results indicate that the likelihood and intensity of non-adult involvement in IGCs were associated with a suite of individual, situational and social factors.

Unsurprisingly, older, and therefore larger, more experienced, non-adults were increasingly likely both to participate and to do so with greater intensity. By the same token, neither males, despite greater weight-for-age (Jarrett et al., 2020), nor females, despite philopatric commitments to territorial defence (Heinsohn et al., 1996; Cords, 2007), were more invested in participation. While rank predicted participation, it had no effect on levels of aggression. In contrast, neophilia, as our index of boldness, although not predictive of participation itself, was associated with higher levels of aggression. The effect is small but in line with general expectation (Briffa, Sneddon, & Wilson, 2015) and, alongside evidence of temperamental consistency in the species (Blaszczyk, 2018), provides evidence for the early emergence of individuals that are 'key' to success in intergroup contests (Glowacki & McDermott, 2022).

Non-adults were also clearly sensitive to numerical asymmetries, being slightly less likely to participate if the overall size of their group was larger than that of their opponents; a finding in line with both theoretical (Olson, 1965) and empirical (Crofoot & Gilby, 2012; Mirville et al., 2018) expectations of increased free-riding in larger groups, at least by adult participants. They were, however, much more likely to participate themselves as the number of active participants—especially those from their own groups—increased (Model 1; Supplementary Figure 1). Rather than shying away from engagement, therefore, their engagement was proximally promoted by numerical advantage, suggesting that this buffered them from the increased risks they faced by virtue of their size and inexperience. Once committed to an IGC, and in line with this, the intensity of their aggression was negatively associated with the number of focal group participants but increased with the number of participants in the opposing group (Model

2). In this regard, their behaviour matched theoretical expectation, with greater commitment in the face of increased threat.

Socio-spatial integration measures were meaningful predictors in Models 1 and 2 but in different directions, with increased grooming EC being positively—and spatial EC negatively—associated with both participation and aggressive intensity. This apparent contradiction may perhaps be accounted for by the fact that grooming and spatial networks are generally dissociated in our population (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013). More specifically, non-adult spatial ties are to other non-adults, while grooming ties are strongly centred on their mothers (Vilette et al., 2023). Increased spatial integration, therefore, binds non-adults to group members who are intrinsically less likely to participate and to do so with lower intensity, while social integration runs through the mother.

By far the strongest positive predictor of non-adult grooming at the time of an IGC event was participation, followed by rank, grooming centrality, and situational conditions (group size, participant numbers) that likely reflected the general tenor and intensity of the IGC. There was no effect of age, despite the increasing likelihood of engagement. At the same time, despite the absence of sex differences in participation and aggression, and unlike the general pattern of grooming (Jarrett et al., 2018), females were more likely to be groomed during IGCs regardless of participation. Narrowing the analysis to participants indicated that grooming with non-adult participants was more likely if they were older, higher-ranking, or female, but that mothers themselves preferentially targeted only younger, more vulnerable offspring.

In concert, and reflecting the value of grooming as a 'carrot' (Arseneau-Robar et al., 2016), these outcomes are consistent with the differential reinforcement of attributes—higher rank, social connectedness and philopatry—likely to be important in the future, and, as indexed by age, current IGC effort. The role of the mother in the induction of offspring should be evaluated in this context. While our non-adults do not inherit maternal grooming networks, they do track them, and maternal self-similarity and integration are predictive of non-adult integration (Jarrett et al., 2018). This, along with the finding that maternal involvement and levels of aggression were the best social predictors of non-adult patterns of participation, suggests that mothers serve both as direct and, through their close adult associates, indirect drivers of differential non-adult engagement in IGCs.

Our findings support the idea that IGC participation can be promoted and potentially inculcated in young non-human animals despite the absence of formal cultural rules and linguistic social practices. There are, as always, reasons to urge caution in the direct extrapolation of these outcomes. First, IGC occurs at very high frequency in our population, and non-adults are exposed both regularly and frequently to aggression of this kind. They consequently have more opportunities simply to acquire the "habit" or "norm" of participation more readily than in other populations. Then, we cannot exclude the possibility that vervets possess some intrinsic potential to behave aggressively toward strange conspecifics, such that they are not being inducted into this behaviour via social processes, but simply maturing into it. This seems unlikely, given the patterning of our findings, but cannot be ruled out. Equally, it is not clear that IGC participation represents any kind of genuine prosocial behaviour, in the sense that animals possess 'other

regarding' preferences and act to generate a public good, and that animals can be free-riders under come conditions. That is, even if we can accept that non-adults are inducted to engage in IGC via social processes, we should still remain sufficiently skeptical, at present, as to whether these findings offer a useful and productive analogue for understanding the evolution of prosocial behaviour in our own species.

Assuming that our findings, at the very least, support the existence of social induction, we still need to characterize exactly what it is that non-adults are learning through development: is it both to respond aggressively to strangers, and to participate in IGC in risk-sensitive ways? Or are they discovering how to moderate an inherently aggressive response to strangers via attunement to the behaviour of their mothers and others, and responding to the contingencies of aggressive action and grooming rewards? Given previous findings on the development of anti-predator vocal communication (Dubreuil, Barrett, Henzi, Notman, & Pavelka, 2023), the latter is more likely, but it remains an open question.

If we accept that induction into (potentially pro-) social behavior occurs, then we can consider some intriguing corollaries. For example, Vygotsky (1997) argued that human children participate in social practices well before they have the capacity to understand them, and that it is only through this participation and—crucially—being treated by adults as though they already have the necessary comprehension, that they are able to develop an understanding of the situations in which they find themselves. Obviously, as stressed in the introduction, this is achieved through exposure to linguistic and highly structured sociocultural environments. Without drawing false comparisons, there is, however, some resemblance to the vervets here, in that much of children's early

cultural participation involves highly interactive, physically embodied activities—to put it colloquially, they simply take part, pitch in and have a go—and they respond, resist and react to the equally embodied social feedback they receive from those around them.

It is in this more limited sense that Vygotsky's ideas resonate with our finding that one of the best predictors of any kind of non-adult participation in our study was their mother's own participation—non-adult vervets also seem to be thrown into a world in which they first participate, and then gradually refine their responses with greater experience. Further, it suggests that a productive route for comparative analyses would be to build from the bottom-up, paying more attention to the kinds of embodied, sensorimotor socially interactive patterns that are shared by humans and non-human primates alike, and how these might form a scaffold for the kinds of highly elaborated sociocultural practices that facilitate the equally elaborate forms of coordination and cooperation that are so characteristic of human groups, both past and present (Barrett, Henzi, & Barton, 2022; see also Graziano, 2017).

CHAPTER 4: MEASURING COSINE SIMILARITY IN INTRAGROUP SOCIAL NETWORKS AND INTERGROUP CONFLICT NETWORKS

4.1 Introduction

Intergroup conflict (IGC) is one of the riskiest behaviours in which animals engage, as conflicts potentially may result in injury or death (De Dreu & Triki, 2022; Thompson, Marshall, Vitikainen, & Cant, 2017; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006). IGC usually occurs in the context of resource defence. This poses a collective action problem because all individuals in the group can reap the benefits won by cooperators regardless of whether they contribute any effort to achieving the goal. Individuals can therefore choose whether to cooperate and incur the risks associated with participation, or defect. Arseneau-Robar and colleagues (2017) have shown that participation in intergroup conflict varies not only between individuals, but also within individuals over time (Arseneau-Robar et al., 2017). Researchers have explored possible explanations for variable participation in IGCs, including individual and social factors (Arseneau-Robar et al., 2017; Koch et al., 2016; Cords, 2007; Chakraborty et al., 2023), as well as the likely nature of punishments and rewards (Arseneau-Robar et al., 2016).

The risks of participation in IGC are intrinsically higher for non-adults as they are both less experienced and smaller than adults. Despite the suggestion that juveniles should therefore be risk-averse and avoid IGC (Janson, 1993), research has shown that juveniles do, in fact, choose to cooperate (Heinsohn et al., 1996; Cords, 2007; Clarke et al., in review). Cords and colleagues (2007) found that there were both age and sex differences in participation among blue monkeys (*Cercopithecus mitis*), with adult females being more likely to participate than males. They also found that juveniles

participated in territorial defence at increasing rates with age and that the sex differences in participation increasingly matched those of the adults as they aged (Cords, 2007).

In the previous chapter, I showed that non-adult vervet monkeys (*Chlorocebus pygerythrus*) also participate in IGC and participate more aggressively as they get older. While this evidence demonstrates that juveniles incur the risks associated with cooperating in IGC, we still do not have a clear understanding of how they come to participate. Here, I offer the beginnings of an investigation into how juvenile participation comes about, making use of social network analysis.

Social network analysis (SNA) has been used to quantify relationships or interactions between individuals. Put simply, a social network consists of individuals (nodes) with interactions (edges) being drawn between them (Fig. 4.1). Gokcekus, Cole, Sheldon, and Firth (2021) suggest using SNA to understand how social structure may influence cooperative behaviours or how cooperation may influence social structure because, in some populations, the organization of individuals within their networks can either influence or impede the spread of cooperative behaviours spreading. As an example, Fehl, van der Post, and Semmann (2011) found that cooperation was more likely in dynamic networks, where human participants in a Prisoner's Dilemma game were given the choice to sever ties with co-participants after each social interaction. Using SNA, it is possible to explore how cooperation is maintained in terms of social structure as a whole rather than only at a dyadic level (Gokcekus et al., 2021).

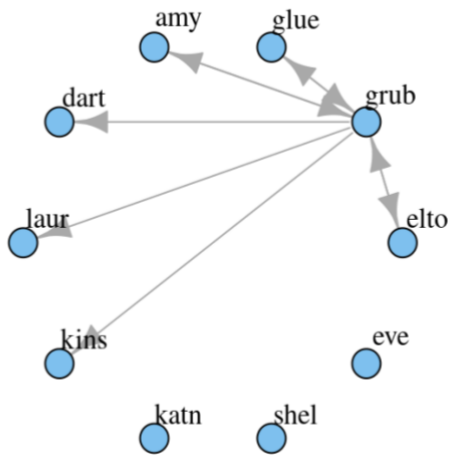


Figure 4.1 An example of a grooming ego network which is a network constructed from the point of view of one focal individual (grub). The nodes (circles) represent the individuals while the edges (arrows) drawn between them show grooming interactions. Interactions in grooming networks can be bidirectional or unidirectional as shown by the arrows. In this example, we can see that grub was observed grooming with some individuals, but not others (i.e., katn, shel, and eve).

There has been extensive research on how IGCs affect intragroup social structure (Radford, Majolo, & Aureli, 2016; di Sorrentino, Schino, Massaro, Visalberghi, & Aureli, 2012; Majolo, de Bortoli Vizioli, & Lehmann, 2016; Grueter, 2013; Mirville et al., 2020). However, the investigation of how intragroup social structure influences participation in IGC has been overlooked and, until recently, investigations on the influence of social structure on cooperation in IGC have been scarce in non-human animals (Chakraborty et al., 2023). In humans, it has been shown that the formation of raiding parties is influenced by social structure (Glowacki et al., 2016; Glowacki & McDermott, 2022). For example, Glowacki et al. (2016) showed that friends of raiding party leaders were more likely to join raids compared to friends of friends. As shown in the previous chapter, grooming and spatial eigenvector centrality measures correlate with

non-adult participation in IGCs. What remains to be investigated is whether and how intragroup social networks (grooming and spatial proximity) are related to IGC participation networks.

4.2 Predictions

Here, I examine whether non-adult intragroup social networks, grooming and spatial association, are similar to their IGC co-participation networks. I use cosine similarity values (Jarrett et al., 2018) to compare the structures of non-adult grooming, spatial association, and IGC participation ego networks across time. Cosine similarity measures how similar the patterns of the values are when comparing two vectors. Cosine values range between 0 and 1 with 0 being non-similar and 1 meaning the vectors are identical. My predictions are as follows:

Given our findings that grooming eigenvector centrality measures had a positive impact on participation while spatial association eigenvector centrality measures had a negative effect, I predict that (i) the grooming and IGC co-participation networks will be the most similar and (ii) that the spatial association and intergroup conflict networks will be the least similar. That is, I expect that individuals who groom each other will be more likely to co-participate in IGCs together. This makes intuitive sense as individuals can more actively choose who their grooming partners are compared to spatial association which is inherently less directed. In addition, grooming can be exchanged as a commodity for other services including cooperation in conflicts (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999). I also predict that (iii) on average, female non-adults will show higher cosine similarity as they age for both the comparison between the grooming and IGC networks and the spatial association and IGC networks than males. Previous research has shown

that female juvenile vervets in our population put increasing effort into their social networks as they age (Jarrett et al., 2018), and so I anticipate that this will hold true when exploring the similarities in the grooming, spatial association, and IGC participation networks.

4.3 Methods

4.3.1 *Social Networks and Data Extraction*

I created weighted, non-directed grooming, spatial association, and IGC participation ego networks (hereafter, networks) for non-adults using the 'netTS' package (Bonnell & Vilette, 2020) in R V 4.3.2(R-Core-Team, 2022). I used a window size of 365 days and a window shift of 90 days with the 'create.window' function to extract edge lists for each year (Bonnell & Vilette, 2020). I created grooming networks by extracting all occurrences of grooming or being groomed for all non-adults. Spatial association networks included all individuals within 3m of the focal individual. Finally, I created IGC participation networks by extracting dyads that included the target individual as well as any individual that was also seen participating in IGCs. I then compared the structure of the ego networks by extracting cosine similarity values between the three types of networks using the 'cosine' function in the 'lsa' package (Fridolin, 2022) which gave me a measure for the similarity between the grooming and IGC networks, the spatial association and IGC networks, and the grooming and spatial association networks.

4.3.2 *Statistical Analysis*

I constructed a model for each of my cosine similarity measures in the Bayesian framework using the 'brms' package (Bürkner, 2017). I used hierarchical generalized

additive mixed models (HGAM), which uses smoothing curves to allow a nonlinear trend to be estimated between explanatory and outcome variables without having to pre-specify the shape (Pedersen, Miller, Simpson, & Ross, 2019). All models were fit using a zero_one_inflated_beta distribution with four chains and 3500 iterations and used weakly informative priors (normal (0,1)). The outcome variable for each model is one of the three cosine similarity measures (model 1: cosine similarity between grooming and spatial association networks model 2: cosine similarity between grooming and IGC networks, model 3: cosine similarity between spatial association and IGC networks). Model 1 was constructed to confirm that the grooming and spatial association networks do not overlap completely and are, therefore, not highly correlated. For model 1, I included the individual's mean age (days) for each year, sex, and average troop size as explanatory variables in my models. I use age (days) and year in my models to control for time. I let the effect of age vary by sex using factor smooths (Pedersen et al., 2019). The number of scans for each year was included to control for sampling effort. I included year and birth cohort as crossed varying intercepts and ID and troop as a nested varying intercept. Models 2 and 3 were constructed using the same variables as model 1, but I added an interaction between age and sex to test my third prediction. All continuous variables were scaled and mean-centred.

I evaluated model performance using the 'pp_check' function in brms (Bürkner, 2017). Additionally, I used R̂s to confirm model convergence with all R̂s=<1.02 (Gelman & Shalizi, 2013). I calculated conditional and marginal R^2 values for the models using the 'bayes_r2' function (Bürkner, 2017) and probability of direction (pd) estimates using the 'p_direction' function in the 'bayestestR' package (Dominique et al., 2019).

To aid interpretation, I generated whole model predictions using the 'fitted' function in the brms package (Bürkner, 2017). I made predictions for variables of interest (age and sex) while all variables that were not of specific interest were fixed to their means (troop size and scan number). These values were then used to generate posterior predictive plots with the 'ggplot2' package (Wickham, 2009). I included 95% credible interval (CI) values due to their interpretative familiarity with estimates in the frequentist framework. Summary statistics for the main effects are listed in the results (Tables 1-3), along with R^2 values and pd estimates.

4.4 Results

4.4.1 *Grooming and Spatial Association Network Similarity*

The grooming and spatial association networks had an average cosine similarity value of 0.39, confirming that the networks do not overlap completely. Cosine similarity values varied across time both within and between the sexes (Table 4.1, Fig 4.2). On average, females had a cosine similarity value of 0.34 compared to 0.25 for the males. There was a negative effect for sex with males being less likely to have higher cosine similarity values, and also the number of scans on cosine similarity (Fig. 4.3). In addition, there was a small positive effect for troop size, but there is some uncertainty around this result as the credible interval range just crosses zero (CI= -0.01 to 0.19). 29% of the variance can be explained by the main effects only while the whole model accounts for 90%.

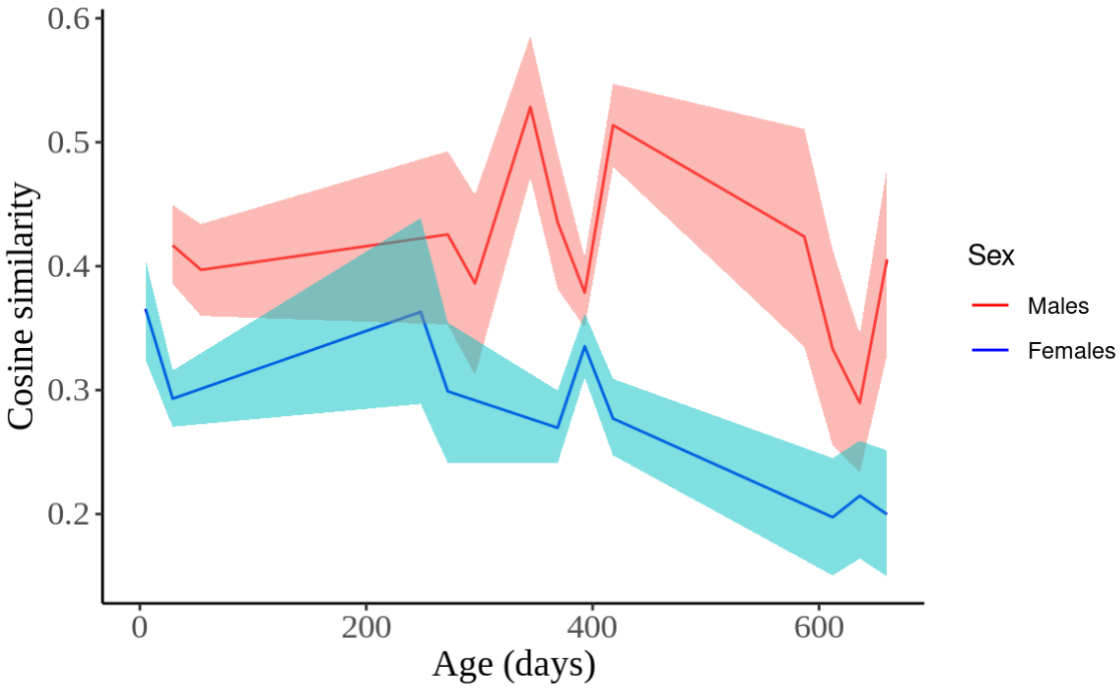


Figure 4.2 Variation in the cosine similarity values for the grooming and spatial association networks by age and sex. The red and blue lines represent each sex respectively, with the lower and upper 95% credible intervals shown with the bands.

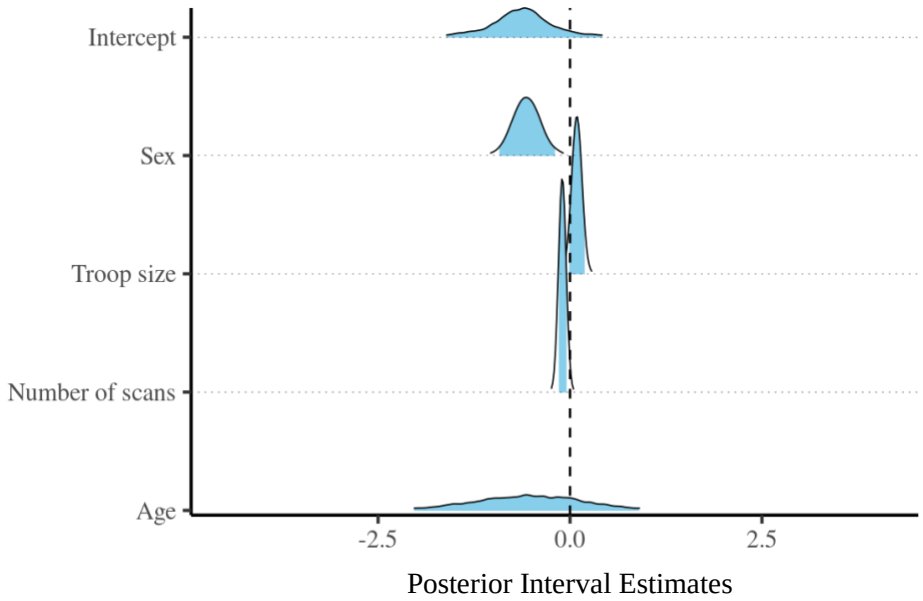


Figure 4.3 Posterior density estimates of the grooming and spatial association networks' cosine similarity in relation to sex (Ref: Female), troop size, and the number of scans.

4.4.2 Cosine Similarity Values Comparison

Contrary to my predictions, on average, the networks with the highest cosine similarity values were the spatial association and IGC networks, with a mean of 0.55. The grooming and IGC cosine similarity values had a mean of 0.49 (Fig 4.4 and Appendix B.4, B.5, and B.6).

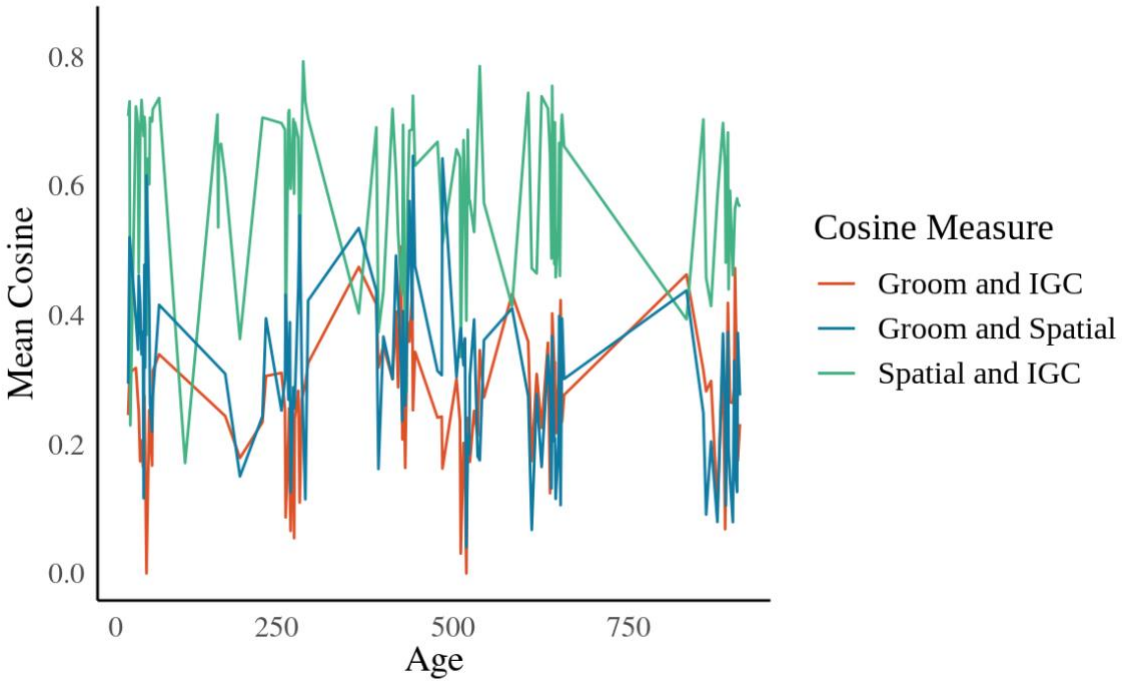


Figure 4.4 Line plot showing changes in the mean cosine similarity values for the three measures with age. Age is shown on the x-axis while the mean cosine similarity value is shown on the y-axis. The colours represent the 3 cosine similarity measures (red= grooming and IGC networks, blue= grooming and spatial association networks, and green= spatial association and IGC networks).

Table 4.1

Posterior estimates of population level changes in cosine similarity measures for the grooming and spatial association networks in relation to age and sex

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	-0.61	0.63	-1.91	0.81	3238	89.87
Sex (reference: female)	-0.57	0.18	-0.92	-0.20	4653	99.93
Troop size	0.09	0.05	-0.01	0.19	7390	95.67
Scan number	-0.10	0.02	-0.15	-0.05	12283	100
Age	-0.55	0.74	-2.05	0.89	6536	77.01

Troop size and scan number were entered as controls. ID and troop were entered as nested varying intercept and cohort and year were entered as crossed varying intercepts. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.29. $R^2_{conditional}$=0.90. N=368.

4.4.3 *Sex Differences Across Time Between Grooming and IGC Network Similarity*

Cosine similarity between the grooming and IGC participation networks were very similar between the sexes across time (Table 4.2: female average=0.28, male average=0.25; Fig. 4.5). I found no meaningful effects for the interaction between sex and age. There was a small positive effect for troop size on cosine similarity and no effect of the number of scans (Fig. 4.6). The main effects account for 13% of the variance, while the whole model accounts for 77%.

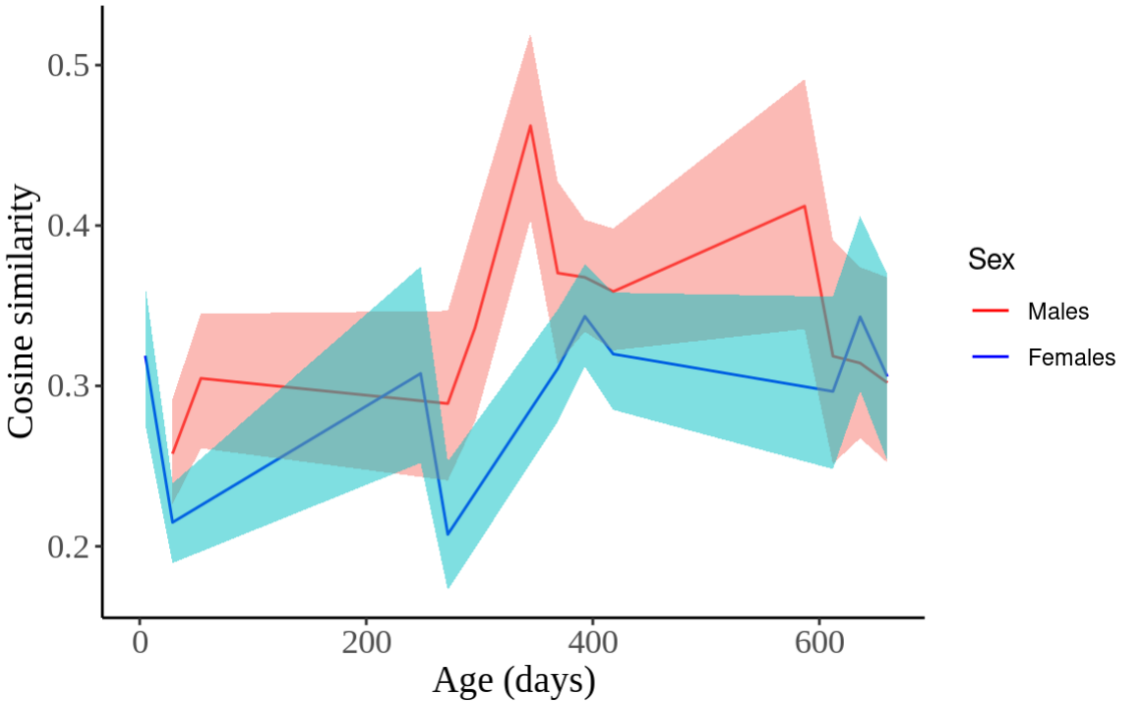


Figure 4.5 Variation in the cosine similarity values for the grooming and IGC participation networks by age and sex. The red and blue lines represent each sex respectively, with shading indicating the lower and upper 95% credible intervals.

Table 4.2

Posterior estimates of population level changes in cosine similarity measures for the grooming and IGC participation networks in relation to age and sex

	β	**SE**	**Lower 95% CI**	**Upper 95% CI**	**ESS**	**PD (%)**
Intercept	-1.02	0.64	-2.25	0.41	3405	95
Troop size	0.19	0.05	0.09	0.29	6451	100
Scan number	0.00	0.03	-0.05	0.06	11227	57.99
Female by Age	-0.26	0.73	-1.66	1.19	5292	64.76
Male by Age	-0.30	0.61	-1.33	1.02	4376	71.01

Troop size and scan number were entered as controls. ID and troop were entered as nested varying intercept and cohort and year were entered as crossed varying intercepts. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.13. $R^2_{conditional}$=0.77. N=368.

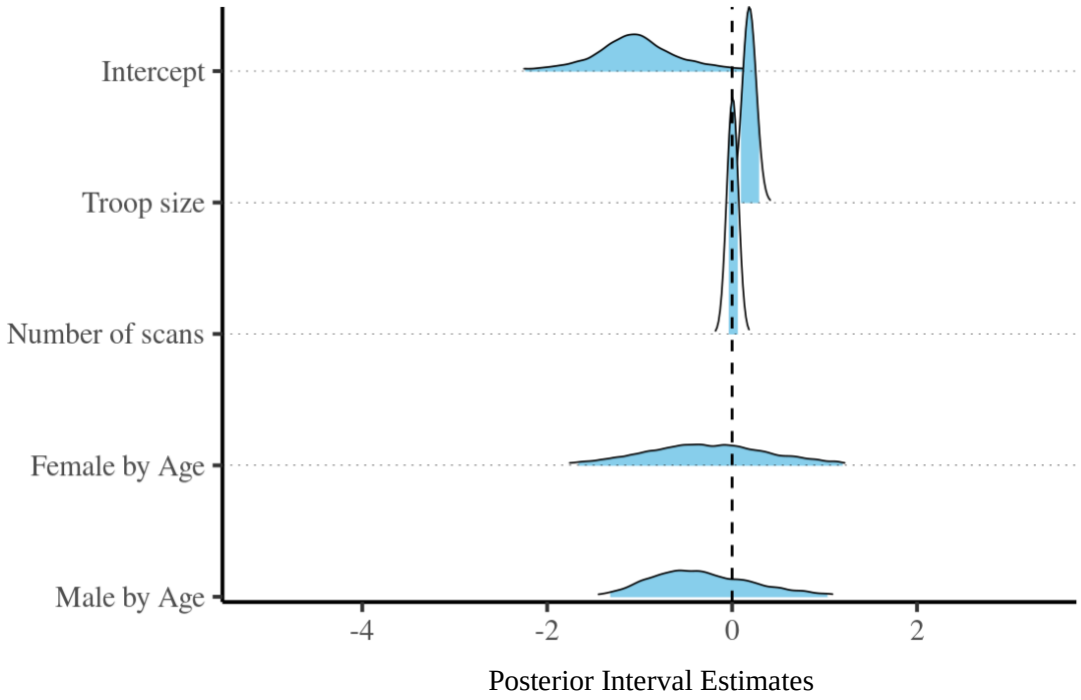


Figure 4.6 Posterior density estimates of the grooming and IGC networks' cosine similarity in relation to troop size, the number of scans, female by age, and male by age

4.4.4 *Sex Differences across Time Between Spatial Association and IGC Network Similarity*

When comparing the spatial association and IGC participation networks, the average cosine similarity values between the sexes are very similar (females=0.60, males=0.61) and I found no meaningful effect for the interaction between sex and age (Table 4.3, Fig 4.7). I found a positive effect for troop size and no effect for the number of scans (Fig. 4.8). 21% of the variance can be explained by the main effects while 90% can be explained by the whole model.

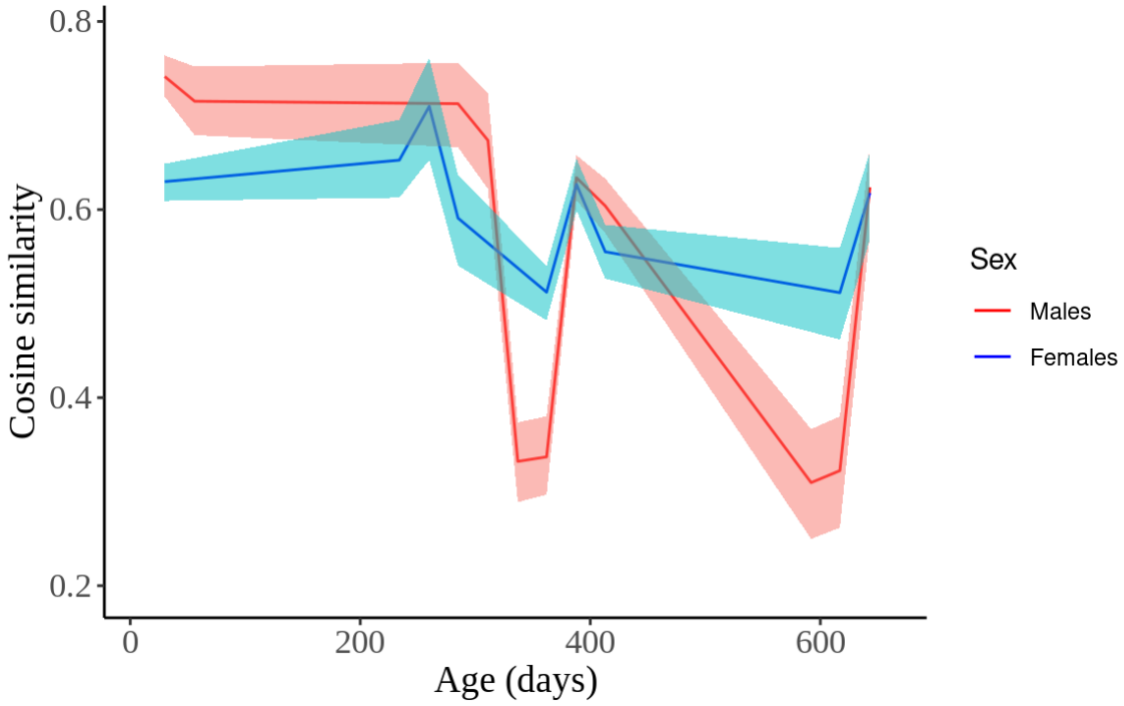


Figure 4.7 Variation in the cosine similarity values for the grooming and IGC participation networks by age and sex. The red and blue lines represent each sex respectively, with the lower and upper 95% credible intervals shown with the bands.

Table 4.3

Posterior estimates of population level changes in cosine similarity measures for the spatial association and IGC participation networks in relation to age and sex

	β	SE	Lower 95% CI	Upper 95% CI	ESS	PD (%)
Intercept	0.36	0.49	-0.71	1.34	4331	86
Troop size	0.36	0.04	0.28	0.44	5164	100
Scan number	0.01	0.02	-0.02	0.05	11460	82.04
Female by Age	-0.82	0.82	-2.28	0.93	6121	84.04
Male by Age	0.26	0.92	-1.49	2.12	10316	61.21

Troop size and scan number were entered as controls. ID and troop were entered as nested varying intercept and cohort and year were entered as crossed varying intercepts. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.21. $R^2_{conditional}$=0.90. N=395.

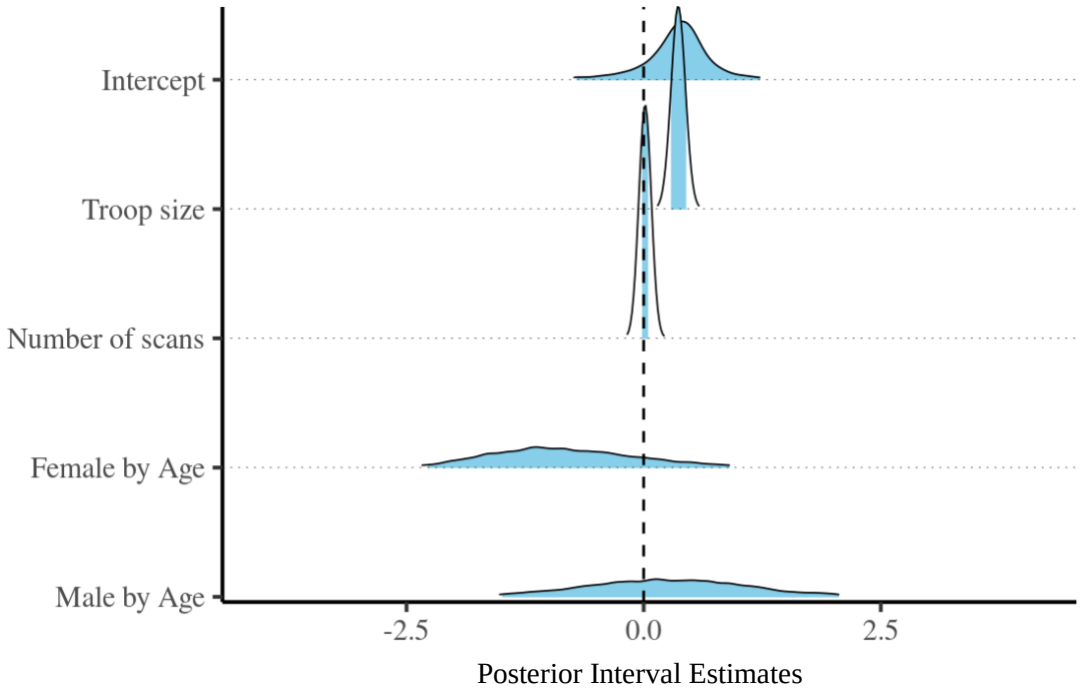


Figure 4.8 Posterior density estimates of the spatial association and IGC networks' cosine similarity in relation to troop size, the number of scans, female by age, and male by age.

4.5 Discussion

Contrary to my prediction, I found that the spatial association and IGC networks were the most similar through time, rather than the grooming and IGC networks—although the latter did show some degree of overlap. As non-adults have more individuals in their spatial association networks compared to their grooming networks (Vilette et al. 2022), this result may simply reflect the greater likelihood that spatial partners will also be participants in IGC, given their greater availability. This, in turn, suggests the possibility that non-adults are not being drawn actively into participating through their spatial association partners, but are acting in an independent but coordinated fashion with others of their cohort.

The fact that the grooming and IGC networks showed some degree of similarity across time suggests there is a relationship between grooming and IGC, although we need to be aware of reverse causality here, where participation in IGC may lead to subsequent grooming partnerships, rather than grooming partners inducing juveniles to participate. Thus, in the case of both spatial and grooming networks, the relationship to IGC remains somewhat inconclusive. This reflects the fact that the real question of interest here is whether *particular* individuals can draw non-adults into IGCs, and this is not something the current analyses can address. Future studies should explore whether specific individuals appear in non-adult social and IGC networks, and if their attributes, such as rank, are influencing the participation networks. Glowacki et al. (2022) have shown that key individuals in human groups draw other members of the group into intergroup violence. While it is unlikely to be the same in non-human primates, it is possible that the attributes of social partners and cooperators may encourage non-adults to participate. Additionally, in my analyses, I did not consider the order in which individuals joined the IGC. It may also be beneficial to consider a sequence of events to determine if there are key individuals joining and others follow suit.

Unexpectedly, I found no meaningful effects for the interaction between sex and age for both cosine similarity comparisons. A non-adult's age and sex does not influence whether their grooming and IGC networks or their spatial association and IGC networks will be similar. My current analyses are correlational and do not allow me to see the mechanisms underlying non-adult participation in IGCs. Future analyses that take a causal approach to investigating the influence of intragroup social structure on IGC participation may find a difference between the sexes.

CHAPTER 5: DISCUSSION AND CONCLUSIONS

In this thesis, I aimed to understand the development of IGC participation in a non-linguistic population of wild vervet monkeys on the Samara Private Game Reserve in South Africa. In Chapter 1, I identified three hypotheses to explain how non-adults come to participate in IGC— that participation is influenced by intrinsic individual and social attributes, that it is regulated through reward, and that it is socially facilitated. Here, I will summarize my findings, list the limitations of my study, and provide directions for future research.

5.1 Is Participation Influenced by Individual, Social, or Situational Factors?

I found that there are individual and social attributes, as well as situational factors, that influence non-adult participation in IGCs. Similar to findings in blue monkeys (Cords 2007), I found that non-adults were more likely to participate in IGC, and to participate more intensely as they aged. In contrast to Cords (2007), I found no sex differences in the likelihood of participation nor the intensity of participation. Dominance rank predicted participation but did not predict the intensity of participation. Specifically, higher-ranking individuals were more likely to participate in IGC, which is in line with both my own prediction and with previous findings in blue monkeys (Cords, 2007). Neophilia, or boldness, predicted the intensity of participation, with bolder individuals being more likely to participate aggressively compared to less bold individuals. However, we found no effect of neophilia on the overall likelihood of participation.

I found that socio-spatial integration influenced both the probability that non-adults would participate in IGC and that they would participate more aggressively.

However, we found that the measures for the grooming and spatial association networks affected participation in opposite ways. A higher eigenvector centrality score for the grooming network increased both the likelihood of participation and its intensity. In contrast, individuals with higher spatial eigenvector centrality scores were less likely to participate and less likely to participate intensely.

Maternal participation increased the likelihood of non-adult participation and its intensity. Non-adults were more likely to participate in IGC if their mother also participated. Additionally, they tracked their mother's intensity of participation. Here, I used maternal participation as a stand-in for their matriline as a whole, as it can be assumed that if one offspring is more likely to participate because their mother does, it is likely that other offspring will do the same. However, we may be able to gain a better understanding of how kin affects participation by also exploring the influence of siblings on non-adult participation.

Non-adults were less likely to participate in IGC as group size increased, which is to be expected given previous findings that free-riding is more likely in larger groups (Olson, 1965; Crofoot & Gilby, 2012; Mirville et al., 2018). However, they were more likely to participate in IGC if there were more contestants from the opposing group and even more likely to participate as the number of participants in their own group grew. This is likely due to numerical superiority where the risks involved in participating are decreased. In line with this, non-adults participated less intensely when there were more contestants from their own group, but participated more intensely when there were more contestants in the opposing group.

5.2 Regulation Through Reward

My findings show that non-adults are more likely to be groomed during IGC if they participated in IGC. As focal group size increased, and the number of contestants in both the focal group and opposing group also increased, so did the likelihood that non-adults would be groomed during IGC. Higher-ranking non-adults were also slightly more likely to be groomed. In addition, grooming and spatial eigenvector centrality scores had the same relationship to grooming as they did with participation: higher eigenvector centrality scores for the grooming networks increased the likelihood of being groomed and higher spatial association decreased the likelihood of grooming. In contrast to our lack of findings for sex, our results here suggested that males are less likely to be groomed during IGC than females. When I narrowed my analyses to only the non-adults who participated, I found that being an older, higher-ranking, or female non-adult increased the likelihood of being groomed during participation in IGC. However, mothers preferentially groomed younger, more vulnerable offspring.

While I aimed to investigate whether grooming could be used as a reward for participating in IGC, it was not possible to establish a sequence of events in the data. All I can state at present is that grooming is indeed more likely during IGC if an individual took part, but I cannot conclude that grooming was used as reward, as I cannot establish whether grooming occurred before or after participation in an IGC. Future research should explore the timing of the grooming relative to participation, to determine whether the latter is regulated through the use of directed grooming as a reward.

5.3 Social Facilitation

I found some support for participation being socially facilitated by intragroup social partners. Unexpectedly, I found no precise effects for age and sex on the cosine similarity values for both of the comparisons.

There are structural similarities between the grooming, spatial association, and participation ego networks. Contrary to my findings that spatial association eigenvector centrality scores decreased the likelihood of participation, I found that spatial association and IGC participation networks were, on average, the most structurally similar. This may be due to non-adults having more spatial partners compared to grooming partners so that there was a higher likelihood of those partners also taking part in IGC, especially when we consider the finding that non-adults were more likely to participate in IGC if more of their group members also participated. This is in line with previous findings from our population that non-adults have more spatial partners than they do grooming partners (Vilette et al., 2022). In the future, it may be beneficial to not only explore structural similarities in the networks, but also determine whether there are key individuals that exert greater influence compared to others, and so draw their social partners into participating in IGC.

It may also be beneficial to consider play networks when exploring how social partners influence juvenile participation. Funk (2022) found that juvenile-juvenile dyads accounted for the majority (94.6%) of play bouts in vervet monkeys, and juvenile-adult dyads accounting for only 5.3% of play bouts. Shimada and Sueur (2018) found that play strengthens social bonds in immature Japanese macaques (*Macaca fuscata*) and suggest that play may be an introduction to juveniles socializing with individuals beyond their

mothers. In future research, it may be beneficial to use a dynamic multilayer network analysis with grooming, spatial association, play, and IGC participation networks to determine which social networks are influencing each other and how these influences change over time.

5.6 Conclusion

Taken together, my findings show that non-adult participation is not only mediated by individual attributes, social factors, situational factors, reward, or social facilitation. Rather, non-adult cooperation in IGC depends on a suite of variables. I found some support for the three hypotheses I tested. There are several individual, social, and situational factors that influence non-adult cooperation in IGCs including rank, personality, age, group size, the number of contestants, and maternal participation. I cannot conclude that non-adults in our population are being rewarded for cooperating due to not having a sequence of events, but I have shown that they are more likely to be groomed during IGC if they have participated. Finally, I found that there are structural similarities in nonadult grooming, spatial association, and IGC co-participation networks which provides evidence that participation may depend, at least to some extent, on whether intragroup social partners are participating.

My findings support the idea that non-adults do participate in IGCs despite the absence of formal cultural norms and language. It is still unclear whether participating in IGCs is in fact prosocial as individuals do still choose to free-ride under some conditions and it is difficult to rule out whether vervets have an intrinsic trait that causes them to behave aggressively toward out-group members. With this in mind, I cannot conclude that participation in IGCs offers a useful comparison for investigating the evolution of

prosocial behaviours in humans. It is possible that non-adults begin participating in IGCs, then alter their responses based on the social feedback they receive from other group members. If this is the case, it suggests that a more productive route for future comparative analyses on the evolution of cooperation would be to take a bottom-up approach by focusing on socially interactive patterns that are shared by humans and non-human primates alike.

REFERENCES

Abbink, K., Brandts, J., Herrmann, B., & Orzen, H. (2012). Parochial altruism in inter-group conflicts. *Economics Letters*, *117*(1), 45-48.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3-4), 227-266.

Arseneau-Robar, T. J. M., Taucher, A. L., Schnider, A. B., van Schaik, C. P., & Willems, E. P. (2017). Intra-and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Animal behaviour*, *123*, 129-137.

Arseneau-Robar, T. J., Taucher, A. L., Müller, E., van Schaik, C., Bshary, R., & Willems, E. P. (2016). Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. *Proc Biol Sci*, *283*, 20161817. doi:10.1098/rspb.2016.1817

Axelrod, R. (1986). An evolutionary approach to norms. *American political science review*, *80*(4), 1095-1111.

Axelrod, R. (2001). The Evolution of Cooperation. *Breakthrough, http://www-ee. stanford. edu/\~ hellman/Breakthrough/book/contents. html*.

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *science*, *211*(4489), 1390-1396.

Barrett, L., Henzi, S. P., & Barton, R. A. (2022). Experts in action: why we need an embodied social brain hypothesis. *Philos Trans R Soc Lond B Biol Sci*, *377*(1844), 20200533. doi:10.1098/rstb.2020.0533

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *266*, 665-670.

Blaszczyk, M. B. (2018). Consistency in social network position over changing environments in a seasonally breeding primate. *Behavioral Ecology and Sociobiology*, *72*(1), 1-11. doi:10.1007/s00265-017-2425-y

Blersch, R. A., Bonnell, T. R., Clarke, M., Dostie, M. J., Lucas, M., Jarrett, J., . . . others. (2023). Maternal social position and survival to weaning in arid-country vervet monkeys. *American Journal of Biological Anthropology*, *181*(1), 3-9.

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Ta\”\i National Park: lethal violence and the female perspective. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *70*(6), 519-532.

Bonnell, T. R., & Vilette, C. (2020). Constructing and analysing time-aggregated networks: The role of bootstrapping, permutation and simulation. *Methods in Ecology and Evolution*, *12*(1), 114-126.

Bossema, I., & Benus, R. F. (1985). Territorial defence and intra-pair cooperation in the carrion crow (Corvus corone). *Behavioral Ecology and Sociobiology*, *16*, 99-104.

Bowles, S. (2008). Being human: Conflict: Altruism's midwife. *Nature*, *456*(7220), 326-327. Retrieved from http://www.nature.com/nature/journal/v456/n7220/full/456326a.html

Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, *324*(5932), 1293-1298.

Boyd, R., & Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1533), 3281-3288.

Briffa, M., Sneddon, L. U., & Wilson, A. J. (2015). Animal personality as a cause and consequence of contest behaviour. *Biology Letters*, *11*(3), 20141007.

Brush, E. R., Krakauer, D. C., & Flack, J. C. (2013). A family of algorithms for computing consensus about node state from network data. *PLoS computational biology*, *9*(7), e1003109.

Bshary, R., Richter, X. L., & van Schaik, C. (2022). Male services during between-group conflict: the 'hired gun' hypothesis revisited. *Philos Trans R Soc Lond B Biol Sci*, *377*(1851), 20210150. doi:10.1098/rstb.2021.0150

Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., . . . van Schaik, C. P. (2014). The evolutionary origin of human hyper-cooperation. *Nat Commun*, *5*, 4747. doi:10.1038/ncomms5747

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software*, *80*, 1-28.

Bürkner, P.-C., & Charpentier, E. (2020). Modelling monotonic effects of ordinal predictors in Bayesian regression models. *British Journal of Mathematical and Statistical Psychology*, *73*(3), 420-451.

Burt, R. S. (2000). The network structure of social capital. *Research in organizational behavior*, *22*, 345-423. Retrieved from http://www.paulallen.ca/documents/2014/10/burt-rs-the-network-structure-of-social-capital-2000.pdf

Butynski, T. M. (1988). *Guenons birth seasons and correlates with rainfall and food. In (A. Gautier-Hion, F. Bourliere, J. Gautier \& J. Kingdon, eds.) A Prinlate Radiation*. Cambridge University Press, Cambridge.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., . . . Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of statistical software*, *76*.

Carter, G. (2014). The reciprocity controversy. *Animal Behavior and Cognition*, *1*(3), 368-386.

Chakraborty, B., Kaburu, S. S. K., Balasubramaniam, K. N., Marty, P. R., Beisner, B., Bliss-Moreau, E., . . . McCowan, B. (2023). Intragroup sociality drives individual participation in intergroup competition in an urban-dwelling nonhuman primate. *bioRxiv*, 2023-2009.

Cheney, D. L. (1981). Intergroup encounters among free-ranging vervet monkeys. *Folia Primatologica*, *35*(2-3), 124-146. Retrieved from http://eutils.ncbi.nlm.nih.gov/entrez/eutils/elink.fcgi?dbfrom=pubmed&id=7196367&retmode=ref&cmd=prlinks

Cheney, D. L., & Seyfarth, R. M. (1987). The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behavioral Ecology and Sociobiology*, *21*(6), 375-386. Retrieved from http://link.springer.com/article/10.1007/BF00299932

Cheney, D. L., & Seyfarth, R. M. (1998). Why animals don't have language. *Tanner lectures on human values*, *19*, 173-210.

Choi, J.-K., & Bowles, S. (2007). The coevolution of parochial altruism and war. *science*, *318*(5850), 636-640.

Chudek, M., & Henrich, J. (2011). Culture--gene coevolution, norm-psychology and the emergence of human prosociality. *Trends in Cognitive Sciences*, *15*(5), 218-226.

Clarke, M., Bonnell, T. R., Blersch, R. A., Nord, C., Vilette, C., Young, C., . . . Barrett, L. (in review). Social Induction and the Developmental Trajectory of Participation in Intergroup Conflict by Vervet Monkeys. *Proceedings of the National Academy of Sciences*.

Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*(7269), 51-57.

Cords, M. (2002). Friendship among adult female blue monkeys (Cercopithecus mitis). *Behaviour*, *139*(2), 291-314.

Cords, M. (2007). Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. *Behaviour*, *144*(12), 1537-1550. Retrieved from http://www.springerlink.com/index/084JP64W430X2722.pdf

Crockett, C. M., & Pope, T. (1988). Inferring patterns of aggression from red howler monkey injuries. *American Journal of Primatology*, *15*(4), 289-308.

Crofoot, M. C., & Gilby, I. C. (2012). Cheating monkeys undermine group strength in enemy territory. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(2), 501-505. doi:10.1073/pnas.1115937109

Crofoot, M. C. (2013). The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors. *American journal of physical anthropology*, *152*(1), 79-85.

Crofoot, M. C., Rubenstein, D. I., Maiya, A. S., & Berger-Wolf, T. Y. (2011). Aggression, grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from social networks. *American Journal of Primatology*, *73*(8), 821-833.

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup aggression in primates and humans: the case for a unified theory. In *Mind The Gap* (pp. 171-195). Springer.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, *1695*, 1-9.

De Dreu, C. K. W., & Triki, Z. (2022). *Intergroup conflict: origins, dynamics and consequences across taxa* (377(1851)). The Royal Society.

di Sorrentino, E. P., Schino, G., Massaro, L., Visalberghi, E., & Aureli, F. (2012). Between-group hostility affects within-group interactions in tufted capuchin monkeys. *Animal Behaviour*, *83*(2), 445-451.

Dominique, M., Mattan, S. B.-S., Daniel, & Lüdecke. (2019). bayestestR: Describing Effects and their Uncertainty, Existence and Significance within the Bayesian Framework. *Journal of Open Source Software*, *4*(40), 1541. doi:10.21105/joss.01541

Dubreuil, C., Barrett, L., Henzi, P. S., Notman, H., & Pavelka, M. S. M. (2023). Age differences in the responses of vervet monkeys, Chlorocebus pygerythrus, to terrestrial alarm calls. *Animal Behaviour*, *201*, 87-100. doi:10.1016/j.anbehav.2023.04.014

Dugatkin, L. (2002). Animal cooperation among unrelated individuals. *Naturwissenschaften*, *89*, 533-541.

Dyble, M., Houslay, T. M., Manser, M. B., & Clutton-Brock, T. (2019). Intergroup aggression in meerkats. *Proceedings of the Royal Society B*, *286*(1917), 20191993.

Fehl, K., van der Post, D. J., & Semmann, D. (2011). Co-evolution of behaviour and social network structure promotes human cooperation. *Ecology letters*, *14*(6), 546-551.

Fehr, E. (2004). Human behaviour: Don't lose your reputation. *Nature*, *432*(7016), 449.

Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young children. *Nature*, *454*(7208), 1079.

Fehr, E. E., & Gächter, S. S. (2002). Altruistic punishment in humans. *Nature*, *415*(6868), 137-140. doi:10.1038/415137a

Foerster, S., Cords, M., & Monfort, S. L. (2011). Social behavior, foraging strategies, and fecal glucocorticoids in female blue monkeys (Cercopithecus mitis): potential fitness benefits of high rank in a forest guenon. *American Journal of Primatology*, *73*(9), 870-882.

Fridolin, W. (2022). *lsa: Latent Semantic Analysis*. Retrieved from https://CRAN.R-project.org/package=lsa

Funk, K. R. (2022). *Play partner preferences in wild vervet monkeys.* Lethbridge, Alta.: University of Lethbridge, Dept. of Psychology.

Gabry, J., & Mahr, T. (2017). bayesplot: Plotting for Bayesian models. *R package version*, *1*(0).

Gao, L., Wang, Z., Pansini, R., Li, Y. T., & Wang, R. W. (2015). Collective punishment is more effective than collective reward for promoting cooperation. *Scientific Reports*, *5*, 17752. doi:10.1038/srep17752

Garber, P. A., & Kowalewski, M. K. (2011). Collective action and male affiliation in howler monkeys (Alouatta caraya) Origins of altruism and cooperation. In (pp. 145-165). Springer.

García, M. G., de Guinea, M., Bshary, R., & van de Waal, E. (2022). Drivers and outcomes of between-group conflict in vervet monkeys. *Philos Trans R Soc Lond B Biol Sci*, *377*(1851), 20210145. doi:10.1098/rstb.2021.0145

Gelman, A., & Shalizi, C. R. (2013). Philosophy and the practice of Bayesian statistics. *British Journal of Mathematical and Statistical Psychology*, *66*(1), 8-38.

Glowacki, L., Isakov, A., Wrangham, R. W., McDermott, R., Fowler, J. H., & Christakis, N. A. (2016). Formation of raiding parties for intergroup violence is mediated by

social network structure. *Proceedings of the National Academy of Sciences*, *113*(43), 12114-12119.

Glowacki, L., & McDermott, R. (2022). Key individuals catalyse intergroup violence. *Philosophical Transactions of the Royal Society B*, *377*(1851), 20210141.

Glowacki, L., & Wrangham, R. W. (2013). The role of rewards in motivating participation in simple warfare. *Human Nature*, *24*(4), 444-460.

Gokcekus, S., Cole, E. F., Sheldon, B. C., & Firth, J. A. (2021). Exploring the causes and consequences of cooperative behaviour in wild animal populations using a social network approach. *Biological Reviews*, *96*(5), 2355-2372.

Graziano, M. (2017). *The spaces between us: a story of neuroscience, evolution, and human nature*. Oxford, UK: Oxford University Press.

Grueter, C. C. (2013). No effect of inter-group conflict on within-group harmony in non-human primates. *Communicative \& Integrative Biology*, *6*, e26801.

Hamilton, W. D. (1963). The evolution of altruistic behavior. *The American Naturalist*, *97*(896), 354-356.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of theoretical biology*, *7*(1), 1-16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of theoretical biology*, *7*(1), 17-52.

Harrison, M. J. S. (1983). Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. *Behavioral Ecology and Sociobiology*, *12*(1), 85-94. Retrieved from http://www.springerlink.com/index/U73NG25282875638.pdf

Hausfater, G. (1972). Intergroup behavior of free-ranging rhesus monkeys (*Macaca mulatta*). *Folia Primatologica*, *18*(1-2), 78-107.

Heinsohn, R., Packer, C., & Pusey, A. E. (1996). Development of cooperative territoriality in juvenile lions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *263*(1369), 475-479.

Henrich, J., & Henrich, N. (2006). Culture, evolution and the puzzle of human cooperation. *Cognitive systems research*, *7*(2-3), 220-245.

Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, *40*(1), 47-59. Retrieved from http://link.springer.com/article/10.1007/BF02557701

Henzi, S. P., Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20120351. doi:10.1098/rstb.2012.0351

Henzi, S. P., Bonnell, T., Pasternak, G. M., Freeman, N. J., Dostie, M. J., Kienzle, S., . . . Barrett, L. (2021). Keep calm and carry on: reactive indifference to predator encounters by a gregarious prey species. *Animal Behaviour*, *181,* 1-11. doi:10.1016/j.anbehav.2021.08.024

Henzi, S. P., Blersch, R. A., Bonnell, T. R., Clarke, M., Dostie, M. J., Lucas, M., . . . Barrett, L. (2023). Estimates of life history parameters in a high latitude, arid-country vervet monkey population. *Am J Primatol*, e23527. doi:10.1002/ajp.23527

Isbell, L. A., Pruetz, J. D., Lewis, M., & Young, T. P. (1999). Rank differences in ecological behavior: a comparative study of patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*). *International Journal of Primatology*, *20*(2), 257-272. Retrieved from http://www.springerlink.com/index/H82M536110913547.pdf

Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (1991). Group fusions and minimum group sizes in vervet monkeys (Cercopithecus aethiops). *American Journal of Primatology*, *25*(1), 57-65.

Janson, C. H. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. *Juvenile primates: Life history, development, and behavior*, 57-74.

Jarrett, J. D., Bonnell, T., Jorgensen, M. J., Schmitt, C. A., Young, C., Dostie, M., . . . Henzi, S. P. (2020). Modeling variation in the growth of wild and captive juvenile vervet monkeys in relation to diet and resource availability. *American Journal of Physical Anthropology*, *171*(1), 89-99. doi:10.1002/ajpa.23960

Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proc Biol Sci*, *285*(1876). doi:10.1098/rspb.2017.2668

Johnson, P. T., Valerio, D. A., & Thompson, G. E. (1973). Breeding the African green monkey, Cercopithecus aethiops, in a laboratory environment. *Laboratory Animal Science*, *23*(3), 355-359.

Kissel, M., & Kim, N. C. (2019). The emergence of human warfare: Current perspectives. *American Journal of Physical Anthropology*, *168*, 141-163.

Kitchen, D., & Beehner, J. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour*, *144*(12), 1551-1581.

Koch, F., Signer, J., Kappeler, P. M., & Fichtel, C. (2016). Intergroup encounters in Verreaux's sifakas (Propithecus verreauxi): who fights and why? *Behavioral Ecology and Sociobiology*, *70*, 797-808.

Kowalewski, M. M., & Garber, P. A. (2015). Solving the collective action problem during intergroup encounters: the case of black and gold howler monkeys (*Alouatta caraya*). In M. M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler Monkeys* (pp. 165-189). New York, NY: Springer New York. doi:10.1007/978-1-4939-1960-4_7

Lazić, A., Purić, D., & Krstić, K. (2021). Does parochial cooperation exist in childhood and adolescence? A meta-analysis. *International Journal of Psychology*, *56*(6), 917-933.

Lee, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. *Primates*, *25*(1), 36-47.

Lewis, R. J., Sandel, A. A., Hilty, S., & Barnett, S. E. (2020). The collective action problem but not numerical superiority explains success in intergroup encounters in Verreaux's sifaka (Propithecus verreauxi): Implications for individual participation and free-riding. *International Journal of Primatology*, *41*, 305-324.

Lukas, D., & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in mammals. *Royal Society open science*, *4*(1), 160897.

Majolo, B., de Bortoli Vizioli, A., & Lehmann, J. (2016). The effect of intergroup competition on intragroup affiliation in primates. *Animal Behaviour*, *114*, 13-19.

Makowski, D., Ben-Shachar, M. S., & Lüdecke, D. (2019). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software*, *4*(40), 1541.

Mathew, S., & Boyd, R. (2011). Punishment sustains large-scale cooperation in prestate warfare. *Proceedings of the National Academy of Sciences*, *108*(28), 11375-11380.

Mertz, J., Surreault, A., van de Waal, E., & Botting, J. (2019). Primates are living links to our past: The contribution of comparative studies with wild vervet monkeys to the field of social cognition. *Cortex*, *118*, 65-81.

Miller, L. (1998). Fatal attack among wedge-capped capuchins. *Folia Primatologica*, *69*(2), 89-92.

Mirville, M. O., Ridley, A. R., Samedi, J. P. M., Vecellio, V., Ndagijimana, F., Stoinski, T. S., & Grueter, C. C. (2018). Factors influencing individual participation during intergroup interactions in mountain gorillas. *Animal Behaviour*, *144*, 75-86.

Mirville, M. O., Ridley, A. R., Samedi, J. P. M., Vecellio, V., Ndagijimana, F., Stoinski, T. S., & Grueter, C. C. (2020). Intragroup behavioral changes following intergroup conflict in mountain gorillas (Gorilla beringei beringei). *International Journal of Primatology*, *41*(2), 382-400.

Moll, H., & Tomasello, M. (2007). Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1480), 639-648. doi:10.1098/rstb.2006.2000

Montgomery, T. M., Lehmann, K. D. S., Gregg, S., Keyser, K., McTigue, L. E., Beehner, J. C., & Holekamp, K. E. (2023). Determinants of hyena participation in risky collective action. *Proceedings of the Royal Society B*, *290*(2011), 20231390.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., . . . Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911-921.

Neumann, C., & Kulik, L. (2020). Animal dominance hierarchies by Elo rating. *https://cran.r-project.org/web/packages/EloRating/EloRating.pdf*.

Nord, C., Bonnell, T., Roth, D., Clarke, M., Dostie, M., Henzi, P., & Barrett, L. (2022). Fear of missing out? Personality and plasticity in food neophilia by wild vervet monkeys, Chlorocebus pygerythrus. *Animal Behaviour*, *191*, 179-190. doi:10.1016/j.anbehav.2022.07.002

Nord, C. M., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2021). Tolerance of muzzle contact underpins the acquisition of foraging information in vervet monkeys (Chlorocebus pygerythrus). *Journal of Comparative Psychology*, *135*(3), 349.

Nord, C. M. (2021). *The contexts of social learning in wild vervet monkeys.* PhD. University of Lethbridge, Lethbridge.

Nunn, C. L., & Deaner, R. O. (2004). Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (Lemur catta). *Behavioral Ecology and Sociobiology*, *57*, 50-61.

Olson, M. (1965). *The Logic of Collective Action: Public Goods and the Theory of Groups*. Cambridge, Mass.: Harvard University Press.

Ostrom, E. (2000). Collective action and the evolution of social norms. *Journal of economic perspectives*, *14*(3), 137-158.

Packer, C. (1977). Reciprocal altruism in Papio anubis. *Nature*, *265*(5593), 441-443.

Palombit, R. A. (1993). Lethal territorial aggression in a white-handed gibbon. *American Journal of Primatology*, *31*(4), 311-318.

Pasternak, G. M., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L., & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe*, *55*, 1-9. doi:10.4102/koedoe.v55i1.1078

Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ*, *7*, e6876.

R-Core-Team. (2022). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Radford, A. N., Majolo, B., & Aureli, F. (2016). Within-group behavioural consequences of between-group conflict: a prospective review. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161567.

Raihani, N. J., Thornton, A., & Bshary, R. (2012). Punishment and cooperation in nature. *Trends in Ecology & Evolution*, *27*(5), 288-295. doi:10.1016/j.tree.2011.12.004

Rand, D. G., & Nowak, M. A. (2013). Human cooperation. *Trends in cognitive sciences*, *17*(8), 413-425.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

RStudio, T. (2018). *RStudio: Integrated Development Environment for R*. Boston, MA: RStudio, Inc. Retrieved from http://www.rstudio.com/

Sashaw, J. J. H. (2012). *Maternal strategies in vervet monkeys.* Lethbridge, Alta.: University of Lethbridge, Dept. of Psychology, c2012.

Shimada, M., & Sueur, C. (2018). Social play among juvenile wild Japanese macaques (Macaca fuscata) strengthens their social bonds. *American Journal of Primatology*, *80*(1), e22728.

Siegel, D. A. (2009). Social networks and collective action. *American Journal of Political Science*, *53*(1), 122-138. doi:10.1111/j.1540-5907.2008.00361.x

Sigmund, K. (2007). Punish or perish? Retaliation and collaboration among humans. *Trends in ecology \& evolution*, *22*(11), 593-600.

Silk, J. B., & Boyd, R. (2010). From grooming to giving blood: the origins of human altruism. *Mind the gap: tracing the origins of human universals*, 223-244.

Silk, J. B., Samuels, A., & Rodman, P. S. (1981). The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (Macaca radiata). *Behaviour*, *78*(1), 111-137.

Smith, E. A. (2010). Communication and collective action: language and the evolution of human cooperation. *Evolution and Human Behavior*, *31*(4), 231-245. doi:10.1016/j.evolhumbehav.2010.03.001

Stamm, J. S. (1961). Social facilitation in monkeys. *Psychological Reports*, *8*(3), 479-484.

Struhsaker, T. T. (1967). Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, *29*, 83-121.

Thompson, F. J., Hunt, K. L., Wright, K., Rosengaus, R. B., Cole, E. L., Birch, G., . . . Cant, M. A. (2020). Who goes there? Social surveillance as a response to intergroup conflict in a primitive termite. *Biology Letters*, *16*(7), 20200131.

Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, *126*, 31-40.

Tomasello, M. (2009). *Why we cooperate*. MIT press.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly review of biology*, *46*(1), 35-57.

Turner, T. R., Schmitt, C. A., & Cramer, J. D. (2019). Introduction. In T. R. Turner, C. A. Scmitt, & J. Danzy Kramer (Eds.), *Savanna Monkeys: The Genus Chlorocebus* (pp. 3-15). Cambridge: Cambridge University Press.

Vasconcelos, M., Hollis, K., Nowbahari, E., & Kacelnik, A. (2012). Pro-sociality without empathy. *Biology Letters*, *8*(6), 910-912. doi:10.1098/rsbl.2012.0554

Vilette, C., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2022). Network formation during social integration in juvenile vervet monkeys. *Animal Behaviour*, *194*, 205-223. doi:10.1016/j.anbehav.2022.10.006

Vilette, C., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2022). Strong ties formation, composition and processes at play during the developmental period of juvenile vervet monkeys. *Animal Behaviour*, *201*, 137-156. doi:10.1016/j.anbehav.2023.05.003

Vilette, C., Bonnell, T., Henzi, P., & Barrett, L. (2020). Comparing dominance hierarchy methods using a data-splitting approach with real-world data. *Behavioral Ecology*, *31*(6), 1379-1390.

Vygotsky, L. S. (1997). *The collected works of LS Vygotsky: Problems of the theory and history of psychology* (4). Springer Science & Business Media.

Warneken, F., & Tomasello, M. (2009). The roots of human altruism. *British Journal of Psychology, 100*(3), 455-471.

Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 68*(2), 161-180.

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wilke, C. O. (2018). ggridges: ridgeline plots in 'ggplot2'. *R package version 0.5, 1*, 483.

Wilkinson, G. S. (1988). Reciprocal altruism in bats and other mammals. *Ethology and sociobiology, 9*(2-4), 85-100.

Willems, E. P., Hellriegel, B., & van Schaik, C. P. (2013). The collective action problem in primate territory economics. *Proc Biol Sci, 280*(1759), 20130081. doi:10.1098/rspb.2013.0081

Willems, E. P., & van Schaik, C. P. (2015). Collective action and the intensity of between-group competition in nonhuman primates. *Behavioral Ecology, 26*(2), 625-631. doi:10.1093/beheco/arv001

Willer, R. (2009). Groups reward individual sacrifice: The status solution to the collective action problem. *American Sociological Review, 74*(1), 23-43.

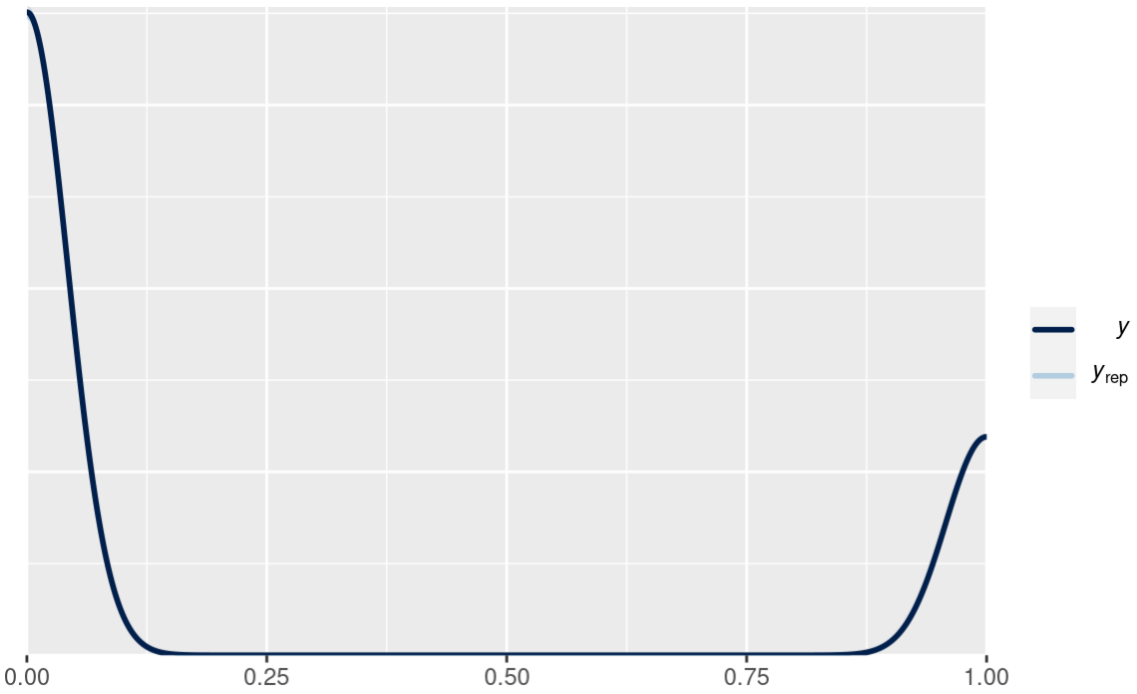
Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., . . . others. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature, 513*(7518), 414.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*(3-4), 262-300.

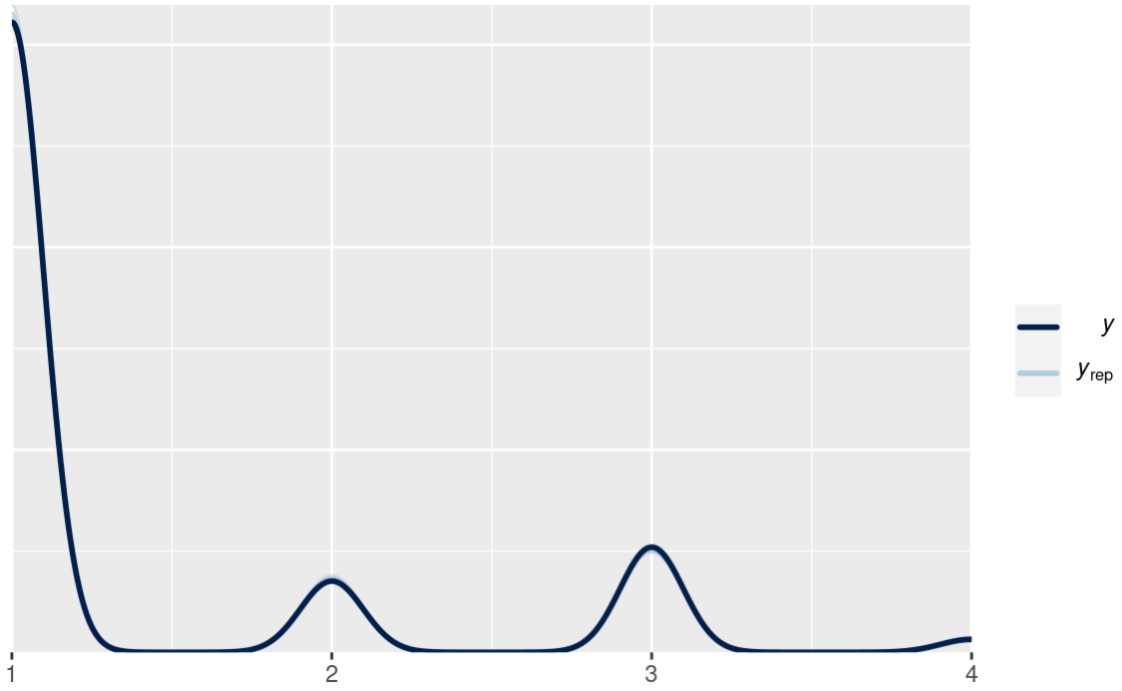
Young, C., McFarland, R., Ganswindt, A., Young, M. M. I., Barrett, L., & Henzi, S. P. (2019). Male residency and dispersal triggers in a seasonal breeder with influential females. *Animal Behaviour, 154*, 29-37.

APPENDICES

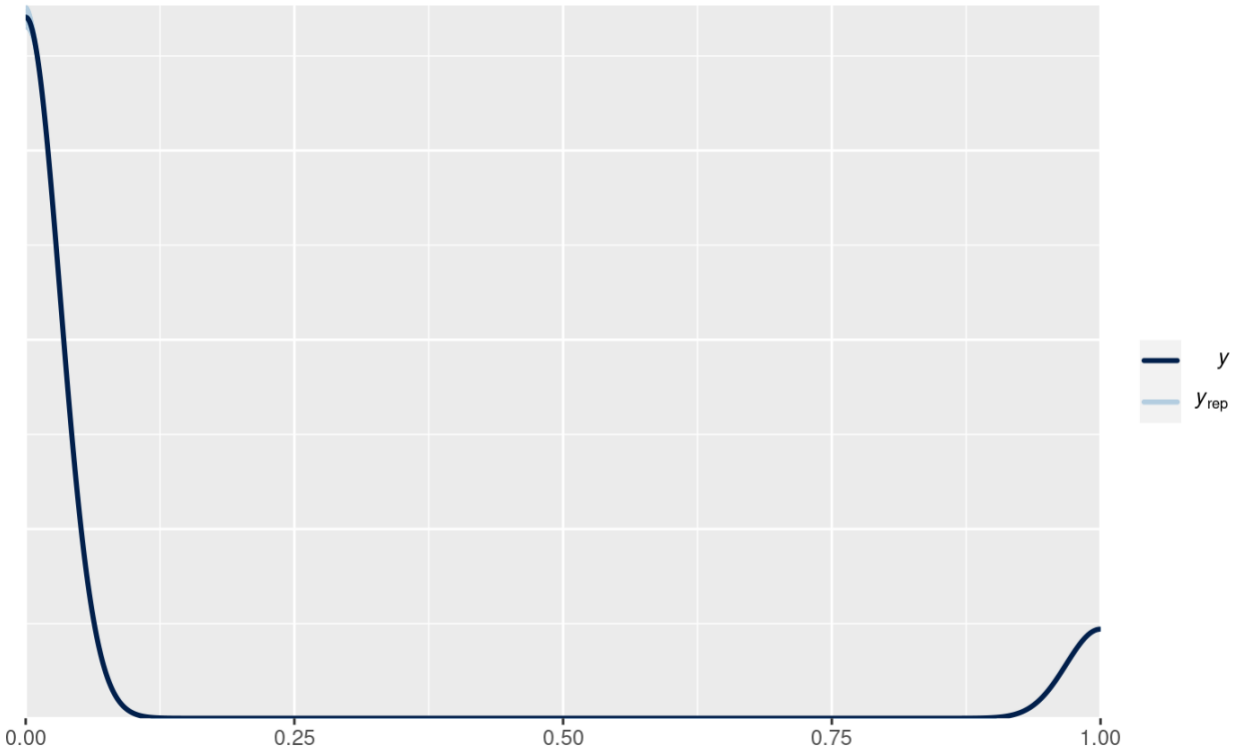
Appendix A: Chapter 3



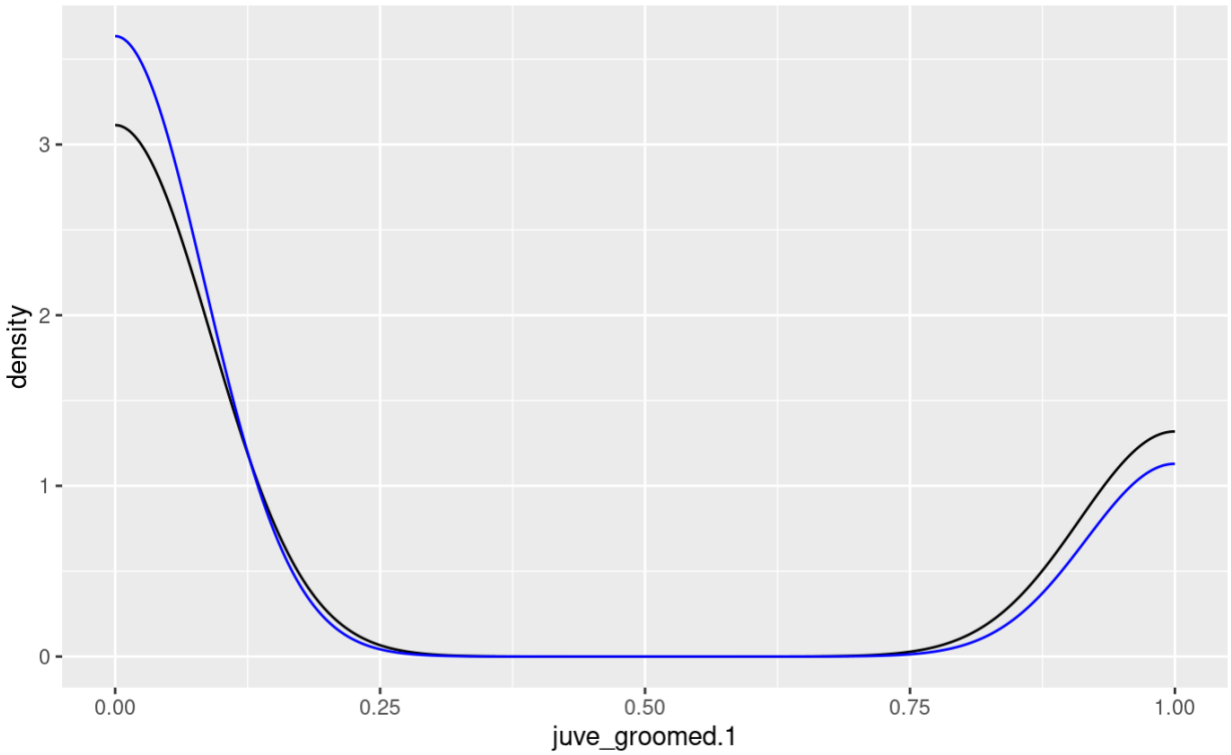
A.1 Model 1 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



A.2 Model 2 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



A.3 Model 3 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



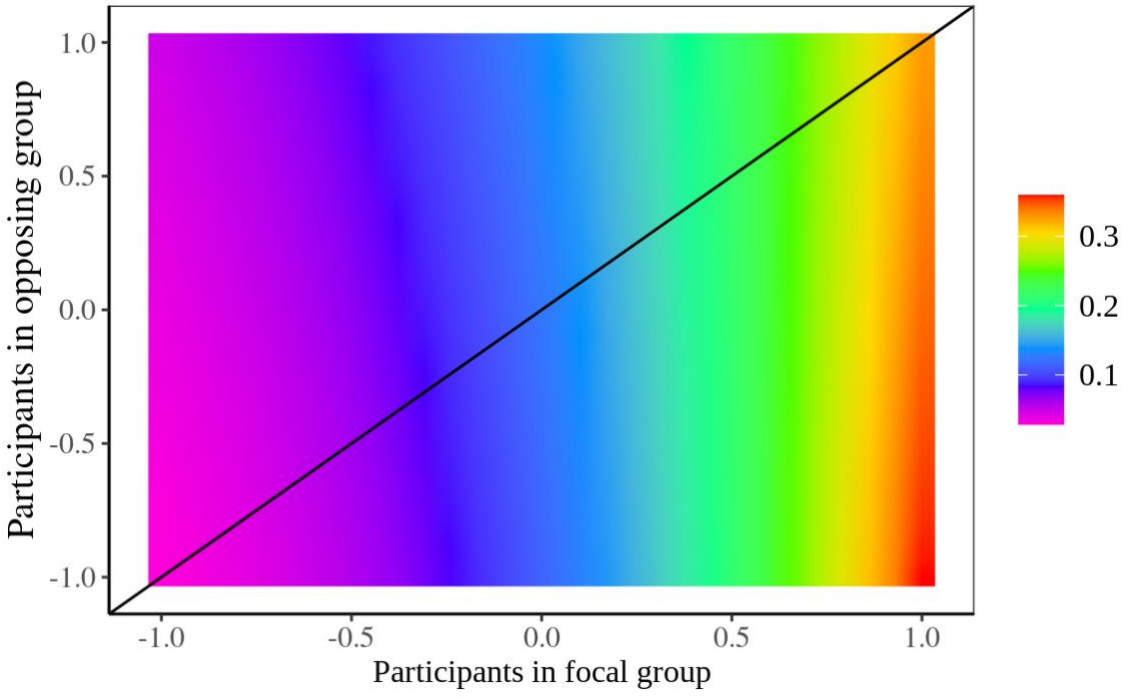
A.4 Model 4 Posterior Predictive Check. The black line represents the actual representations from the model while the blue line shows the possible model representations.

A.5. *Posterior estimates of the probability of participation (Y/N) in intergroup conflict in relation to age, sex (Ref: Female), the number of individuals in the troop, rank, grooming eigenvector centrality (EC), spatial eigenvector centrality, personality, the number of participants from the focal and opposing group (and their interaction), and maternal participation.*

	β	**SE**	**Lower-95% CI**	**Upper-95% CI**	**ESS**	**PD (%)**
Intercept	-2.03	0.22	-2.47	-1.57	2480.44	100
Age	0.27	0.02	0.24	0.30	7659.36	100
Sex (Ref: Female)	0.24	0.15	-0.06	0.54	3537.04	94.68
Maternal participation	0.52	0.03	0.47	0.57	9834.34	100
Number of individuals in the focal group	-0.10	0.01	-0.12	-0.08	8629.77	100
Rank	0.09	0.02	0.04	0.13	9242.08	99.98
Grooming EC	0.13	0.02	0.09	0.17	8756.68	100
Spatial EC	-0.09	0.01	-0.12	-0.07	10508.19	100

Personality	-0.03	0.08	-0.18	0.12	3527.23	65.44
Number of participants from the focal group	1.2	0.01	1.18	1.23	9135.45	100
Number of participants from the opposing group	0.13	0.01	0.11	0.16	9315.71	100
Interaction between numbers of participants from the focal and opposing groups	-0.17	0.01	-0.18	-0.16	8118.61	100

ID, nested in troop, and opposing troop identity were entered as crossed random intercepts. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.24. $R^2_{conditional}$=0.29. N=66,724.



A.6. Predictive marginal means for the relationship between the probability of non-adult participation and the interaction between numbers of focal and opposing group participants.

A.7. *Posterior estimates of changes in the level of aggressive intensity in relation to age, sex (Ref: Female), the number of individuals in the focal group, rank, grooming eigenvector centrality (EC), spatial eigenvector centrality, personality, the number of participants from the focal and opposing groups (and their interaction), and maternal aggressive intensity.*

	β	SE	Lower-95% CI	Upper-95% CI	ESS	PD (%)
Intercept [1]	1.72	0.18	1.33	2.05	3696.85	100
Intercept [2]	0.31	0.18	-0.09	0.63	3632.83	95.25
Intercept [3]	3.26	0.19	2.85	3.61	3841.40	100
Age	0.44	0.03	0.39	0.48	10710.29	100
Sex (Ref: Female)	0.20	0.13	-0.06	0.45	6411.63	93.8
Number of individuals in the focal troop	-0.00	0.02	-0.04	0.03	13115.51	58.86
Rank	0.00	0.03	-0.07	0.07	11053.30	50.34
Grooming EC	0.16	0.03	0.09	0.22	12190.95	100
Spatial EC	-0.09	0.02	-0.13	-0.05	14290.55	100
Personality	0.15	0.06	0.03	0.28	6475.63	99.11
Number of participants from the focal group	-0.08	0.02	-0.11	-0.04	12966.23	100
Number of participants from the opposing group	0.21	0.02	0.17	0.25	12225.39	100
Interaction between the number of participants from the focal and opposing groups	0.00	0.01	-0.01	0.02	11522.66	71.09
Maternal aggressive intensity	0.29	0.03	0.24	0.34	9363.26	100

ID, nested in troop, and opposing troop identity were entered as crossed random intercepts. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.08. $R^2_{conditional}$=0.13. N=16,918.

A.8. *Posterior estimates of the probability of grooming (Y/N) in relation to participation (Y/N), age, rank, personality, spatial eigenvector centrality, grooming eigenvector centrality, sex (Ref: Female), the number of individuals in the focal group, the number of participants from the focal and opposing groups.*

	β	SE	Lower-95% CI	Upper-95% CI	ESS	PD (%)
Intercept	-2.58	0.08	-2.74	-2.41	2673.28	100
Non-adult participation	1.40	0.03	1.33	1.46	8861.34	100
Age	0.02	0.02	-0.02	0.06	7203.83	84.51
Rank	0.07	0.03	0.01	0.13	6160.57	99.47
Personality	0.04	0.06	-0.08	0.16	2521.25	76.5
Spatial eigenvector centrality	-0.17	0.02	-0.20	-0.14	8876.59	100
Grooming eigenvector centrality	0.09	0.03	0.03	0.14	6655.81	99.96
Sex (Ref: Female)	-0.31	0.11	-0.53	-0.09	2428.51	99.71
Number of individuals in the group	0.12	0.02	0.09	0.15	7670.87	100
Number of participants from the focal group	0.23	0.02	0.19	0.26	7672.86	100
Number of participants from the opposing group	0.29	0.016	0.26	0.32	7820.93	100

ID and troop were entered as nested random intercept. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. $R^2_{marginal}$=0.09. $R^2_{conditional}$=0.12. N=57,138.

A.9. *Posterior estimates of the probability of grooming (Y/N) in relation to age, rank, and sex (Ref: Female).*

	β	SE	Lower-95% CI	Upper-95% CI	ESS	PD (%)
Intercept	-0.83	0.01	-1.31	-0.27	615	99
Age	0.14	0.00	0.13	0.15	2267	100
Rank	0.12	0.00	0.09	0.14	4126	100
Sex	-0.28	0.00	-0.53	-0.05	1479	99.05

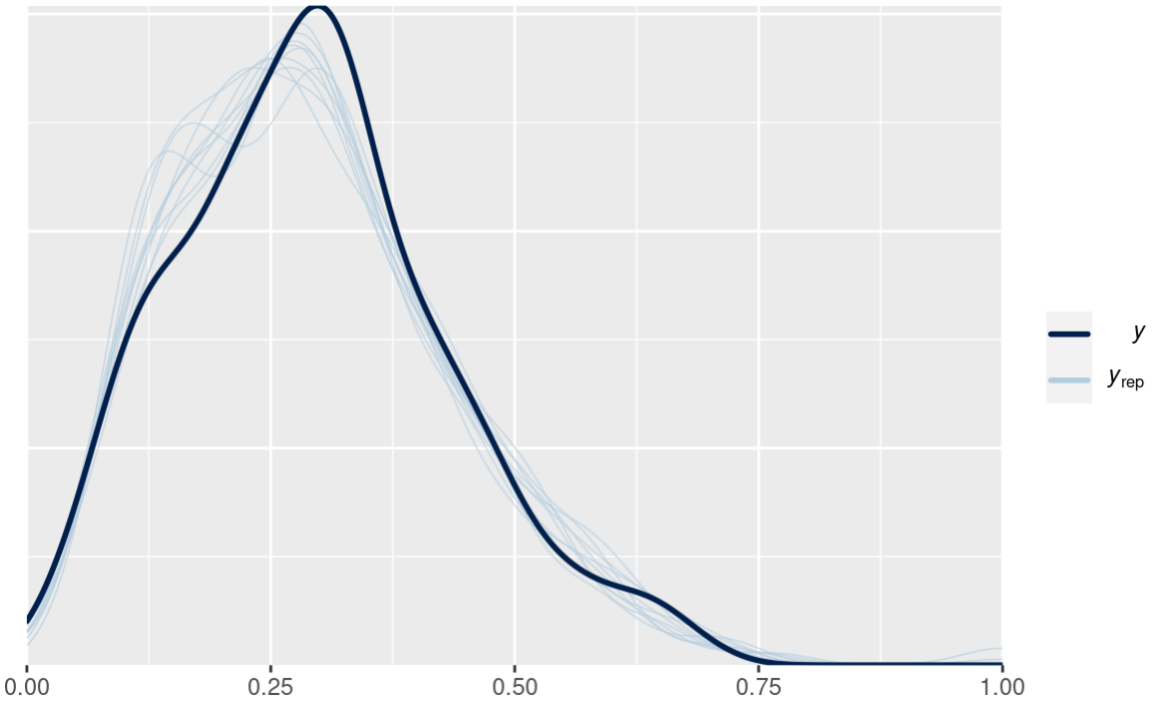
ID, mother ID, and troop were entered as nested random intercept. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. AUC= 0.62 (full model) 0.54 (main effects).

A.10. *Posterior estimates of the probability of mother grooming (Y/N) in relation to age, rank, and sex (Ref: Female).*

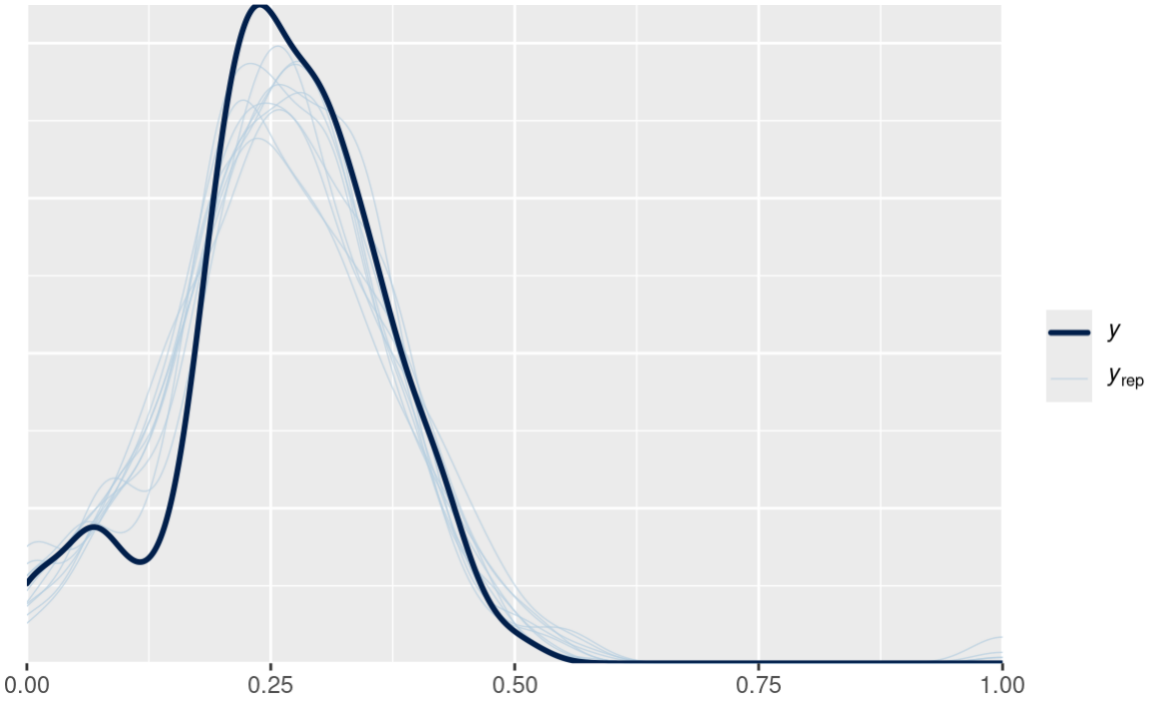
	β	**SE**	**Lower-95% CI**	**Upper-95% CI**	**ESS**	**PD (%)**
Intercept	-1.22	0.02	-2.37	0.14	1417	96.35
Age	-0.74	0.00	-0.77	-0.70	3631	100
Rank	0.05	0.00	0.00	0.11	3375	97.4
Sex	-0.22	0.01	-0.93	0.44	1741	72.55

ID, mother ID, and troop were entered as nested random intercept. β: slope of the predictor; SE: standard error of the estimate of β; CI: credible interval; ESS: effective sample size; PD: probability of direction. AUC= 0.77 (full model) 0.63 (main effects).

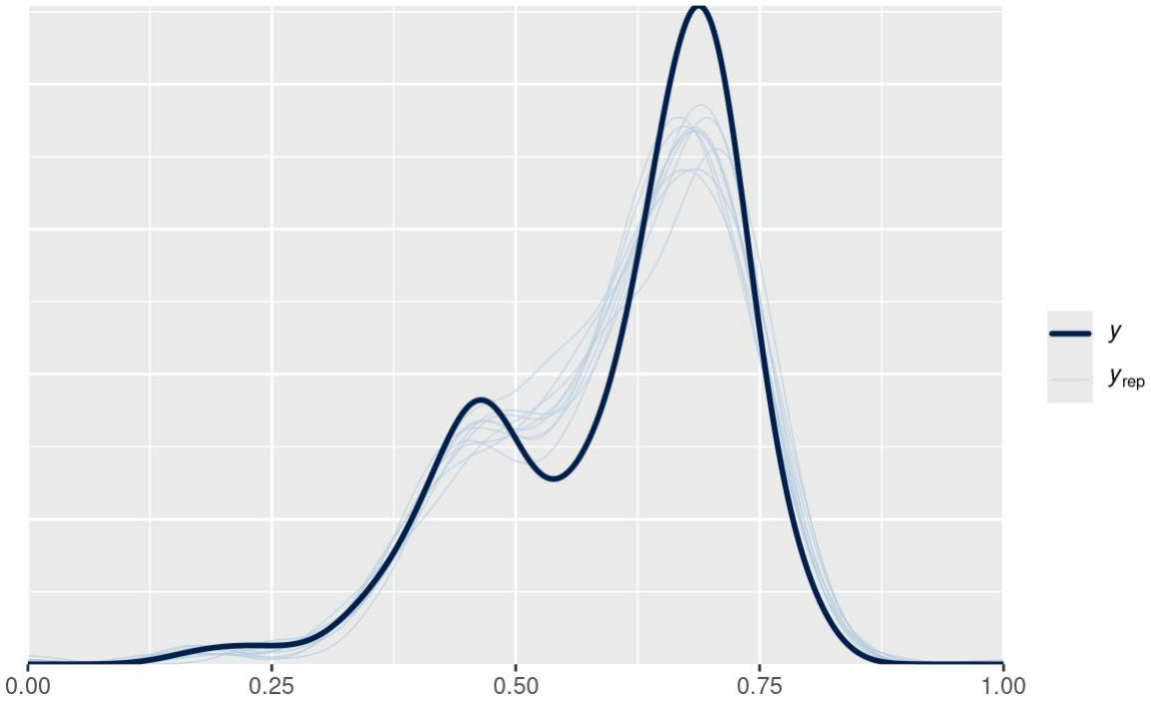
Appendix B: Chapter 4



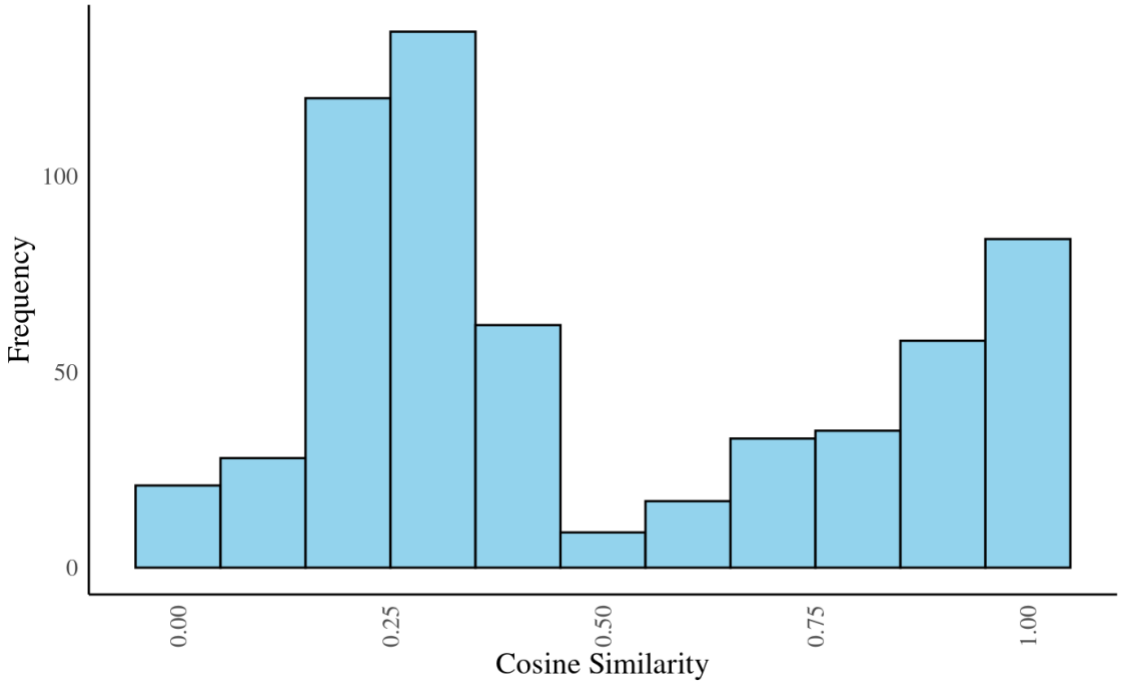
B.1 Model 1 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



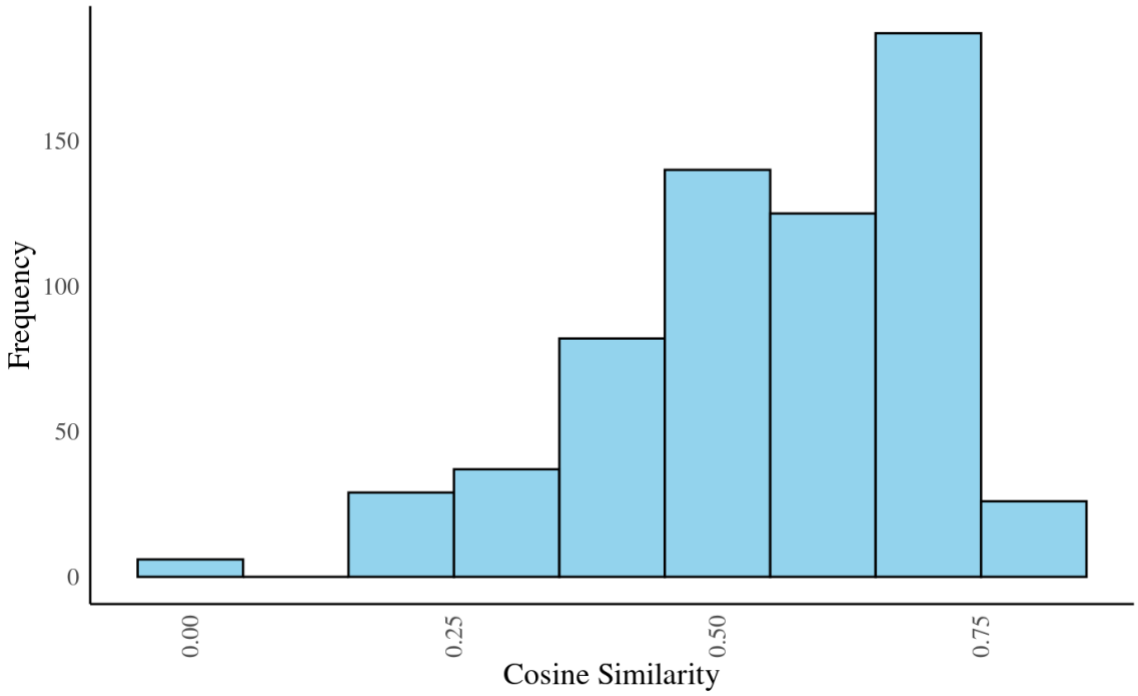
B.2 Model 2 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



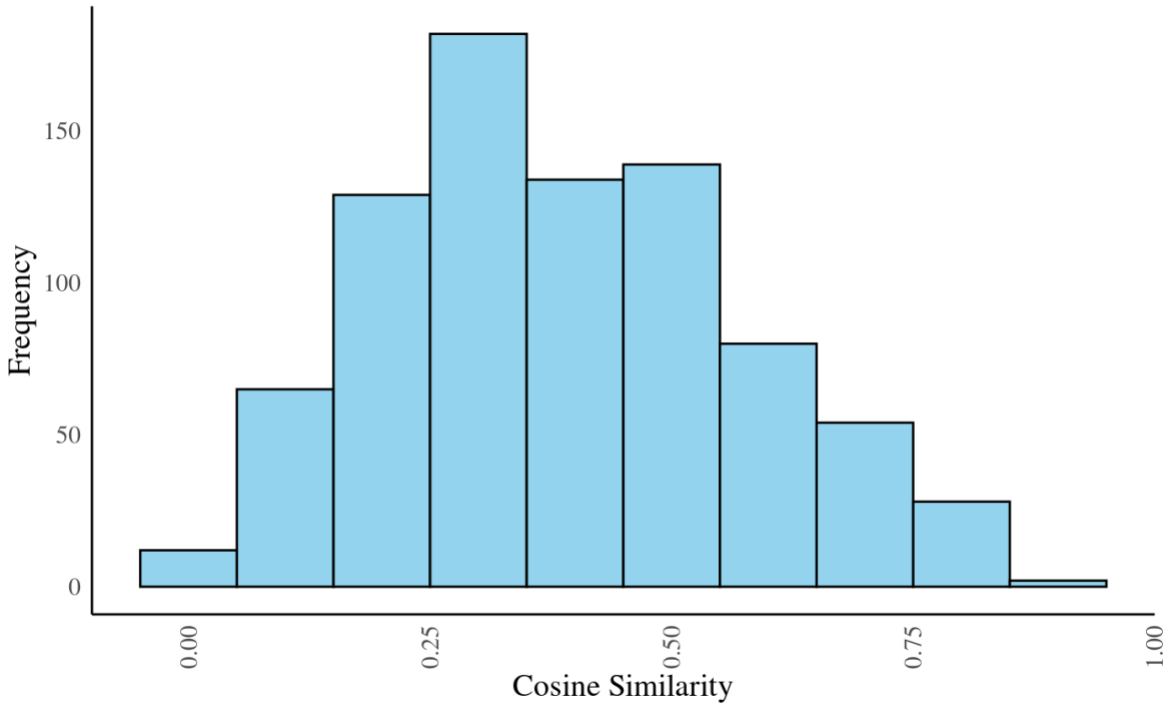
B.3 Model 3 Posterior Predictive Check. Y represents the actual representations from the model while Y_{rep} shows the possible model representations.



B.4 Histogram showing the distribution of the cosine similarity values between the grooming and IGC co-participation networks.



B.5 Histogram showing the distribution of the cosine similarity values between the spatial association and IGC co-participation networks.



B.6 Histogram showing the distribution of the cosine similarity values between the grooming and spatial association networks.