Strategic decision making around social behaviours in wild vervet monkeys (*Chlorocebus pygerythrus*)

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"Strategic decision making around social behaviours in wild vervet monkeys (Chlorocebus pygerythrus)"

sur le rapport des membres du jury composé comme suit:

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Neuchâtel, le 19 juillet 2021

Le Doyen, Prof. A. Bangerter

To my grandparents Jacinto and Isabel and my mother

“Go through the motions Adam.

Act out being alive, like a play.

And after a while, it will be true.”

(John Steinbeck, East of Eden)

“What I must do is all that concerns me, not what the people think. This rule, equally arduous in actual and in intellectual life, may serve for the whole distinction between greatness and meanness. It is the harder because you will always find those who think they know what is your duty better than you know it. It is easy in the world to live after the world’s opinion; it is easy in solitude to live after our own; but the great man is he who in the midst of the crowd keeps with perfect sweetness the independence of solitude… Men imagine that they communicate their virtue or vice only by overt actions, and do not see that virtue or vice emit a breath every moment… Life only avails, not the having lived. Power ceases in the instant of repose; it resides in the moment of transition from a past to a new state, in the shooting of the gulf, in the darting to an aim… Nothing can bring you peace but yourself. Nothing can bring you peace but the triumph of principles… To err on the side of passion is human and right and the only way I’ll live.”

(Ralph Waldo Emerson, Self-Reliance)

“When the wind blows

the tree must bend

or be pulled out by its roots.”

(Patagonian Proverb)

“We wish to check if our aspirations are always the same, or in what measure they have changed. To do so, we need to have recourse to a situation difficult to reach, midway between blind self-approval and real scorn, between the presumption you have been of some use to people and the subtle, painful fear you haven’t… Nor should one forget that the great mountains are the measure of the man who tests himself against them – otherwise they are no more than heaps of stone... Obviously, nothing I have done is important in any absolute sense, but it belongs to me completely, and identifies me.”

(Walter Bonatti, The summits of my life)

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curiosity generated in all the many hours I spent with the monkeys was only possible thanks to the trust you deposited in my abilities. I am honoured to have been an IVP researcher and to have attempted different projects that benefitted hugely from the existence of a 10 years-long database and to have been supported to explore uncharted waters.

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RÉSUMÉ GÉNÉRAL

Les animaux vivant dans des groupes sociaux stables sont confrontés à des défis quotidiens pressants pour se nourrir, se déplacer et se socialiser, même si les individus prennent des décisions qui ne peuvent pas se contenter de satisfaire leurs propres intérêts. Au contraire, les décisions individuelles doivent être adaptées à un collectif dont les besoins peuvent varier en fonction de l'âge, de l'état physiologique ou du rang. Par conséquent, les individus ont évolué vers une capacité à intégrer un ensemble large et flexible d'options qui prennent en compte les conflits d'intérêts qui surviennent en raison de la concurrence pour prendre des décisions comportementales. Le même ensemble d'éléments a très probablement favorisé le développement d'interactions coopératives stratégiques entre les individus qui permettent d'apaiser les tensions, de créer des liens, de restaurer les conflits, et finalement de faciliter la cohésion du groupe et la synchronie collective. Les sociétés de primates sont exquisément variées dans leurs structures de groupe, leurs habitats, leurs régimes alimentaires et leur socialité, mais une généralité clé qui ressort parmi les sociétés liées aux femelles est le rôle prédominant que le comportement social des femelles joue dans la coexistence des groupes. Dans cette thèse, j'ai étudié comment la prise de décision individuelle et de groupe affecte la dynamique coopérative, et quels sont les facteurs qui influencent l'émergence de tels comportements, et comment les dilemmes sociaux peuvent survenir dans certains cas chez les singes vervets sauvages (Chlorocebus pygerythrus). Pour ce faire, j'ai mené un mélange d'études empiriques et corrélationnelles en me concentrant sur les femelles adultes comme sujets d'étude dans certains cas, ou sur le comportement de groupe dans d'autres, en essayant de dévoiler quels facteurs pourraient déclencher les différentes stratégies sociales qui se manifestent par des résultats comportementaux concrets et observables. Pour ce faire, j'ai combiné des scénarios de coopération et de conflit en utilisant différentes dimensions temporelles.

Dans le **Chapitre I**, j'ai exploré les mécanismes de réciprocité directe des échanges de toilettage pour la tolérance chez les femelles adultes de singe vervet. Des expériences avec des boîtes contenant de petits aliments permettent de tester la dynamique tolérance/agression et de la relier aux interactions sociales précédentes à court terme (quelques minutes à quelques

heures). De plus, les vervets sont désireux de participer à de telles expériences et discernent rapidement les couvertures de couleur personnelles, de sorte qu'ils ne s'approchent de leurs boîtes que lorsque des dyades de femelles sont testées. J'ai découvert que la femelle dominante de la dyade ne basait pas sa réciprocité envers un partenaire de toilettage précédent aux boîtes installées sur la qualité de la relation qui les a déliés (lien) ni sur la différence de contribution au toilettage que les individus ont fait. Au lieu de cela, les femelles dominantes variaient leur disposition de tolérance en fonction de la durée totale de l'interaction de toilettage comme une forme de réciprocité attitudinale où les sensations positives de l'interaction de toilettage renforçaient la bienveillance du dominant en étant tolérant. Les dominants fournissaient de la tolérance d'une manière qui imite un sablier où le sable qui tombe est le déclin de la tolérance et la tolérance était échangée contre du toilettage pendant jusqu'à trois heures. De plus, les femelles n'ont pas diminué leur réciprocité malgré le fait d'avoir eu des partenaires supplémentaires, ce qui indique que si cela s'est produit, cela n'a pas provoqué une sorte de saturation cognitive.

Dans le **Chapitre II**, j'ai élargi la dimension temporelle de la dynamique de réciprocité basée sur le toilettage. J'ai nourri expérimentalement huit sujets (quatre de haut rang, quatre de bas rang) dans quatre groupes voisins. En nourrissant un sujet à la fois, j'avais l'intention de leur fournir un "surplus de temps" pour d'autres activités et j'ai évalué s'ils changeaient leur socialisation et comment cela se traduisait dans leur positionnement dans le réseau social. En étudiant le toilettage donné comme une source d'investissement social stratégique, j'ai évalué les femelles nourries et constaté qu'elles augmentaient significativement leur allocation de toilettage aux autres pendant qu'elles étaient nourries, par rapport aux deux phases de contrôle autour du traitement. Elles ont également augmenté leur allocation de toilettage (force), ont donné plus que ce qu'elles ont reçu, et ont spécifiquement ciblé les femelles liées, les proches et les adultes comme partenaires de toilettage préférentiels. Il est intéressant de noter que les femelles de haut rang et de bas rang ont réagi de façon similaire au traitement d'alimentation, démontrant des stratégies de toilettage similaires en donnant plus de toilettage qu'elles n'en recevaient. Ces résultats ont montré que les réseaux sociaux de toilettage sont dynamiques et font allusion aux capacités d'intelligence machiavélique comme fondement probable des individus qui tentent de se promouvoir socialement dans leurs groupes en fournissant des services de toilettage.

Dans le **Chapitre III**, j'ai étudié le sujet des rencontres intergroupes comme une forme de problème d'action collective entre quatre dyades de groupes. J'ai créé un mélange de variables écologiques et territoriales et les ai calculées du point de vue d'un groupe focal, mais en incluant le point de vue du groupe qu'ils ont rencontré. Cela permettait de savoir si le groupe focal appréciait plus ou moins la zone où se situait le conflit. Les variables écologiques reflétaient également des dimensions temporelles distinctes (ici et maintenant, moyenne de l'année, maximum de l'année). Les résultats ont montré que les rencontres se concentraient davantage dans les zones centrales (très utilisées), dans les zones où le NDVI actuel est plus élevé (verdure comme indicateur de la disponibilité de la nourriture) et où les valeurs maximales du NDVI de l'année sont plus élevées. Il apparaît que la volonté des vervets de combattre des groupes rivaux est modulée par les valeurs de perception qui intègrent les informations présentes, futures et passées sur la qualité d'un site spécifique. J'ai trouvé que parmi les facettes écologiques et territoriales possibles qui pourraient influencer les résultats (gagner/perdre), aucune ne semblait être critique, même si des aspects comme la distance relative au noyau ou l'intensité relative de l'utilisation étaient considérés. Il est frappant de constater que ce qui semblait augmenter la probabilité de gagner était d'être plus petit que son rival. On peut mieux comprendre ce phénomène en utilisant le dilemme du volontaire, selon lequel les groupes plus importants peuvent moins bien réussir à rassembler suffisamment de volontaires pour combattre le groupe rival en raison des chances plus élevées de tricherie. Cette découverte passionnante pourrait être mieux comprise si l'on considère l'importance de la recherche d'un consensus avant d'engager un combat contre un autre groupe. Si les groupes plus importants ont une proportion significative de leurs individus qui utilisent des sources de nourriture alternatives à celle qui est en jeu lors de la rencontre intergroupe, cela pourrait expliquer qu'il y ait moins d'accord et donc un manque de synchronisation pour surpasser les groupes rivaux de plus petite taille mais avec une meilleure coordination de groupe.

Dans le **Chapitre IV**, j'ai étudié le phénomène des fissions de groupes dans trois groupes voisins qui ont eu lieu au milieu d'une grave sécheresse qui a touché l'Afrique australe (2014-2016). Ici, j'ai étudié la variation des budgets d'activité, les comportements de toilettage, certains paramètres du réseau social au niveau individuel et collectif (femelles adultes), et la dispersion du groupe comme mesure de la cohésion du groupe. J'ai constaté que les différents groupes semblaient suivre des voies quelque peu différentes pour faire face aux conditions écologiques difficiles. Contrairement à ce qui était attendu, je n'ai pas trouvé de détérioration progressive convergente de la cohésion du groupe et tous les groupes ont adopté des réactions relativement flexibles. J'ai évalué si la connectivité du réseau social par le biais du toilettage et de la proximité serait un indicateur de la manière dont la composition finale des deux groupes de filles a été déterminée, mais un seul des trois groupes a suivi cette logique. Enfin, j'ai sélectionné une série de facteurs qui pourraient être informatifs de la condition physique des femelles afin d'étudier si elles joueraient le rôle de "rester" (averses au risque) ou de "rester". (aversion au risque) ou "partir" (prise de risque). J'ai constaté que les femelles de rang inférieur partaient toujours, que celles de rang supérieur restaient et que celles de rang intermédiaire pouvaient choisir n'importe quelle option. De manière surprenante, le fait d'avoir vécu le décès d'un membre de la famille proche était fortement corrélé à l'adoption de la stratégie "rester".

En résumé, ces résultats apportent la preuve que les singes vervet, et les femelles en particulier, sont capables d'afficher des répertoires sociaux très flexibles dans des contextes de coopération et de conflit. Comme les individus utilisent leurs capacités acquises au cours de l'évolution pour faire face à des conditions changeantes (sociales, environnementales), il n'est pas surprenant qu'ils puissent adopter des processus décisionnels stratégiques qui favorisent leur connectivité sociale dans le réseau. En outre, la nature multicouche inévitable des groupes en fait une plateforme idéale où se déroulent les conflits d'intérêts. De tels contextes représentent des dilemmes sociaux intéressants qui nécessitent un certain niveau d'action de coordination des coopérateurs afin de compenser les non-coopératifs.

GENERAL ABSTRACT

Animals living in stable social groups find daily pressing challenges to feed, move and socialise although individuals make decisions that cannot just satisfy self-driven interests. Instead, individual decision-making needs to be tuned to a collective that may have different needs due to age, physiological state or rank status. As a result, individuals have evolved a capacity to integrate a wide and flexible set of options that take into consideration conflicts of interest that arise due to competition to make behavioural decisions. The same set of elements has most probably favoured the development of strategic cooperative interactions between individuals that help to ease tensions, building bonds, restoring conflicts, ultimately facilitating group cohesion and collective synchrony. Primate societies are exquisitely varied in their group structures, habitats, diets and sociality, but one key generality that stands out among female-bonded societies is the predominant role that females' social behaviour play in the groups' coexistence. In this thesis, I investigated how individual and group decision-making affects cooperative dynamics, and which factors influenced the emergence of such behaviours, and how social dilemmas could arise in some instances in wild vervet monkeys (*Chlorocebus pygerythrus*). For that, I conducted a mix of empirical and correlational studies focusing on adult females as subjects of study in some instances, or on group behaviour in others, trying to unveil which factors might spark the different social strategies manifested in concrete and observable behavioural outputs. I did so by combining cooperative and conflict scenarios using different time dimensions.

In **Chapter I**, I explored the mechanisms of direct reciprocity exchanges of grooming for tolerance in adult female vervet monkeys. Experiments with boxes that contain small food items permit testing tolerance/aggression dynamics and relate it to previous social interactions in the short term (minutes to hours). Further, vervets are eager to participate in such experiments and quickly discern personal colour-covers so they would only approach their boxes when testing female dyads. I found that the dominant female of the dyad did not base her reciprocity towards a previous grooming partner at the boxes set up based on the relationship quality that untied them (bond) nor on the difference in grooming contribution that individuals did. Instead, dominant females varied their tolerance disposition on the total time

the grooming interaction lasted as a form of attitudinal reciprocity where the positive sensations of the grooming interaction reinforced the dominant's benevolence by being tolerant. The dominants provided tolerance in a way that mimics an hourglass where the sand that falls is the tolerance decay and tolerance was exchanged for grooming for up to three hours. What is more, females did not lower their reciprocity despite having had additional partners, indicating that if this happened, it did not cause a sort of cognitive saturation.

In **Chapter II**, I widened the time-dimension of grooming-based reciprocity dynamics. I experimentally fed eight subjects (four highest-ranking, four bottom-ranked) in four neighbouring groups. By feeding one subject at a time I intended to provide them with a "surplus time" for other activities and evaluated whether they changed their socialisation and how this would translate into their social network positioning. By studying grooming given as a source of strategic social investment, I assessed the fed females and found that they significantly increased their allocation of grooming to others while being fed, compared to two control phases around the treatment. They also increased their allocation of grooming (strength), gave more than what they received, and specifically targeted bonded, kin and adult females as preferential grooming partners. Interestingly, the high and low-ranking females reacted similarly to the feeding treatment evidencing akin grooming strategies by giving more grooming than they received. These results showed that grooming social networks are dynamic and hint at Machiavellian Intelligence abilities as a probable foundation for individuals to attempt social promotion in their groups through the provisioning of grooming services.

In **Chapter III**, I studied the topic of intergroup encounters as a form of collective action problem between four group dyads. I created a blend of ecological and territorial variables and calculated them from the perspective of a focal group, but including the perspective of the group they encountered. This allowed a sense of whether the focal group valued more or less the area where the conflict lay. The ecological variables also reflected distinct time-dimensions (here and now, year average, maximum in the year) The results showed that encounters concentrated more in core areas (highly used), in areas with higher current NDVI (greenness as a proxy of food availability), and with higher NDVI maximum year-values. As it appears, vervets' willingness to fight rival groups is modulated upon perception values that integrate the present, future, and past information about the quality of a specific site. I found that among the possible ecological and territorial facets that could shape outcomes (winning/losing) neither appeared to be critical, even if aspects like relative distance to the core or relative intensity of use were considered. Strikingly, what seemed to increase the likelihood of winning was being smaller than your rival was. This is better understood using the volunteer's dilemma, whereby bigger groups may be less successful in putting together enough volunteers to fight the rival group due to higher odds of cheating. This exciting finding could be better understood if one considered the importance of building consensus before initiating a fight against another group. If bigger groups have a significant portion of their individuals using alternative food sources than the one at stake during the intergroup encounter, that could explain that there is less agreement and therefore a lack of synchrony to outcompete rival groups of smaller size but higher group coordination.

In **Chapter IV**, I studied the phenomenon of group fissions in three neighbouring groups that took place amid a severe drought that affected Southern Africa (2014-2016). Here, I two full years before the groups fissioned using three months time windows to investigate the variation of activity budgets, grooming behaviours, some social network parameters at the individual and collective level (adult females), and group dispersion as a measure of group cohesion. I found that the different groups seemed to follow somehow different routes in their dealing with challenging ecological conditions. Contrary to expected, I did not find convergent progressive deterioration of the group cohesion and all groups adopted relatively flexible reactions. I assessed whether social network connectivity through grooming and being in proximity would be indicative of how the final composition of the two daughter groups was determined, but only one of the three groups followed that logic. Finally, I selected a suite of factors that could be informative of the females' fitness to investigate whether they would play "stay" (risk-averse) or "leave" (risk-taking) strategies. I found that bottom-ranked females always left, top-ranking stayed, and middle-ranking could choose any option. Surprisingly, having experienced the death of a close family member was highly correlated with playing the "stay" strategy.

In summary, these results bring forward evidence that vervet monkeys, and females, in particular, are capable of displaying highly flexible social repertoires in contexts of cooperation and conflict. As individuals use their evolutionary acquired abilities to cope with changing conditions (social, environmental), it is no surprise that they can adopt strategic decision-making processes that assist their social connectivity in the network. Beyond, the inevitable multi-layered nature of groups makes an ideal platform where conflicts of interest unfold. Such contexts represent interesting social dilemmas that require a certain level of coordination action of cooperators so to make up for the non-cooperative ones.

GENERAL INTRODUCTION

I.1. Group living

Animals living in groups, including humans, benefit greatly from doing so. Depending on the species, the population size, the social system, and habitat quality, groups differ widely in composition and social interaction patterns (Struhsaker and Leland, 1979; Terborgh and Janson, 1986; Krause and Ruxton, 2002). One of the essential foundations on which group living is built is the increased safety from predators (van Schaik and van Hooff, 1983). This can be achieved directly thanks to antipredator behaviour rules like the selfish herd, confusion, detection and dilution effect (Gillett, Hogarth and Jane Noble, 1979; Foster and Treherne, 1981; Delm, 1990). A different key foundation for group living is the capacity to defend resources against rival groups (Barton, Byrne, & Whiten, 1996; Janson & van Schaik, 1988; Sterck, Watts, & van Schaik, 1997). Groups can defend food resources indirectly thanks to having home ranges and territories that groups rely on to cover the different needs (Burt, 1949; Maher and Lott, 1995; Anich, Benson and Bednarz, 2009; Spencer, 2012). Animal groups can collectively defend food sources by confronting and outfighting neighbouring competitors (Whiting, 1999; Johnsson, Carlsson and Sundstrom, 2000; Gray, Jensen and Hurst, 2002; Campbell *et al.*, 2005).

However, safety from predators and food resources alone do not cover the entire spectrum of benefits that distil from group living. Living with other peers – in a more or less stable fashion – is one of the bedrocks for the emergence of social relationships (Hamilton, 1964b; Trivers, 1971; Hofmann *et al.*, 2014). Commonly, many taxa have evolved migratory mechanisms on one of the sexes after reaching sexual maturity to avoid inbreeding (Kurvers et al., 2013; Lehmann & Perrin, 2003; Neff & Sherman, 2002; Young & Wang, 2004), which leads to the formation of two chief grouping systems; those that are female or male philopatric. Such group categorisation influences greatly the genetic structure of groups, mating behaviours and social styles (Clutton-Brock & Lukas, 2012; Greenwood, 1980; Hatchwell, 2009; Ishizuka et al., 2018; Lehmann & Perrin, 2003; Lucia et al., 2008; Perrin & Mazalov, 1999; Sterck et al., 1997; Wolf & Trillmich, 2008; Wong, 2010). Beyond the apparent unity or homogeneity of groups, individuals are confronted with conflicts of interest; be it because of access to food or access to social and mating partners. It is believed that hierarchical systems evolved to avoid or limit the extent of agonistic interactions between group peers (Kaufmann, 1983; Enquist and Leimar, 1987; Mesterton-Gibbons and Dugatkin, 1995; Lauer, 2001; Hobson, Monster and DeDeo, 2018; Leimar, 2021). In that frame, group-living animals behave as units, and although different degrees of behaviour plasticity can exist (i.e. fission-fusion, metapopulations), sharing space and time facilitates the development of social relationships just as much as it creates a fertile ground for conflicts and aggression. Hence, the panoply of conditions emanating from a social group, the challenges set by the distribution and variability of food resources, and the competition for food (within, between groups) are fundamental tenets for the evolution of advanced intelligence (Humphrey, 1976; Jolly, 1966) and the development of sophisticated cognitive abilities as the Machiavellian Intelligence Hypothesis posits (Byrne, 1988; Byrne & Whitten, 1997; Jolly, 1966). As a result, the complex social environment that animal societies represent is a suitable space for the study of social interactions, the development of social relationships, and the underlying strategies and decisions that animals make in different contexts. In figure 1 I try to illustrate, some of the ramifications of group living concerning some aspects that I investigated in the different chapters of my thesis.

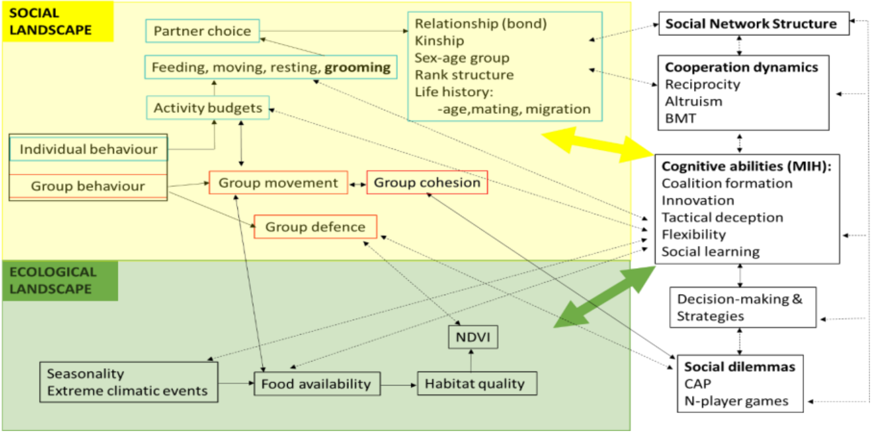

Figure 1. Scheme summary of the individual and group behaviour traits connected to social and ecological landscapes. These have ramifications linking to the configuration of groups' social networks, the emergence of decision-making and strategies, cooperation, and social dilemmas. Underlying these facets, group-living animals have evolved cognitive abilities that assist them to manoeuvre social and ecological challenges.

I.2. Machiavellian intelligence

I.2.A. Evolution and advancement of cognitive abilities

As it could not be otherwise, living in a social group where there are individuals of different ages, sexes, kinship ties, and bond relationships abiding by certain society rules set the stage for complex social life. Here, the meaning of complex does not intend to deepen into how cognitively-brainpower demanding are the tasks and ventures that animals undergo in their daily lives. Instead, by complex, I aim to encompass the convoluted and multifaceted social arena that leads way to sophisticated, purpose-driven behaviours that animal societies inexorably irradiate. Some distant and yet compelling pieces of evidence of how sophisticated behaviours are present in distinct animal society architectures are manifested in varied taxa, from insects like ants (*Leptothorax albipennis*) or honey bees "house-hunting" information pulling (Franks *et al.*, 2002) to social surveillance in termites (*Zootermopsis angusticollis*) (Thompson *et al.*, 2020). Among reptiles, lizards (*Anolis evermanni*) can process information and solve problems at levels comparable to endothermic species (Leal and Powell, 2012), and bearded dragons (*Pogona vitticeps*) have shown the ability to socially learn by imitation (Kis, Huber and Wilkinson, 2015). Among the amphibian class, there is evidence of strategic planning around tadpole transport in Neotropical poison frogs (*Allobates femoralis*) (Houston and Mcnamara, 1999), the common frog (*Rana temporaria*) can practice a form of clutch piracy (Vieites *et al.*, 2004) and more generally, anurans exhibit a broad scope of parental care behaviours (Furness and Capellini, 2019). Birds like ravens' (*Corvus corax*) can integrate what others have seen into their actions – tactical deception (Bugnyar and Heinrich, 2005), are efficient learners by observing others solve tool use tasks in kea parrots (*Nestor notabilis*) (Huber and Gajdon, 2006), or can form intricate multilevel societies like guinea fowls (*Acryllium vulturinum*) (Papageorgiou *et al.*, 2019). Among fish, cleaner *Labroides dimidiatus* can have up to 2000 daily interactions with clients which allows the ingestion of over 1200 parasites (Grutter, 1996) and can engage in inter-species cooperative hunting – moray eel (Vail, Manica and Bshary, 2013). Also cooperatively breeding cichlid *Neolamprologus pulcher* raised under different social conditions can develop varying social competence skills (Taborsky *et al.*, 2012). Among mammals, Ethiopian foxes (*Canis simensis*) foraging efficiency increases when roaming around gelada monkeys (*Theropithecus gelada*) without opting to predate accessible juvenile monkeys (Venkataraman *et al.*, 2015) in what may constitute a form of mutualistic behaviour (foxes hunt rodents that compete for food with geladas). Groups of banded mongooses (*Mungos mungo*) can self-organise and outcompete rival neighbours in highly organised ways and engage in contingent cooperation actions (Furrer *et al.*, 2011; Kern and Radford, 2018). Further, chimpanzees (*Pan troglodytes*) show remarkable tool-based foraging technique repertoires that allow teaching, learning, planning of the future (Byrne, Morgan, & Sanz, 2013; Estienne, Robira, Mundry, Deschner, & Boesch, 2019; Gruber et al., 2015; Lamon, Neumann, Gier, Zuberbühler, & Gruber, 2018; Yamamoto, Humle, & Tanaka, 2009). Moreover, chimpanzees are capable of highly sophisticated and well-structured group arrangements around group defence (Amsler, 2009; Wrangham & Glowacki, 2012). And bonobos (*Pan paniscus*) provide a notable example of peaceful coexistence – sometimes involving merging - of neighbouring groups (Lucchesi *et al.*, 2020), and food sharing between individuals of different groups (Hohmann and Fruth, 1996).

In that frame, it should be clear that animal societies of any clade are equipped to deal with, a priori, non-trivial challenges to resolve the interesting and sometimes unpredictable nuances of social life. Hence, one wonders about the underlying proximate mechanisms that regulate different animal taxa to solve the complications that come with social life. Which are the strings that were pulled by the engines of evolution, for such wealth of behavioural ranges to exist? Even if this ample quest feeds the wishes of naturalists and scientists alike, we must acknowledge the difficulty to dissociate possible causal factors and evolution drivers from by-product behavioural adaptations (McNally, Brown and Jackson, 2012). Consequently, even if some theories have advanced relevant explanations linking the different layers of group living and the evolution of sophisticated brain systems, most notably, the Social Brain Hypothesis (Dunbar & Shultz, 2007; Dunbar, 1998; Lehmann, Andrews, & Dunbar, 2010), I will only occasionally speculate about how some behaviour examples may relate to the advancement of cognitive processes that allow individuals to successfully exploit their social environments. Social complexity is regarded as a convenient platform for the evolution of social intelligence (Humphrey, 1976) and the opening behavioural routes like social manipulation, cooperation and defection. This view comprehends intelligence as a trait favoured by natural selection pressures because more advanced forms of intelligence would permit animals to exploit their social environments better than less advanced ones (Ashton, Kennedy, & Radford, 2020; Burkart, Schubiger, & van Schaik, 2017; Byrne, 1988; Reader & Laland, 2002; Whiten & Byrne, 1988; Jolly, 1966). Notwithstanding, one cannot neglect the relevance that complex ecological landscapes present to group-living animals to efficiently cover nutritional needs in changing environments due to climatic, seasonality, and territory holding potential issues (Ohsawa and Dunbar, 1984; Chaline *et al.*, 2000; Marlowe, 2005; Godfrey, Sih and Bull, 2013; Majolo and Mcfarland, 2013; Campos *et al.*, 2014; McFarland *et al.*, 2014; Maldonado-Chaparro *et al.*, 2015). The Machiavellian Intelligence Hypothesis suggests that advanced cognitive processes or abilities were acquired as evolutionary traits to assist animals to solve complex day-to-day social scenarios that are also affected by ecologically-changing landscapes (Byrne, 1988; Byrne & Whitten, 1997). Thus, this theory includes adaptations that helped solve personal gains through deception but also cooperation (Byrne & Whitten, 1997). The evolution of social intelligence grants a legacy of importantly varied adaptations that do not necessarily express as a whole package. Some such adaptations comprise behavioural flexibility, social learning, innovation, tactical deception, coalition and alliance formation, social priorities or strategies around relationships, and conflict-solving options like reconciliation, consolation, or third party conflict resolution (Byrne & Whitten, 1997). Consequently, it is paramount to think of how these abilities can enable animals to perform behaviours that are beneficial for them.

I.2.B. Why are these social abilities important?

Individuals per se are not evolving machines, instead, species evolve, gene frequencies change, but individuals make use of what has evolved before and is available for them. In this context, complex cognitive abilities are very useful for individuals to solve the problems of group living. Some basic adaptations that permit individuals to go about their social environments are the recognition of individuals with whom one is living. Beyond that, individuals can recognise individuals' particular kinship ties with others in the same group and the rank positions of others (Bergman, Beehner, Cheney, & Seyfarth, 2003; Borgeaud, Alvino, van Leeuwen, Townsend, & Bshary, 2015; Range & Noë, 2005). Moreover, group-living individuals may have the capacity to amass information about other individuals' social relationships (or friendships) and incorporate this into the regulation of one's behaviour as observed in baboons'

(*Papio hamadryas ursinus*) information used to achieve “sneaky” mating opportunities (Crockford, Wittig, Seyfarth, & Cheney, 2007). Similar findings were made thanks to the use of playback experiments, i.e. chimpanzees recognise the bonds of others by looking longer times after listening to the vocalisation of bond partners of an individual with whom they had had an agonistic interaction (Roman M Wittig *et al.*, 2014).

Therefore, group-living animals not only develop an affinity with particular individuals (kin, non-kin) and form bonds that act as useful interdependencies in collaborative-cooperative contexts but also have memory abilities to distinguish how others are connected in the social group. Such capacity for social knowledge spans out allowing individuals to selectively engage in coalitions, as seen in different bird species that show a preference for certain bond partners (reviewed in Emery, Seed, Von Bayern, & Clayton, 2007), or male dolphins (*Tursiops spp.*), where socially bonded non-relatives interact in highly-cooperative ways like herding behaviours or fighting with other males during mating season (Gerber *et al.*, 2021). Further, by knowing other’s rank position within the hierarchy system relative to the self, individuals can make strategic decisions about getting involved in providing support to others so as not to get aggressed by superior-ranking individuals as observed in Japanese macaques (*Macaca fuscata*) (Schino, Polizzi Di Sorrentino and Tiddi, 2007). Further, primates can scan one’s perimeter and the rank of nearby neighbours to make strategic decisions about exchanges of grooming for tolerance (audience effects) as experimentally tested in vervet monkeys (*Chlorocebus pygerythrus*) (Borgeaud, Schnider, Krützen, & Bshary, 2017). A similar expansion of such capacity to relate other group peers to the self is brought by a chimpanzee study that shows that victims of aggression can exaggerate their calls whenever the potential audience contained individuals that matched or surpassed the aggressor’s rank (Slocombe and Zuberbuhler, 2007). Abundant studies of social learning inform that observing others can have fitness implications through learning feeding techniques, as seen in cottontop tamarins (*Saguinus Oedipus*), or chickadees (*Poecile gambeli*).

An additional prolongation of social animals’ cognitive abilities is shown in the capacity of baboons (*Papio ursinus*) to show phenotypic assortment that may have implications in information flow (Carter *et al.*, 2015), and information transfer in groups of ravens (Kulahci *et al.*, 2016). Beyond, studies conducted in Trinidadian guppies (*Poecilia reticulate*) relate assortment to the maintenance of cooperation around predator inspection (Croft *et al.*, 2009), or solving social dilemmas (theoretical model) (Aydogmus, Cagatay and Gürpinar, 2019). Likewise, studying variation in social environments illustrates how different foraging strategies can be learned in wild birds (Aplin and Morand-Ferron, 2017) but also, that groups can show hunting habit signatures that are rather independent of ecological factors, as seen in bonobos (Samuni, Wegdell, & Surbeck, 2020). This lays some of the foundations for the evolution of culture as known in the context of chimpanzee tool use or humpback whale song (*Pan troglodytes, Megaptera novaengliae* ; Gruber, Poisot, Zuberbühler, Hoppitt, & Hobaiter, 2015; Andrew Whiten, 2021; Garland et al., 2011;). Further, groups seem to recognise some key individuals because of the role they can display as leaders, so others follow during group movement decisions as shown in different animal taxa like broad-winged hawks (*Buteo platypterus*) (Maransky and Bildstein, 2001), African elephants (*Loxodonta africana*) (McComb *et al.*, 2011), black howler monkeys (*Alouatta pigra*) (van Belle, Estrada and Garber, 2013), grey wolves (*Canis lupus*) (Peterson *et al.*, 2002), vervet monkeys (Lee & Teichroeb, 2016), chacma baboons (Stueckle and Zinner, 2008), wild bonobos (Tokuyama and Furuichi, 2017), or humans (*Homo sapiens*) (Dyer *et al.*, 2009). In this thesis, I will investigate strategic decision-making around some of the features abovementioned like behavioural flexibility, cooperation, bonds, phenotypic assortment or individual preference, speculate about the importance of leader-follower dynamics, and the importance of strategies to solve conflicts of interest or social dilemmas. In this context, the chapters of this thesis will concentrate on the measurement of behaviours that reflect underlying decision-making rules at both the individual and group level. In this panorama cooperative behaviours stand out as a behavioural option that animals can put on display that still bewilders scientists.

I.3. Cooperation

The topic of cooperation is a puzzling one and evolutionary biologists have been trying to resolve how it works, especially when behavioural strategies are unconditional ("always defect", "always cooperate") because individuals' behaviour is flexible to changing circumstances (Bshary and Bergmüller, 2008). Here, I will refer to cooperation as behavioural actions that are mutually beneficial or as investment by the actor incurs in that benefit the recipient (Bshary and Bergmüller, 2008). This definition, however, challenges one of Darwin's natural selection theory precepts (Darwin, 1859); that natural selection cannot produce modifications good for another species (here species can be understood as another individual). Hamilton brought to attention beneficial acts that have previously unlooked genetic characteristics (Hamilton, 1964a, 1964b) which led to the formalisation of kin selection theory (Maynard-Smith, 1964). Still, how non-kin individuals engage in cooperative acts like predator vigilance, group mobbing behaviour, alarm calling, support to injured group peers, giving up one's reproduction to help others' reproduction, cooperative hunting, food sharing, body cleaning of parasites, care-giving, nursing someone else's infants, defending territories or fighting rival groups remained contending issues (Clutton-Brock, 2002; Dugatkin, 1997). Once the main distinction of cooperative acts was made, resolving whether interactions involved related individuals or not, opened the way for additional conceptual options of cooperation. Trivers contributed to the idea of reciprocity using behavioural examples of cleaning symbioses, warning cries of birds, and human reciprocal altruism (Trivers, 1971). This concept was further developed by Axelrod and Hamilton that applied Prisoner's Dilemma games to deduce the impact of behavioural strategies between individuals that have the opportunity to cooperate when interacting (Axelrod and Hamilton, 1981). At this stage, individuals that can benefit from a cooperative partner and reciprocate, but instead do not play cooperatively was interpreted as a form of defection, cheating or free riding.

Generally, reciprocity consists of the alternation that two individuals undertake when giving and receiving benefits obtained thanks to the partner's acts, especially if the individuals have ample opportunities to interact because they live in the same group (Trivers, 1971). A key difference between reciprocity and mutualism is that the second is a type of cooperation that takes place between species (Bshary and Bergmüller, 2008; Johnstone and Bshary, 2008). Game theory approaches to animal behaviour initially based in Prisoner's Dilemma-like scenarios (Axelrod & Hamilton, 1981; Maynard-Smith, 1982) benefited from additional two-player games' options like hawk and dove (Maynard-Smith, 1982), the stag-hunt game (Skyrms, 2004), and the snow drift game (Sugden, 2004). One of the reciprocity explanations that derived from the reciprocity scheme was the tit-for-tat strategy that explained how cooperative interactions could persist despite the risk of cheating if individuals played the same strategy of their partner (“cooperate when your partner cooperates, defect when your partner defects”) (Axelrod and Hamilton, 1981). However, this theory needed the individuals to engage in a series of “continuous” interactions. Beyond, the biological market theory (BMT) assumed there is no cooperation riddle because individuals control their offers, so exchanges only happen when the interactants agree, which automatically implies that there is no cheating taking place (Noë, van Schaik and van Hooff, 1991; Noë and Hammerstein, 1994). Further, the BMT put the focus on payoff distributions among cooperators according to partner choice (and partner switching) and competition (and outbidding competition) fluctuations (Noë, van Schaik and van Hooff, 1991; Noë and Hammerstein, 1994). When studying such dynamics, it is important to distinguish whether the cooperative act that one individual provides to the partner is dependent or independent of the partner’s presence as if the act itself would take place independently, such cooperative act could be better interpreted as by-product mutualism (Dugatkin, 1997b). Furthermore, generalised reciprocity aimed to explain situations under which individuals of a group decide to cooperate based on the previous interaction they experienced independently of whom with whom they had interacted before (Pfeiffer *et al.*, 2005). In a similar vein, indirect reciprocity assumes that individuals behave in cooperative manners with others upon having observed them behaving in cooperative ways with someone else (Axelrod and Hamilton, 1981; Alexander, 1987), although this concept still raises important issues such as how cooperative acts like grooming between individuals that help bond formation would fit into this logic. However, the “reputation-based partner choice” idea, formerly considered competitive altruism (Roberts, 1998), suggests that cooperation can be linked to individuals building a reputation that helps them be more eligible by others and facilitates the establishment of cooperative partnerships (Sylwester and Roberts, 2010) as reported in cleaner fish (Bshary and Noë, 2003) or as sometimes hypothesised in humans (Barclay and Willer, 2007; Fu *et al.*, 2008).

Because animals living in the same group they are likely to engage in repeated interactions. Accordingly, it is thought that reciprocity can work only if the partners have the tendency to be cooperative and there is a probability that they will interact again (Lehmann & Keller, 2006). This reasoning is based on the assumption that an interaction between a cooperator and a recipient will be likely to be repeated if the likelihood that individuals interact again is greater than the cost to benefit ratio perceived by the co-operator (Axelrod & Hamilton, 1981; Lehmann & Keller, 2006; Trivers, 1971). For this to occur, individuals are presupposed to have the necessary abilities to identify each other and to keep track of the previous interactions (Fehr and Fischbacher, 2003), which is widely assumed in humans, but sometimes more debatable in non-human animals. Hence, reciprocity was traditionally expected to rely on memory mechanisms that grant individuals the capacities to recall details about specific interactions with particular partners to avoid cheating partners and favour cooperative ones (Fehr and Fischbacher, 2003).

In that frame, reciprocity processes (cooperative actions spaced in time and indirect reciprocity is discarded) are explained by different possible mechanisms. The mechanism of attitudinal reciprocity posits that individuals opt to reciprocate their partners following the logic of mirroring past interactions that imprinted a positive emotional stand favouring future cooperation actions (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006; de Waal, 2000). Third, emotion-based reciprocity can be interpreted as an extension of the previous one, but here the emotion component elicited by interactions can bear fruit over longer periods since the individuals interacting are socially bonded (Schino & Aureli, 2009), although the underlying principle is rather equivalent. A shortcoming of this last proposition though would be its limitation to bonded partners that are naturally in interdependency states (sort of ineludible obligation), which would constrict such partnerships sensibly within a group, and perhaps constitute an exchange type for cooperative behaviours different from kinship and reciprocity (Roberts, 2005). As it appears, attitudinal reciprocity could have an emotional component, as positive salient emotional states could be drivers of the mirroring of behaviours. In addition, studies linking neuro-hormone variations like oxytocin to prosocial behaviours (in chimpanzee studies: grooming bonded partners, sharing food, group defence during intergroup encounters: Crockford et al., 2013; Samuni, Mielke, & Preis, 2019; Wittig, Crockford, Deschner, et al., 2014) cannot exclude (nor explain) the cognitive basis (emotions) of physiology yet. Lastly, calculated reciprocity suggests that individuals base their decision of whether to reciprocate a social partner or not based on the mental abilities that permit scorekeeping of the previous interactions (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006). Thus, the different forms in which cooperative behaviours can be explained and interpreted are of much relevance to address possible conflict of interest-like contexts that represent dilemmas to the collection of individuals that compose animal groups.

I.4. Social dilemmas

Beyond the one-to-one context in which dyads can act cooperatively, there are situations when collectives of individuals are part of the cooperation game. Again, similarly to two individual setups, collective setups offer the possibility to study behaviour and make predictions about underlying strategies (strategies as a list of behavioural stances or outputs under different subjective situations that are open to consideration in some instances of the game; Hammerstein & Riechert, 1988). Because groups are aggregates of individuals that share home ranges or territories and move more or less cohesively to perform different activities, there is remarkable potential for conflicts of interest to arise.

These issues are very well illustrated in the foraging context of groups, as it is a central activity to individuals' wellbeing, but also conditioned by the distribution of food resources (Schoener, 1971). Therefore, the individuals of a group are confronted with potentially different optimal foraging decisions. Thus, foraging decisions are embedded within another collective game, that is, movement coordination. It is thought that individuals make spatial positioning decisions that obey different trade-offs as they benefit from diminishing the predation risks while assuming a certain degree of within-group foraging competition (Hirsch, 2007; Morrell and Romey, 2008). It is thought that a group's spread is the result of the combined (collective) balance of costs and benefits of the individual parts that integrate the collective (Parrish and Edelstein-Keshet, 1999). This raises interesting questions such as how group movement decisions are orchestrated. For groups to move cohesively, there is either a certain degree of consensus or some individuals can impose their decision on others (Conradt & Roper, 2005). In the case of consensus building, the individuals must coordinate to favour one option and exclude other alternatives for synchrony to materialise (Conradt & Roper, 2003; Conradt & List, 2009).

Under that framework, there is the possibility that consensus becomes a reality following a chain of behaviours where a leading figure initiates movement and it is up to others whether to follow or not (Stueckle and Zinner, 2008; King and Cowlishaw, 2009; Petit *et al.*, 2009). But achieving coordination as a group through consensus building has obvious costs for those that give up on alternative options, such as sacrificing one's preferred destination (Conradt & Roper, 2010; King & Cowlishaw, 2009). The role of leaders has been described widely across the animal taxa, and different attributes have been suggested as relevant, i.e. rank position and temperament in mountain gorilla (*Gorilla gorilla beringei*) (Fossey, 1972), grey wolves (Peterson *et al.*, 2002), or chacma baboons (King *et al.*, 2008). In other instances, leaders seem to be knowledgeable about food sources in vervet monkeys (Lee & Teichroeb, 2016), broad-winged hawks (Maransky and Bildstein, 2001) or golden shiner fish (*Notemigonus crysoleucas*) (Reebs, 2000). Beyond, group decision-making could be conceptualised as an extension of cooperative behaviours, even if some individuals have to give up personal preferences (costs) to build up consensus. This generalisation could be looked at through the lens of game theory with n-players during public good games (Kagel and Roth, 2000; Doebeli and Hauert, 2005) to pinpoint the mechanics of decision-making (Brosnan, Beran, Parrish, Price, & Wilson, 2013). However, some distinctions could be made here as in a coordination game around group movement; the role of defectors could be re-interpreted as decision-maker agents embodying disagreement visions. While individuals having a highlighted role in movement decision making are not explicitly opting to defect, by imposing their will they are nevertheless better off than other individuals that are not in such position. The would-be joiners or individuals that do not get to "vote" could be seen as co-operators instead. As an example, chimpanzees can coordinate as a group when moving (Fletcher, Warneken and Tomasello, 2012), but they are also capable of choosing not to do so when some individuals prefer alternative options that are more beneficial (Rekers, Haun and Tomasello, 2011). However, they seem to prioritise coordination and give up on individual preferences when the benefits achieved are higher than those driven by individual interest would be (Bullinger *et al.*, 2011). On that ground, to address the nature of decision-making at the individual level or the group level, it is useful to think in terms of payoff matrices that can represent what the alternative strategies can offer to the different players (Brosnan, 2013; Wubs, Bshary, & Lehmann, 2016).

As seen before, decision-making at the group level is a process that encapsulates decisions (following individual strategies, plus group strategies' influences) contingent on prior decision choices (Brosnan, Beran, Parrish, Price, & Wilson, 2013). This game theory look at group movement links well to the underlying decision-making that is likely to be part of animal populations when foraging, hunting, resting, crossing rivers or using open areas. Moreover, similar challenges arise when animals aim to resolve group coordination issues during intergroup encounters as the potential benefits of the contest are at stake when coordination problems arise (Nunn and Lewis, 2010). The specific context of intergroup encounters is relatively well studied across the animal taxa, from banded mongooses to lions (*Panthera leo*), howler monkeys or humans (Mosser and Packer, 2009; Furrer *et al.*, 2011; Van Belle and Scarry, 2015; Pisor and Surbeck, 2019). These situations appear when two groups that are naturally linked to a home range or territory find each other nearby, which commonly elicit defensive reactions to safeguard the territory against the rival group (Hinsch & Komdeur, 2017; Maynard-Smith & Price, 1973; Switzer, Stamps, & Mangel, 2001).

More concretely, behavioural ecology is interested in the study of fitness, which makes the topic of intergroup encounter interesting due to the many internal (perception value) or external (environmental characteristics) aspects that may condition territoriality and fight between groups (review in Lucchesi et al., 2020). The territories and the resources contained within represent a collective action problem, insofar as they represent a collective good that requires a concerted effort of the parties involved (group individuals) to actively defend and dissuade the opponent group (Olson, 1965). What is more, as, in the case of group movement, synchrony and coordination, groups are expected to perform in a relatively coordinated fashion to successfully expelling a rival group. This implies dealing with risks associated with the emergence of cheaters or free-riders (Nunn and Deaner, 2004; Willems, Hellriegel and van Schaik, 2013; Willems and van Schaik, 2015). Again, what could be first deemed as group behaviour becomes more challenging when the individual players of the group are considered as single, somewhat independent decision-making entities. Theoretically, those that are benefitting more from defending the territory (and resources) are expected to display higher levels of participation in the defence action and this should be reflected in the potential payoffs that integrate investment of costs (Olson, 1965). These costs can be characterised by risk of injury or even death in some species like meerkats, grey wolves, chimpanzees, or modern humans as well as Australopithecines (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Dyble, Houslay, Manser, & Clutton-Brock, 2019; Wrangham & Glowacki, 2012). Costs can also be the loss of an opportunity to perform an alternative activity, more beneficial (in the short-term) activity like foraging.

There is abundant literature reporting that individual factors like the philopatric sex, rank position, number of kin individuals in the group are associated with participation in intergroup encounters (Mirville et al., 2018; Samuni, Mielke, Preis, Crockford, & Wittig, 2020; Wright, 2007; Beehner & Kitchen, 2007; Koch, 2016; Majolo, de Bortoli Vizioli, & Lehmann, 2016). In the philopatric society of vervet monkeys, it seems that females are more driven to participate in group defence, and while males are also collaborating, females sometimes use punishment and rewards to accentuate males' involvement (Arseneau-Robar et al., 2016). Males have sometimes been regarded as having fewer stakes on "group causes" than females in philopatric societies so their behaviour has been interpreted as 'hired guns' (Fashing, 2001; Perry, 1996; Wrangham, 1980). However, it could also be that males' decisions to participate in intergroup encounters could represent a by-product of inter-sexual cooperation whereby they engage in cooperative behaviour with the females (in female-philopatric groups like vervet monkeys) but benefit also by increasing their reputation and perhaps investing in possible future mating opportunities (Arseneau-Robar, Müller, Taucher, van Schaik, & Willems, 2016).

Beyond the male-female distinctions that may motivate payoff asymmetries, defending an area is fundamental due to the importance of its spatial and ecological connotations (food, water, shelter) (Arseneau-Robar et al., 2018; Beehner & Kitchen, 2007; Sakamaki, Ryu, Toda, Tokuyama, & Furuichi, 2018). For these reasons, the context of intergroup encounter provides a phenomenal suite to explore group decision making as n-player games and speculate about the essential factors that may shape strategies manifested in concrete decisions that offer measurable behavioural outputs. Because outfighting a rival group would demand more than one or just a few players, one can discard snow-drift or stag-hunt games (Bullinger et al., 2011; Connor, 2010; Hauert & Doebeli, 2004; Kümmerli et al., 2007; Luo, Liu, & Chen, 2021; Pacheco, Santos, Souza, & Skyrms, 2009; Silk, 2007; Skyrms, 2004; Van Veelen & Nowak, 2012). Instead, there is a possibility that strategic behaviours of this kind can benefit from original applications that combine collective action problems in conjunction with the volunteer’s dilemma (Archetti, 2009; Archetti & Scheuring, 2010; Archetti et al., 2011) and coordination problems (Archetti, 2009; Silk, 2007; Van Vugt, Hogan, & Kaiser, 2008) to better understand some n-player games.

Hence, group coordination, group synchrony, group movement and group defence are contexts where there may be conflicts of interest between the different individuals of a group due to the underlying payoff asymmetries involved. As a result, group conflicts require helpful leaders whereas group movement may yield egoistic leaders. Crucially, payoff asymmetries are of maximum interest because herein may lay interesting aspects that condense strategic decision making around behaviour adjustment (Van Vugt, 2006) in specific group predicaments like group movement or fighting a rival neighbouring group. In principle, leadership can be effective if only a small fraction of the group leads (Couzin *et al.*, 2005; Dyer *et al.*, 2009), while in collective action problem situations like intergroup encounters may require a certain number of volunteers to take action as the volunteer’s dilemma suggests (Archetti, 2009; Archetti, 2011). Beyond, both contexts would need the figure of initiators (group movement, group defence) to whom other individuals could join in the action, both with potentially subjacent different decision-making rules.

Ultimately, leadership may represent an evolutionary co-opted trait that allowed the efficient solving of social dilemmas like collective action problems like intergroup conflicts, group foraging, group movement or peace-making (De Cremer & Van Vugt, 2002; King, Johnson, & Van Vugt, 2009; Van Vugt, 2006). Albeit, one cannot exclude that leaders may have (to some extent) self-driven motivations to lead as being a leader is a non-zero-sum game (actor interests partly overlap and partly conflict with the rest of the group) (Rapoport, 1967). Therefore, it appears unlikely that evolution would have favoured the emergence of leader figures if their decisions were not more positive than negative to the overall group (Van Vugt & Cremer, 1999). For that reason, the resolution of such collective action problems require strategies that could be represented as equilibria games (both leaders and followers are better off playing the same strategy) (Maynard-Smith, 1982; Van Vugt, 2006). The study of these aspects could incorporate some concepts of the collective action problem theory and volunteer's dilemmas to give a glimpse on wider fundamental aspects like group's manageability, cohesion, and stability, especially considering that bigger groups are more likely to fail in coordination games (van Huyck, Battalio and Beil, 1990; Robert and Frey, 2010). For the moment, it appears that evolution primed animals' assertiveness, understood as a capacity to reach consensus and behave synchronously and in cooperative ways even if imperfectly, while leaving some space to free riding and payoff asymmetries. Furthermore, group's payoffs are subject to variation not only due to the different individual perceptions and behaviours but also due to environmental, climatic and demographical variation, adding and amplifying layers of complexity to decision-making around social behaviours.

I.4.1. The dynamicity and flexibility dimension of life in a social group

Life in social groups is inherently a changing one. In addition to the spatially mobile component of most animal societies, groups undergo fundamental changes across time due to different influxes like demographic changes, rank instability periods, life history (growth, social development or maturity, migration needs, sexual activation), social products like bonds or friendships and the establishment of family lines. This blend of considerations is subject to the caprices of climatic, environmental and ecological hazards. Given the abundant elements that can influence life in social groups, it could be expected that natural selection would have penalised rigidity and favoured flexibility and adaptability to changing environments - both social and ecological. Behavioural flexibility is therefore a means by which individuals can achieve adaptation to local and changing environments (van Schaik, 2013).

Some pertinent examples illustrate greatly how animals can benefit importantly from exhibiting flexible behaviours; bird migration strategies (Both and Visser, 2001; Alerstam, Hedenström and Åkesson, 2003; Eggeman *et al.*, 2016), coral reef swimming behaviour varies according to hydrodynamic conditions (Heatwole and Fulton, 2013), vervet monkeys and chacma baboons' activity budget adaptation to climatic-seasonal changes (Hill et al., 2003; McFarland et al., 2014; Young et al., 2019). Lions groups adapt to ecological conditions by subgrouping depending on prey availability (Mbizah *et al.*, 2020), and baboon foraging behaviour indicates important diet changes as the habitat changed in Amboseli National Park (Kenya) across 15 years (Alberts *et al.*, 2005). Likewise, grazer ungulates of Kruger National Park changed their diets compared to that of browsers in response to drought conditions that altered the grasses distribution and abundance (Abraham, Hempson and Staver, 2019). Similar buffering strategies may be seen in species as phylogenetically distinct as spotted sand lizards in Southern Kalahari alter hunting strategies when their habitats degraded (*Pedioplanis l. leeoocellata*) (Blumroeder, Eccard and Blaum, 2012). Chacma baboons individuals show adaptable strategizing and role-taking around producer-scrounger dynamics across spatial scales (larger and indefensible versus shorter and more monopolisable) (Lee & Cowlishaw, 2017). Sustained exposure to stable ecological variations may have assisted different animal taxa to acquire flexible grouping structuring, i.e. fission-fusion (Aureli *et al.*, 2008; Sueur *et al.*, 2011), as seen in Asian elephants (E*lephas maximus*) (Silva *et al.*, 2011), lions (Mbizah *et al.*, 2019), primates like spider monkeys (*Ateles geoffroy yucatensis*) (Asensio, Korstjens and Aureli, 2009; Ramos-fernández *et al.*, 2009); ungulates like woodland caribou (*Rangifer tarandus caribou*) (Lesmerises, Johnson and St-Laurent, 2018), many bird species (Silk, Croft, Tregenza, & Bearhop, 2014), guppy fish (*Poecilia reticulata*) (Kelley *et al.*, 2011), or sand tiger sharks (*Carcharias taurus*) (Haulsee *et al.*, 2016).

Moreover, animals can also respond flexibly to changes due to social variation which links well with the concept of social competence that presupposes variability of behaviour and optimisation relative to the availability of social information (Oliveira, 2009; Taborsky and Oliveira, 2012). Some examples are observed in Japanese macaques' grooming variation concerning changes in group size and composition (Kurihara, Nishikawa and Mochida, 2019) shaping intra-group competition dynamics and the extent of kin-biased grooming networks (Majolo *et al.*, 2009). Similarly, chimpanzees change their grooming patterns during periods of dominance instability (Koyama, Ronkainen and Aureli, 2017). Also, female chacma baboons respond to the death of a close partner by increasing the grooming network (Engh *et al.*, 2006). Age also seems to shape social interaction strategies, as seen in older rhesus macaques

(*Macaca mulatta*) that become more recipients of grooming interactions as they grow old (Liao *et al.*, 2018). Another example of flexibility in sociality is provided by rhesus macaques' response to a hurricane, where a general group trend of sociality increase was more accentuated in the subset of individuals that were more isolated before the extreme event (Testard *et al.*, 2021). Within the gambit of the group, narrow-stripped mongooses (*Mungotictis decemlineata*) showed a positive relationship between social learning and behavioural flexibility when tested in cognition tasks like reversal learning (Rasolofoniaina, Kappeler and Fichtel, 2020). Also, the Caribbean cleaning goby (*Elacatinus prochilos*) showed flexible social organisation when two phenotypes (pair living, group living) were tested in group manipulations, where both formed clear dominance hierarchies (Mazzei, Soares and Bshary, 2021).

This is important because ecological circumstances can vary rather unpredictably through extreme droughts, hurricanes, typhoons or the likes (Parmesan, Root and Willig, 2000; Foley, Pettorelli and Foley, 2008; Walls, Barichivich and Brown, 2013; Knoll and Nowak, 2017; Herring *et al.*, 2018) that may constitute ecological tipping points (Lenton, 2013; Riche, Johannessen and Macdonald, 2014; Botero *et al.*, 2015; Moore, 2018). Also, such circumstances facilitate animals' adoption of proximate adjustments, as seen in cleaner fish increase in strategic sophistication after the supply of clients and the demand rules of cleaners had changed (Triki *et al.*, 2018). In cichlid fish *Simochromis pleurospilus,* an increase in social learning tasks regarding food (Kotrschal and Taborsky, 2010) followed severe ecological alteration (the first based on wild fish brought to lab, the second with ecological conditions mimicked in the lab with lab-raised fish). Moreover, a study on 69 bird species attested that the degree of behavioural flexibility and the capacity to display foraging innovations in combination with larger brains seemed to determine success in invasion success to New Zealand novel environments (Sol, Timmermans and Lefebvre, 2002), and the same invasion potential relies on the Australian cane toad behavioural flexibility capacity (*Rhinella marina*) (Webb *et al.*, 2014). Behavioural diversity, therefore, adapts to ecological diversity, as a study using 144 wild chimpanzee communities reports considering tool use and environment variability (Kalan *et al.*, 2020). Furthermore, behavioural flexibility is not an evolutionary trait limited to endotherms, as lizards (*Anolis evermanni*) respond flexibly to new and challenging ecological conditions when tested in multiple cognitive tests (Lea *et al.*, 2020), nor of vertebrates, as a study shows that hermit crabs (*Pagurus berhardus*) adapt of startle responses to risk conditions (Briffa and Bibost, 2009). In this frame, social network approaches offer various measures to study behavioural variation, group structure and cooperation through the study of dyadic interactions (Whitehead, 2008; Krause, Lusseau and James, 2009; Farine and Whitehead, 2015).

I.4.2. Social networks as a platform to study the processes of group living

Social networks comprise individuals (nodes) and the relationships (interactions, associations) between them through edges (ties or links) (Whitehead, 2008). Edges can be measured differently thanks to the use of weights and directionality and inform of individual relationships. Social networks approaches can be incorporated into individual or group measures (Wey, Blumstein, Shen, & Jordán, 2008) making them valuable tools to capture behaviour dynamics (i.e. grooming, proximity between neighbours). The social interactions of the group's different individuals shape the group's social structure (Hinde, 1976) that build upon certain group composition (multi-male, multi-female in the case of vervet monkeys). The information of social structure is key to understand some relevant characteristics of animal societies like information transmission, the persistence of cooperation dynamics, the spread of diseases, or the emergence of individual roles (Eguíluz *et al.*, 2005; Hamede *et al.*, 2009; Farine *et al.*, 2015; Fotouhi *et al.*, 2018).

For example, social networks can reflect group structure variation due to life-history changes (birth, mating) as seen in rhesus macaques (Brent *et al.*, 2013). Likewise, male passerine birds *Carpodacus mexicanus* of less elaborated phenotype changed their associations more frequently than more elaborated ones which helped them increase their attractiveness (Oh and Badyaev, 2010). Similarly, better-connected male Wire-tailed manakins (*Pipra filicauda*) experienced a more pronounced social rise which may have effects on their reproductive success (Ryder *et al.*, 2008). Seasonality can also influence group structures, as seen in giraffes (*Giraffa Camelopardalis giraffe*), that present more multi male-multi female subgrouping during winder even if giraffes are not seasonal breeders, suggesting that summer female-female clustering may facilitate bond formation (Wolf, Ngomo, Bennett, Burroughs, & Ganswindt, 2018). Likewise, social weaver birds' (*Philetairus socius*) markedly decreased their network cohesion (highly connected to cooperative behaviours) under extreme temperatures (Rat *et al.*, 2020). In the case of species that live in multi-level societies like Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*), food abundance conditions seem to shape inter-unit relationships, hence configuring a complex and variable social network (Adams *et al.*, 2021). On the same token, changes in the social environment precipitated alterations in aggression and affiliative dynamics that were visible in the network structure that led to a mass-eviction phenomenon in rhesus macaques (*Macaca mulatta*) (Larson *et al.*, 2018). Comparably, network parameters like modularity indicated deterioration of group cohesiveness and progressive sub-grouping before chimpanzees and killer whales' (*Orcinus orca*) groups fissioned into two daughter groups (Feldblum *et al.*, 2018; Stredulinsky *et al.*, 2021). Human-caused habitat modifications can also provoke network changes as shown in Australian bottlenose dolphins (*Tursiops aduncus*), where individual network properties exhibited remarkable resilience following intensive human fishing activity (Ansmann *et al.*, 2012). Finally, if groups' cohesiveness weakens due to rank instability, this can also reflect physiological stress levels, as found in female chacma baboons (Wittig *et al.*, 2008).

Likewise, group size increases decreased the influence individuals can have on a group as well as the potential transmission of information in yellow-bellied marmots (*Marmota flaviventris*) which was observable through the decrease of centrality and betweenness (Maldonado-Chaparro, Hubbard and Blumstein, 2015). In the same species, affiliative networks were highly influenced by age and kinship, being tighter in younger individuals whereas agonistic networks were higher in older individuals (Wey & Blumstein, 2010). In philopatric societies, like that of vervet monkeys, females connectivity (measured through different parameters) was consistently higher across seasons compared to that of males (Blaszczyk, 2018). In the same way, in the female-philopatric society of spotted hyenas (*Crocuta crocuta*) females' network seem influenced by rank (Turner, Bills and Holekamp, 2018). Sometimes, the connectivity of individuals can be highly conditioned by the family niche in which individuals are born, as observed in Australian zebra finches (*Taeniopygia guttata*) or spotted hyenas (Ilany & Akçay, 2016), suggesting that early life experiences have an imprint on future social trajectories.

Moreover, social networks can aid to visualise cooperation dynamics and rewiring of connections (Rand, Arbesman and Christakis, 2011). Fruteau et al. showed that individuals who had learned a new foraging task increased their connectivity, and similarly, ring-tailed lemur (*Lemur catta*) individuals that had learned a food extraction technique became more central in the network (Kulahci, Ghazanfar and Rubenstein, 2018). Furthermore, collective decision-making around group movement is connected with the network structure in Tibetan macaques (*Macaca thibetana*) and in black howler monkeys (*Alouatta pigra*), where more connected females acted as leaders and made movement decisions faster (Fratellone et al., 2019; van Belle et al., 2013). Finally, social connectivity studied through the individuals' position in the group network can shed light on the fitness implications via effects on survival, as found in killer whales and Barbary macaques (Ellis et al., 2017; Lehmann, Majolo, & McFarland, 2016). Studies in resident killer whales demonstrate that mothers and daughters association varied with births and deaths involving the maternal line or the connectivity with males in the group (Ellis *et al.*, 2021). Altogether, social networks can help visualise, identify, and link social interactions to specific socio-ecology conditions.

In this thesis, I studied individual connectivity status through metrics like degree (number of edges to which a node is connected), strength (overall rate of interaction frequency), and betweenness (number of shortest paths between other nodes that pass through a given node)- as defined in Whitehead's social network analysis book (Whitehead, 2008). Similarly, I used global network metrics of social structure using females as a collective of individuals through the metrics of density (number of connected edges in the network relative to the possible total edges), transitivity (proportion of triads as trios of nodes that have three edges divided by the number of triads that have two edges) – as defined by Farine and Whitehead (Farine and Whitehead, 2015), and modularity (indicates how well a given population is subdivided into clusters or subgroups; Whitehead, 2008). Concretely, I used food treatment (mimicking ecological conditions) to evaluate variation in individual-based metrics in Chapter II by comparing the treatment to two control periods (one before, one after). Likewise, I examined how an extreme drought affected sociality would impact both individual and group network metrics (of adult females) across two years using time windows.

I.5. Species of study and study site

For my PhD, I studied vervet monkeys (*Chlorocebus pygerythrus*), a semi-terrestrial Old-word monkey species belonging to the genus *Chlorocebus* widely distributed across the African continent, from the Ethiopian Highlands to the southern-most tip of South Africa. Vervet's diet is highly omnivorous, as they forage on shrubs, trees, herbaceous plants, and insects (Whitten, 1983; Isbell and Jaffe, 2013). Vervet monkeys live in densities that range from 9 to 104 individuals per square kilometre (Isbell and Jaffe, 2013). They adapt to an extensive range of habitat types from savannah to woodland, or forest-grassland mosaics (Isbell and Jaffe, 2013). They live in multi-male and multi-female groups of up to 38 individuals (Isbell, Cheney and Seyfarth, 2002; Isbell and Jaffe, 2013), although in Amboseli groups have been reported of sizes up to 53 individuals (Struhsaker, 1967) and at the Inkawu Vervet Project (IVP) groups have been recorded bigger than 60 individuals (personal observation). The different chapters of this thesis are based on vervet monkeys from the IVP, in Kwazulu-Natal (28° 00.327S, 031° 12.348E, South Africa) where six groups of vervet monkeys are habituated to humans and live in adjacent territories with ample overlapping areas (van de Waal, 2018) and even some sleeping sites are shared (personal observation). Vervets are active from sunrise to sunset and range their territory almost all day except during summer when long breaks and naps are needed to cool off due to the high temperatures (McFarland *et al.*, 2014; Mcfarland *et al.*, 2019).

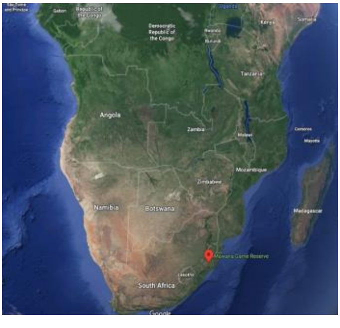

Figure 2. Map of Southern Africa with Mawana Game Reserve highlighted in red, where the IVP is located, in Kwazulu Natal, South Africa.

In the society of vervet monkeys, females are the philopatric sex and stay in their natal group throughout their entire lifespans (Cheney & Seyfarth, 1990), although there are cases when groups fission and females form a daughter group together with some males and juveniles (van de Waal, van Schaik, & Whiten, 2017). Vervet's society is a rather hierarchical one, where females inherit their rank from that of their mothers (younger offspring higher-rank than older offspring) which is relatively rigid and stable. Kinship ties are reflected among mother-offspring but also grandmother-grand offspring relationships (Fairbanks, 1988). Male vervets migrate upon reaching sexual maturity (Cheney & Seyfarth, 1983; Struhsaker, 1967) which helps avoid consanguinity (Melnick, 1983). Males' rank is determined by male-male competition and therefore more susceptible to variation (Cheney & Seyfarth, 1990). Direct intergroup conflict sometimes takes the form of intergroup encounter, where two groups face each other and take both indirect (mostly vocal, gestural displays) and direct action (chases, bites) to force the other group to retreat (Cheney, 1981; Struhsaker, 1967). Among the different social behaviours that vervets can exhibit (cuddling, mouth to mouth, infant-carrying, infant-handling and caressing), grooming is the most conspicuous and permits exchanging roles. Such interactions further enable relationship building between individuals (Fruteau, Lemoine, Hellard, van Damme, & Noë, 2011; Seyfarth, 1977, 1980; van de Waal, Spinelli, Bshary, Ros, & Noë, 2013) beyond the most obvious grooming benefits of parasite removal and relaxing-state induction (Mooring, Mckenzie and Hart, 1996; Shultz and Dunbar, 2010). Vervets are capable of recognising dominance relations within the group, rank orders, and matrilineal kinship relations (Cheney & Seyfarth, 1985; Seyfarth & Cheney, 2000) from an early age – 3 years (Cheney & Seyfarth, 1986) and to make inferences about others' ranks, what is known as third-rank relationship knowledge (Borgeaud et al., 2015).

Because vervet's habitats are highly conditioned by marked seasonality, they can behave flexibly concerning their managing of activity budgets, ranging habits, a social engagement which has been shown to alter the structure of their networks and clique sizes. This reflects that different strategies are adopted to varying degrees of within-group competition (Borgeaud, Sosa, Bshary, Sueur, & Carter, 2016; Canteloup, Borgeaud, Wubs, & van de Waal, 2019; Isbell & Young, 1993). Even if they commonly spread out during the dry season, when they most rely on scattered, low-quality fallback foods, vervets are cognitively capable of keeping track of group movement when other individuals are not within a visual range and far away without using vocalisations (Noë and Laporte, 2014). Females are known to present a vast array of strategic behaviours like coalition formation after grooming interactions as an early study documented using playbacks (Seyfarth and Cheney, 1984) and support provisioning during conflicts, usually directed toward high-ranking individuals (Borgeaud & Bshary, 2015; Cheney, 1977). Encounters with other groups (intergroup encounters) represent a form of collective action problem (Olson, 1965) and therefore a social dilemma situation where individuals can either participate or not (Willems *et al.*, 2013; Willems and van Schaik, 2015). In this context, females strategically exert aggression as a form of punishments and grooming as a form of reward as social incentives to promote males' participation (Arseneau-Robar et al., 2016). Moreover, females can flexibly interchange grooming for tolerance in a clear example of direct reciprocity (Borgeaud & Bshary, 2015). Additionally, during such instances, females showed integration of audience information (third-party relationships) to make strategic decisions about reciprocity and aggression by the dominant toward the subordinate when deciding to be tolerant or not (Borgeaud & Bshary, 2018; Borgeaud et al., 2017). Females of older age are also more successful in leading group movement while foraging in a sort of consensus decision-making (Lee & Teichroeb, 2016).

In the social world of vervet monkeys, high-ranking individuals (Grampp *et al.*, 2019) and females are influential figures from whom the juveniles learn (Renevey, Bshary and van de Waal, 2013) which expands into the prominent role of matrilines (van de Waal, Krutzen, Hula, Goudet, & Bshary, 2012) and even to the group level as shown in the colour-corn preference signatures of different neighbouring groups (van de Waal, Borgeaud, et al., 2013). Vervet monkeys are a very suitable species to study in general, and at the IVP in specific, because of the great access that researchers have to several neighbouring groups and the accumulated knowledge thanks to the research conducted on communication, social learning and cooperation (Borgeaud & Bshary, 2015; Canteloup, Hoppitt, & van de Waal, 2020; Fedurek et al., 2019). In this thesis, I present two chapters based on experiments conducted in adult females and two chapters that concentrate on group behaviour dynamics around intergroup encounters and during an extreme drought that led to the fission of three groups. One of the key advantages of the IVP study site is that the different groups are rather accessible from the house and the important workforce that nourishes several teams daily allow keeping track of the demography variations of all groups and daily intergroup encounter dynamics (focal group, encounter group). Most notably, the agreements with the South African Ezemvelo KZN Wildlife Board and the University of Cape and permission from the family owning the land where IVP is located allow testing specific behaviours using experimental approaches.

I.6. PhD thesis topic

Initially, this thesis is composed of a first block that addresses issues like grooming reciprocity dynamics across several hours using boxes experiments and food provisioning to selected individuals to investigate behavioural flexibility and strategic decision-making (Chapter I and II). These two sections set the focus on adult female vervet monkeys that are key in their societies (Wrangham, 1980) and attempt to shed light on how reciprocity operates across different time scales. While the first chapter concentrates on direct reciprocity exchanges of grooming for tolerance within a short time scale (several hours), the second aims at a similar enterprise, but uses a more ample time scale thanks to exposing to a 2-week feeding treatment. The purpose of adopting similar but slightly different approaches to studying grooming dynamics enabled to gather information about the mechanisms that facilitate reciprocity interactions (Brosnan & de Waal, 2002; Gabrielle Schino & Aureli, 2009) and the possible strategic dimension of such dynamics in combination with the improvement of one's connectivity with other group peers. This second aspect aspires to obtain preliminary ideas about the Machiavellian component of flexible and strategic grooming behaviour. Even if I interpret the results of the first two chapters in the light of social strategies, I will not speculate about the cognitive-brain implications of these abilities.

The original intent was to complement the first block with a second that concentrated on the physiological underpinnings of such affiliative-cooperative behaviours via urinary oxytocin (through grooming exchanges and participation-defection during intergroup encounters as ideal Chapter III and IV). Unfortunately, this part could not be terminated in time due to unexpected laboratory delays. Still, the samples were collected during three consecutive field seasons and laboratory protocols were developed for cortisol/testosterone and oxytocin analysis (see Appendix section). As a result of that mishap, I readjusted the second part of the thesis as is presented here, incorporating the topic of intergroup encounters (Chapter III) and the different behavioural dynamics (activity budgets, grooming, group dispersion, social networks, preferential assortment, strategy stay or leave) registered during two years before three groups fissioned in 2015-2016 (Chapter IV). Hence, the first block puts the focus on resolving reciprocity and behavioural flexibility as expressions of strategic decision making of adult female vervet monkeys through analysing grooming dynamics. The second block aims to tackle group decision making, more concretely how groups deal with social dilemma-like scenarios using group behaviour data in Chapter III, and a mix of female and group behaviour data in Chapter IV. Group encounters have helped us understand how groups resolve collective action problems (Willems, Hellriegel and van Schaik, 2013) so I approached this theme using an approach perspective value that may influence strategic decision making. Additionally, I explored if the imminent group fission events are preceded by observable trends informative social strategy development, through the females' social interactions to assess the impact on their social network.

I.7. Thesis chapters

In Chapter I, I concentrated on the strategic decision making of adult females around a boxes set-up to test the reciprocity dynamics of grooming and tolerance from a dominant to a subordinate individual after previous grooming interaction. I used a short-term scale of different time-lapses (hourglass) that spanned from a few minutes to a few hours hoping to fill a gap in the literature that mostly concentrates on shorter time scales (minutes) or long-term trends (months of data). While studies in tufted capuchins (C*ebus apella*) found no proof for exchange of grooming for tolerance in the short time scale (minutes) (Molesti and Majolo, 2015), other studies confirmed positive results in grooming reciprocation under similar time scales in the same species (Schino, Di Giuseppe, & Visalberghi, 2009). My project was conducted in two neighbouring groups and constitutes an extension of previous studies launched at the IVP where dominant females efficiently exchanged grooming for tolerance in a form of direct reciprocity within approximately 15 minutes (Borgeaud & Bshary, 2015). With my study, I aimed to evaluate which mechanisms may govern reciprocity dynamics (attitudinal reciprocity, calculated reciprocity) (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006; de Waal, 2000) over a three hours timescale.

In Chapter II, I analysed strategic grooming decision making in adult females in four groups when they are primed with food provisioning during two weeks that offered "surplus time" (as a sort of time voucher) that could be potentially invested in other activities. I evaluated the extent to which adult females behaved in strategic ways and "did something smart" with the extra time they had. Such experimental study intended to compare the fed females with those that were not fed (fed females: one dominant and one bottom-rank per group). More generally, this platform also allowed me to assess if females exhibited flexible strategic grooming behaviours by comparing the treatment period with two control phases; one before and one after the treatment. The dynamics of grooming that the females showed allowed me to assess reciprocity dynamics and to withdraw interpretations about how females' improvement of social connectivity links with the Machiavellian Intelligence Hypothesis (Byrne & Whitten, 1997). Hence, the grooming dynamics shown in this chapter led to a broad assessment of strategic decision-making and behavioural flexibility, social network dynamicity, preferential grooming targeting, and reciprocity.

In Chapter III, I explored the dynamics of cooperative behaviours that are represented in the intergroup encounter context where I brought an original approach using ecological and ownership measurements that considered both the focal and the encounter group. Mainly, I concentrated on ecological measurements based on NDVI (Normalised Difference Vegetation Index) as a proxy of food abundance (Willems, Barton and Hill, 2009) and territorial aspects (core areas, overlapping areas). I used this information to estimate value perception at different time scales (here now, maximum year, average year) and to determine where encounters were more likely to happen over four years (2016-2019). This temporal distinction is novel and allowed me to make inferences about strategic decision making concerning value perception that may allow some speculation about underlying cognitive abilities thanks to the different time-scale of the resources' value. I addressed these issues in four neighbouring groups that constitute four dyadic combinations and also investigated which factors help tip the balance for groups to harvest victories. I interpret some of these results using animal game theory options like the Bourgeois strategy (Riechert, 1998), assuming that groups would have a higher perspective of value on a given area based on ecological and/or territorial aspects and hence fight more, which should help to outcompete the rivals.

Although not explicitly tested, I pondered over the capacity of groups to effectively solve collective action problems that are inherently susceptible of free-riders using the volunteer's dilemma theory (Archetti, 2009).

In Chapter IV, I selected different measures of adult females' behaviour (activity budgets, grooming) and analysed their social networks, and group behaviours like dispersion, to explore the linkage with group fissions that took place during a severe drought that affected South Africa (Lottering, Mafongoya and Lottering, 2020). Beyond, I delved into the possible motivations that may have influenced the adult females to adopt two alternative strategies of staying in the original group or leaving the original group. For those that left, I attempted to clarify whether their decision of whom to stay was based on personal relationships (proximity, grooming) and/or kinship. Ultimately, I evaluated if factors like the number of dependent offspring, the occurrence of a close family member, and rank position conditioned the risk-taking or risk-averse strategies encapsulated in the decision to leave or stay. I hypothesised that group movement and group synchrony and cohesiveness maintenance may have posed conflicts of interest as different strategies may have appeared in the groups if alternative leaders emerged that disagreed to follow the traditional leaders. Hence, the last two chapters exemplify situations akin to social dilemmas since individuals can opt to play cooperative strategies or more self-interest driven strategies that may oppose the cooperative option and could be perhaps understood as an uncooperative/defection alternative.

I.8. References

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CHAPTER1. Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys (*Chlorocebus pygerythrus*)

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1.1. Abstract

Grooming is the most common cooperative behaviour in primates. It has helped advance our understanding of how animals achieve reciprocal cooperation without using precise counting strategies. For example, attitudinal reciprocity refers to recipients making short-term adjustments like reciprocated grooming or tolerance at food sources based on a change in emotional states. Here, we use an experimental set-up to investigate in unprecedented detail the building blocks of attitudinal reciprocity that govern wild dominant females' tolerance around food after a grooming interaction with a subordinate female partner in vervet monkeys (*Chlorocebus pygerythrus*). We measured the tolerance of the dominant females towards their previous grooming partner within four hours after a grooming interaction. Tolerance levels remained elevated compared to baseline for the entire period, showing a significant negative slope projecting that the tolerance window would close after approximately six hours. The slope in the decline of tolerance levels was not affected by relationship quality between females, nor by further grooming received from other group members. Also, the surplus grooming that the dominant received relative to what it gave did not yield a prolonged increased tolerance increase. Instead, lengthier grooming services by the subordinate influenced the dominant’s tolerance positively. These results suggest that tolerance temporal dynamics are best described with grooming triggering the start of a partner-specific sand-clock, where the amount of remaining sand equates to the dominant’s current tolerance level above baseline. Furthermore, the results challenge the notion that dominants use scorekeeping regarding their grooming debts towards subordinates to make decisions about reciprocating with tolerance.

Keywords: Attitudinal reciprocity, cooperative behaviour, experiment, grooming, tolerance, vervet monkeys (*Chlorocebus pygerythrus*)

1.2. Introduction

In evolutionary biology, helping is defined as an act that increases a recipient’s direct fitness (Lehmann & Keller 2006). Nature is full of examples where help to others cannot be explained by kin selection but instead yields direct fitness benefits through cooperation (Sachs *et al.*, 2004; Bshary and Bronstein, 2011; Taborsky, Frommen and Riehl, 2016). Cooperation often involves investments, i.e. behaviour that reduces the actor’s current payoff (Bshary & Bergmüller, 2008). Therefore, a question that arises is how investments are stable against cheating so that they yield more than just compensating future benefits. The problem is best captured in the so-called iterated prisoner’s dilemma game, in which mutual cooperation brings higher payoffs than mutual defection, but defecting yields a higher payoff no matter how the partner behaves (Dugatkin, 1997). Cooperative solutions to the problem are based on reciprocity, i.e. helping being contingent on the partner helping as well. Reciprocal decision rules suggested by theoreticians in their analyses can be described as counting or calculated reciprocity as individuals are assumed to have rather precise knowledge, typically of the last interaction, and act in highly predictable ways based on that knowledge (Dugatkin, 1997). However, the extent to which animals have memory capacities that allow for such counting abilities or scorekeeping is not clear (Emery, Dally and Clayton, 2004; Clayton, 2017). Some studies attest potent memory-response abilities in species like pigeons or baboons (Fagot and Cook, 2006), while some tests have revealed ravens’ capacity to distinguish prosocial partners lasting up to weeks or even months (Müller *et al.*, 2017), which can be further enhanced when the information retained is biologically meaningful (Lind, Enquist and Ghirlanda, 2015). On the other hand, emotional states may play a major role in decision-making. Certain social interactions might generate gratitude (Trivers, 1971) as a result of a positive emotional valence or salience as social interactions can stimulate the amygdala, leading to a strengthening of memory abilities by facilitating "*preferential perceptual processing*"(Dolan, 2002) as opposed to interactions devoid of emotional salience observed on amygdala- injured patients (Kensinger, 2004). A flow of positive emotions as incentive cues (Aureli & Schaffner, 2002; Schino & Pellegrini, 2009; Schino & Aureli, 2009) may eventually allow for reciprocity contingencies or the mirroring of behaviours (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006; Suchak & de Waal, 2012), bringing about the possibility of cooperation without a precise accounting or scorekeeping of past interactions. In this context, field primatologists have led empiricists in realizing that animal decision rules may not fit the theoretical ones. Two non-mutually exclusive decision rules have been proposed to describe empirical data, namely attitudinal reciprocity and emotional bookkeeping.

Attitudinal reciprocity is thought to occur over short-term periods and is motivated by mirroring attitudes of the social partner that can also be influenced by positive emotional states (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006; de Waal & Berger, 2000). On the other hand, emotional bookkeeping reciprocity may be triggered by long-term emotional states that promote bond affiliation between social partners as a result of past interactions (de Waal, 2000; Frank & Silk, 2009; Schino, 2007; Schino & Aureli, 2009; Schino, Polizzi Di Sorrentino, & Tiddi, 2007). Contrary to calculated reciprocity's precise scorekeeping of previous interactions (Brosnan and de Waal, 2002; Dufour et al., 2009; Barroso et al., 2014), attitudinal reciprocity has its foundations on emotional scorekeeping (de Waal, 2000). This mechanism of reciprocity is less cognitively demanding as it does not require scorekeeping of past given and received services (Brosnan and de Waal, 2002) as de Waal's classic capuchins' study illustrates whereby positive attitudes around a food set-up can beget reciprocity of food sharing (de Waal, 2000). A recent study on adult female vervet monkeys showed evidence for both attitudinal reciprocity and emotional bookkeeping using an experiment that demonstrated the exchange of grooming for tolerance as grooming between a female dyad led to higher tolerance levels by the dominant toward the subordinate (Borgeaud and Bshary, 2015).

Grooming interactions are the most conspicuous of primate social behaviours. Grooming permits ectoparasite removal (Mooring, Mckenzie and Hart, 1996; Akinyi *et al.*, 2013), improves thermoregulation (Barrett and Henzi, 2006), facilitates relaxation decreasing heart rates (Boccia, Reite and Laudenslager, 1989; Aureli, Preston and de Waal, 2005) and endorphin release (Keverne, Martensz and Tuite, 1989; Russell and Phelps, 2013), and allows individuals to build and reinforce relationships through trust reinforcement (Dunbar, 1991; Sutcliffe *et al.*, 2012). Although mainly beneficial (de Waal, 1997), grooming can impose an opportunity cost to perform other activities like feeding, resting (Dunbar, 1992), or watching out for predators (Mooring and Hart, 1995). In species like vervet monkeys (*Chlorocebus pygerythrus*) females are the philopatric sex and hence central in the social organisation of groups, being preferred grooming partners with higher centrality in the social network (Cheney and Seyfarth, 1990; Wu, Bischof and Kingstone, 2013). Females also play an important role in social learning (van de Waal, Borgeaud, & Whiten, 2013; van de Waal, Renevey, Favre, & Bshary, 2010) as they hold important ecological knowledge. Among the females, the dominants are perceived as attractive grooming partners because they can offer benefits to those that groom them (Seyfarth, 1977; Tiddi, Aureli and Schino, 2012). Indeed, grooming can also be exchanged for tolerance around food resources (Henzi and Barrett, 1999; Leinfelder *et al.*, 2001; Borgeaud and Bshary, 2015) or support during conflicts (Carne, Wiper, & Semple, 2011; Hemelrijk, 1994; Schino et al., 2007; Seyfarth, 1977; Seyfarth & Cheney, 1984; Seyfarth et al., 2010). Here, we trained adult female vervet monkeys to approach individualised boxes at an experiment set-up containing high-quality food, that was opened by the experimenter via remote control. Putting two boxes close to each other allowed testing how recent grooming would affect the dominants' tolerance levels. In line with the concept of emotional bookkeeping, the distance between boxes was adjusted to the particular tolerance levels during the trial phase between the different female dyads to obtain baseline tolerance levels in the control condition (without prior recent grooming involved), as done by Borgeaud and Bshary (Borgeaud and Bshary, 2015).

Here, following on recent findings (Borgeaud and Bshary, 2015), we studied the attitudinal reciprocity aspect in unprecedented detail. We kept the general experiment design (Borgeaud and Bshary, 2015) but varied the time delay or time-lapse between a grooming interaction and the presentation of the boxes set-up. Such time sequences or lapses have been mostly investigated around short-term grooming dynamics (Barrett, Gaynor, & Henzi, 2002; de Waal, 2000; Molesti & Majolo, 2015; Schino & Pellegrini, 2009). However, some studies have investigated grooming relationships over long periods (Gomes, Mundry, & Boesch, 2009; Manson, Navarrete, Silk, & Perry, 2004; Schino et al., 2007), although the contingency of behaviours are harder to disentangle because different behaviours can easily overlap in the dynamic mesh of a social group (Aureli & Schaffner, 2001; Fehr & Mcelreath, 2019; Jaeggi, de Groot, Stevens, & van Schaik, 2013; Schino & Aureli, 2008). This may explain the paucity of empirical studies incorporating time lapses to the study of cooperative interactions in the wild (Sánchez-Amaro and Amici, 2015).

With this experimental approach, we expected to verify the previous results of attitudinal reciprocity whereby tolerance among female dyads increases as a result of dominants' increased benevolence toward their subordinate counterparts after a grooming interaction– confirmatory question (Borgeaud and Bshary, 2015). For up to four hours, we monitored the dominant female from the grooming interaction and noted if she had any other grooming interactions (i.e., additional grooming partners). During this time, we looked for the subordinate female from the initial grooming interaction (i.e., original grooming partner) and when the original dominant-subordinate dyad was next to each other, we set up the experiment to measure tolerance between them. Our main prediction was an increase in aggressive outcomes by the dominant towards her original grooming partner as a function of time since the original grooming (variable A). Moreover, we explored four variables related to time-lapse and the original grooming (B-E). B) If the relationship quality or dyadic bond between the original dyad influenced reciprocity as found in other studies (Luttrell and de Waal, 1988), we predicted original grooming bouts among bonded partnerships would elicit a more positive valence (de Waal, 2000), slowing the decline of tolerance with time compared to non-bonded dyads. The opposite prediction would posit that in dyads that rarely groom the resulting positive valence of the interaction would be greater (de Waal, 1997; Henzi & Barrett, 1999) and have a diminishing effect of the decreasing function of tolerance with time. C) We considered the possibility that the dominants' additional grooming partners beyond the original partner from the time the original grooming was over until we tested the dominants' tolerance with the original grooming partner may affect tolerance levels. How many partners' interaction details an individual can track simultaneously (Schweinfurth and Call, 2019), and whether holding this information could impose memory interference effects ultimately affecting reciprocity remains an open subject. If vervet monkeys can only have a temporary tolerant attitude toward a single group member at a time, we expected any additional grooming event to decrease tolerance towards the original partner. Alternatively, if female vervets can alter attitudes towards several partners independently, we did not expect any effect of additional grooming partners on tolerance levels. D) We calculated what we call here surplus grooming received (what the dominant received minus what she gave) to test whether it affects the dominant's tolerance levels. The surplus of grooming received describes best the debt that a dominant has towards the subordinate grooming partner; a negative surplus value or close to zero values would mean that dominants had already reciprocated by paying in kind for the grooming they received. Thus, if vervet monkeys exchange grooming for tolerance in a 'calculated tit-for-tat like reciprocity' way (without implying that individuals measure the time of grooming given minus received in a precise fashion), we expected that dominants would be more prone to reciprocate at the boxes set-up by being tolerant the more surplus grooming they had received. Conversely, a negative surplus value should not alter tolerance levels relative to baseline. E) Further, we tested whether lengthier grooming services received by the dominants influence the dominants' tolerance levels (time duration grooming received). If dominants make use of a sort of personal sand-clock that stores the positive valence of a past grooming interaction with a given partner, this should result in longer-lasting tolerance levels displayed toward partners that provided longer grooming services. Lastly, we used the model to describe the decay of the dominants' tolerance beyond the time window we were able to cover(196 min) to predict how long it would take for tolerance to return to baseline levels (control conditions).

1.3. Methods

1.3.1. Subjects of study, training and trial phases, and the reference distance

The study was conducted in adult females of two neighbouring groups of vervet monkeys at the Inkawu Vervet Project (Mawana Game Reserve, KwaZulu-Natal, South Africa) from May to October 2017. The two groups, Noha (NH) and Baie Dankie (BD) had a total number of 32 and 46 individuals, with 6 and 12 adult females respectively. Vervet monkeys live in female-bonded groups (Wrangham, 1980) so by selecting the adult female subset of the population we focussed on the age/sex class that shows the higher proportion of affiliative interactions among adults, whereas males tend to be socially integrated into smaller cliques (Cheney, 1992; Cords, 2012).

Adult female individuals (Table A.1. in Appendix) were trained from sunrise to 2 PM to approach personalised boxes containing a piece of apple two months before the onset of the experiment. Human experimenters opened the boxes using a remote control when the correct subject touched the box. Each female subject was assigned a distinctive personal colour cover that was placed on top of the box. During the initial training phase, each individual was presented with two boxes, one with her assigned colour pattern and one with a different pattern (that would change in different trials), until the accuracy of the individuals' right choice was above 70%. Following, we trained females to come in pairs (dyads henceforth) and two boxes were presented. Later, we carried out trials to collect data on distances between two boxes and the outcome as either tolerance or aggression. By testing each dyad at different distances we gathered a specific reference distance, i.e. a distance where baseline tolerance levels – tolerance levels without recent prior grooming – that is rather low but not zero (i.e. tolerance on around 10-20% of the trials, more details in the Appendix). Pair-specific distances with low tolerance levels enabled the detection of increased tolerance levels ensuing grooming interactions. By the end of the trial period, a total of five and eight adult females (hereafter subjects) were considered suitable for the experiment in NH and BD groups, composing 29 dyads (10 in NH, 19 in BD) with reference distances ranging from 0.7 to 4 meters (mean ± s.d = 2.57 ± 0.77). All subjects were tested in control and grooming conditions.

1.3.2. Experiment design and data collection

We collected samples in two conditions: control and grooming experiments. Control experiments offer a baseline measure of tolerance levels without the influence of recent grooming interactions. In this condition, we assured that the two subjects of the dyad had not engaged in previous grooming by collecting focal follows (Altmann, 1974) that started early in the morning as the monkeys descended from the sleeping trees. Upon observation of dyadic grooming interactions with a potential female partner for which we had a reference distance (original grooming for the interaction henceforth), we gathered relevant information about the grooming interaction. Thus, we collected data (see Table A.3. in Appendix) on the identity of the female subjects, time start and time end, who initiates and who stops, the time when they resume the (each) interaction, who gives grooming, and who receives grooming. After that, we focal followed the dominant female of the original grooming dyad to register information about possible additional affiliative interactions during a time-lapse that ranged from a few minutes to more than three hours until we could present the boxes experiment set-up to the original dyad. We focal followed the dominant individual of the original dyad since this individual will later decide whether to be tolerant or not towards a subordinate partner. Following the grooming between the original grooming dyad and during the focal follow of the dominant female, we waited until we had suitable conditions for the conduction of a grooming experiment, i.e. having the two female subjects in close vicinity and absence of bystanders within 15 meters (also applicable for control conditions) to avoid audience effects (Borgeaud and Bshary, 2018).

We conducted controls and grooming experiments from early morning to 2 PM. Although we intended to space out our grooming experiment collection evenly across time, the individuals composing the original dyad at the boxes experiment was not always feasible, so we assumed certain opportunism when good conditions materialised. By and large, suitable conditions to find the original grooming dyad were higher during the first and second hours although we collected data until a maximum that extended until four hours (196 minutes) from the original grooming interaction to the grooming experiment. Generally, the difficulties to find again the dyad in proximity increased for time-lapses beyond the second hour as grooming often took place in general group grooming contexts, and subsequent changes of general group behaviour (moving, feeding, resting) were more probable as time passed, which further reduced our ability to conduct experiments. Besides, all our potential dyads did not include combinations involving individuals with relatedness at the level of mother-offspring which might have conditioned a lower likelihood of females in proximity (Chapais & Berman, 2004; Grampp, Sueur, van de Waal, & Botting, 2019; Silk, 2009). Lastly, although low food availability conditions during the winter-dry season motivate the monkeys to engage in food experiments (Arseneau-Robar, Müller, Taucher, van Schaik, & Willems, 2016; Borgeaud & Bshary, 2015; Borgeaud, Schnider, Krützen, & Bshary, 2017), higher spatial distances between females may have been influenced by highly scattered food availability during the winter-dry season, leading to large group spreads (Alberts *et al.*, 2005), further complicating experiments' requirements.

1.3.3. The outcome of the experiment

The outcome of the boxes experiment set-up was defined based on the behaviour of the dominant female toward the subordinate counterpart (Borgeaud and Bshary, 2015). The outcome was scored as a binary option, either aggressive or tolerant, and was measured from the time when the boxes simultaneously opened that enabled access to the apple piece until the ensuing fifteen seconds. Aggressive behaviours could be aggressive calls, stare, stare-attack, approach-take place and displace, steal the food item, chase, bite any body part or hit on top of the head. Any of such behaviours, alone or in combination with others were estimated as outcome aggression. Alternatively, tolerance was interpreted as the absence of any of the above-described aggressive behaviours (representation of the experiment in Appendix, Figure A.1.).

1.3.4. Ethical note

Ethical permission for the conduction of this study was given by Ezemvelo Wildlife Board (KwaZulu-Natal, South Africa), the University of Cape Town, and the van der Walt family that owns the private property where the Inkawu Vervet Project is located. The study adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research. All individuals were wild adult females from four neighbouring groups habituated to researchers during the last ten years and trained to the boxes set-up without humans directly interacting with them. We attracted adult females to the boxes set-up by clicking the tongue, a sound they were trained to associate with upcoming control and experiment conditions during the training, trial and sample collection phases. Subjects approached their boxes voluntarily, so only individuals that initially showed interest in participating ended up in the training phases and were apt for the experiment. Subjects did not have dependent infants at any stage of the study; hence the boxes experiment did not impose possible additional stress on them. The experimental set-up did not cause dominant females to physically aggress their subordinate counterparts, and hence no wounds were caused by our experiments. Instead, we typically observed mild levels of aggression, i.e. behavioural displays such as staring and stare-attack, and chases were extremely rare. The presentation of the boxes set-up (control or grooming) and its development took place within a couple of minutes from setting up to picking up after the boxes set-up, causing only a short break from usual activities and therefore not provoking the subjects' isolation from the rest of the group. Both control and grooming samples were interspersed throughout the entire period of study for all dyads. The food provisioned at the boxes consisted of a small piece of apple grown for regular human consumption. Apples were cleaned beforehand and handled with gloves to avoid the possible transmission of diseases.

1.3.5. Rank and bond calculation

We used six months’ ad libitum agonistic interaction data before the onset of the study with a clear winner to calculate rank hierarchies with David Scores (DS) in the Elo-Rating package (Neumann *et al.*, 2011) using R (R Development Core Team, 2016). We calculated the relationship quality or dyadic bond index between individuals using a sociality index R package (Neumann, 2016), incorporating data about grooming interactions that play a vital role in primates’ social bonding (Dunbar, 2010; Seyfarth and Cheney, 2012; Brent *et al.*, 2014). For that, we also used six months’ grooming data before the onset of the experiment. The social index scores measuring the dyadic bond were normalised using the scale function in R (R Development Core Team, 2016). Our 10-year old database did not allow us to exclude paternal siblings, although there is a lack of evidence of kin recognition at that level (Silk, 2020; Widdig, 2013). Finally, none of the female dyads included mother-offspring or maternal sibling relationships. (See Tables A.4. and A.5. of the Appendix).

1.3.6. Statistical analysis

We carried out generalized linear mixed-effects models (GLMM) (Zuur, Ieno and Elphick, 2010) using R (R Development Core Team, 2016) to examine the effect of the original grooming interactions and the associated characteristics of such interactions and the particular individuals composing the dyad around the experiment set-up where we measured tolerance levels of the dominant individual in the dyad toward the subordinate female partner (tolerance was coded as 1, aggression as 0). We used the function *glmer* available in lme4 R packages (Bates *et al.*, 2014). We compared the different models to the null models while preserving the random factors, to validate the robustness of our models. As a first analysis, we ran a model to verify if female vervet monkeys engaged in reciprocity through the exchange of grooming for tolerance as found in a previous study (confirmatory question) (Borgeaud and Bshary, 2015). Control and experiment samples were used to investigate the effect of sample type condition on the outcome of the boxes set-up. We used a GLMM and included the outcome as a binary response variable (tolerance or aggression) and sample type condition (grooming or control) as the predictor variable and incorporated the identity of the dominant and subordinate individuals that composed the original grooming female dyad to account for the variability of the different female subjects and the time (hour) in which the tolerance was tested at the box set-up as random factors.

To test whether the time-lapse (time-questions, A to E) that spanned from the original grooming to the experiment boxes set-up influenced the tolerance predisposition of the dominant toward the subordinate partner we ran a full model that only included the outcome registered in grooming condition experimental set-ups. This full model included additional questions about the aspects related to the original grooming that we aimed to investigate (questions A to E). Therefore, we integrated all variables of interest in one full model since they could presumably have interaction effects and influence the outcome. The outcome was a binary response variable, i.e. tolerance or aggression. A) The time-lapse, measured in minutes, was our key predictor factor and it was the only variable we actively manipulated by choosing the good conditions when the two individuals of an original grooming dyad were fulfilling the requisites for an experiment set-up to take place. The additional variables involving the original grooming dyad and the characteristics of the dyad were the following: B) the dyadic bond; C) additional grooming partners by the dominant; D) time duration of grooming that the dominant received minus what it gave (termed ‘surplus grooming received’ henceforth, though few data points had negative values); and E) the time duration that the dominants received grooming by the subordinate partner. The bond between the original dyads was included in the model as a continuous scaled variable. Note that while dyads with stronger bonds were exposed to experiments at shorter reference distances to obtain similar baseline dyadic tolerance levels (Borgeaud and Bshary, 2015), we were interested in studying whether the social bond affects the change in tolerance levels after grooming. Additional grooming partners by the dominant were accounted for as a binary variable (yes, no).

The variable time-lapse was measured in minutes, while the surplus and the time that the dominant was groomed were measured in seconds to better adjust to the timescales of each event. All measures involving time were divided by hundred and centred to mitigate the skew of their distributions. The variables surplus and the time duration that the dominant received groomed (questions D, E) allow to address different reciprocity mechanisms: the terms ‘scorekeeping’ or ‘calculated reciprocity’ are typically used to describe strategies investigated by game theoreticians, like tit-for-tat (Boyd, 2006; Lehmann *et al.*, 2008; Wubs, Bshary and Lehmann, 2016; Schweinfurth and Taborsky, 2020). Although the term ‘calculated’ may be misleading as it implies a rather precise counting mechanism while animals may rather use rules of thumb. The term ‘attitudinal reciprocity’ refers to short-term changes in emotional states that consequently affect behaviour in the short-term (Brosnan & de Waal, 2002; Schino & Aureli, 2010). As random factors, we included the identity of the dominant and subordinate individual that composed a total of 29 possible dyads as well as the time-hour (with no effect on the outcome) in which the tolerance was tested at the box set-up. Initially, we included all interactions between the time-lapse and the other descriptive factors relative to the original grooming (questions A-E) in the full model and proceeded to do stepwise backward model simplification (Forstmeier and Schielzeth, 2011), removing in each step the least significant of interaction terms, until the model design would contain no non-significant interactions. Lastly, we excluded grooming samples where the dominant was the only individual giving grooming (groomer) and not receiving because of the scarcity of observations (sample size N=10 versus, N=67, and 75 for when the dominant only received and when the dominant gave and received grooming). F) Finally, we used the model to predict the decay function of tolerance with time until the baseline tolerance levels (without grooming) would be reached again after the grooming interaction. We did this by conducting an extrapolation provided by the predictions of our model that extended beyond the time that our grooming samples covered. More precisely, we averaged all continuous predictors and attributed to the binary ones the option more represented in our data to launch the prediction, thus calculating the predictions in 30-minute time slices incorporating the data we collected.

1.4. Results

1.4.1 Confirmatory question: exchange of grooming for tolerance

In a general linear mixed-effects model (GLMM) we compared the outcome of the two conditions, control experiment samples (N= 172; mean ± s.d =5.93 ± 4.61 per dyad), and grooming experiment samples (N= 142; mean ± s.d =4.89 ± 5.24 per dyad, see data in Table A.2. of the Appendix) to verify the previous findings (Borgeaud and Bshary, 2015). The dominant individuals tolerated subordinates in 9.6% of the control samples, which constitutes the general tolerance baseline levels, versus 73.9% of all grooming samples, i.e. dominants were 7.7 times more likely to be tolerant in the grooming samples than in the control samples ($X^2_{df = 1}$= 83.67; P < 0.001).

1.4.2. Effect of time-lapse and original grooming factors on the outcome (time questions: A-E)

In the GLMM time-questions model, we evaluated the influence of the different factors: time-lapse (A), dyadic bond (B), additional grooming partners (C), surplus grooming received (D), and time duration that the dominant received groomed (E) on the outcome (Table 1, Figure 1). Regarding the main effects, tolerance significantly decreased as time progressed ($X^2_{df = 1}$=5.45; P =0.0193). Tolerance probabilities evolved as follows when grouped per hour: first hour 81.52% (N= 92 samples), second hour 63.88% (N= 36 samples), third hour 58.33% (N= 12 samples), and fourth hour 0% (N=2) respectively. None of the interactions between time-lapse (A) and the different grooming factors (B-E) was significant. When looking at whether the different grooming factors influenced the outcome of the experiment (tolerance or aggression), we found the following: B) dyadic bond did not affect the tolerance levels ($X^2_{df = 1}$=0.199; P =0.655); C) whether or not the dominant individual of the original dyad had additional grooming partners did not influence the dominants' tolerance levels ($X^2_{df=1}$=0.008; P =0.928); D) the surplus grooming received that the dominant received relative to what it gave did not affect the tolerance ($X^2_{df=1}$=2.22; P =0.136); and E) the time that the dominant received grooming had a positive effect on the tolerance ($X^2_{df=1}$=4.73; P =0.0296).

1.4.3. Prediction of tolerance decay (F)

The prediction of the tolerance function decline with time was built on the model and calculated tolerance levels every 30 minutes up until 6 hours. Following our findings, tolerance decreased with time during the time-lapses we sampled and the slope of the decline was maintained beyond this time until the fifth hour when the slope of the tolerance decline slowly flattens (Figure 2., and data in Appendix in Table A.5.).

1.5. Discussion

We had asked how being groomed affects dominant female vervet monkeys' subsequent tolerance levels over time. Our results confirm previous findings by Borgeaud and Bshary (Borgeaud and Bshary, 2015) that dominant female vervet monkeys increase tolerance selectively towards females that groomed them recently. Furthermore, in line with the concept of attitudinal reciprocity, tolerance levels declined over time. The slope of this decline was not affected by relationship quality. In general, subordinates have an extended time window of several hours to reap the benefits of their grooming investment, independently of the dominant having further grooming interactions with additional grooming partners. This latter result could indicate that a grooming interaction causes dominants to fill a sort of individual-based 'sand-clock' or hourglass, where the filling state represents the current extra-tolerance level available for past grooming partners. Although our data did not specifically test for this, it appears that dominant individuals can keep track of several grooming partners' past interactions details simultaneously and the tolerance sand-clock function in parallel. Clearly, the physiological basis for this mechanism, as well as potential memory limits, warrant further investigation. Perhaps most surprisingly, dominants did not adjust subsequent tolerance levels to the degree to which they had reciprocated grooming but to the absolute time, they had received grooming. Taken together, these results imply that the general increase in tolerance is not a function of the dominants' current debt to subordinates but due to the positive valence of close social interactions that persists for a few hours after the original grooming. We discuss each of these points below.

We could verify that the time dimension of the grooming and the contingency with the posterior tolerance at the boxes set-up persists at least three hours from the original grooming that involved the female dyad. This contrasts with the findings of Molesti and Majolo (Molesti and Majolo, 2015) where there was no contingency between grooming and food tolerance in Barbary macaques, although is in line with a previous study on vervet monkeys (Borgeaud and Bshary, 2015). Indeed, tolerance levels during the third hour were 6.07 times higher than baseline levels. Nevertheless, the trend of the model's prediction (line in Fig. 1-a, Fig. 2) was negative, yielding a 33% reduction in the probability of the dominant being tolerant for about 200 min after the grooming event. Extrapolating from the steepness of the slope and assuming a linear decline in tolerance levels, the baseline level would be reached around the sixth hour. The decrease of tolerance within a few hours supports the hypothesis that attitudinal reciprocity (Brosnan & de Waal, 2002; de Waal & Brosnan, 2006) underlies short-term exchanges of grooming for tolerance in female vervet monkeys.

The dominants' short-term shifts in attitude toward subordinates changed after the grooming interaction independently of the bond or relationship quality of the dyad. Interdependencies or bonds cultivated over long periods do not constitute a defining trait shaping reciprocity processes (Schino & Aureli, 2008; Schino & Aureli, 2009) nor was it the case in our study. As in Borgeaud and Bshary's previous investigation (Borgeaud and Bshary, 2015), strong bonds warranted short distances between the two food boxes to obtain low baseline tolerance levels. This finding further supports the attitudinal reciprocity scheme as an underlying mechanism. This is interesting because research on other primate species has shown that grooming interactions (or sharing food) between bonded individuals cause changes in hormonal and neurohormonal profiles that differ from the effects of grooming between non-bonded individuals (Crockford *et al.*, 2013; Wittig *et al.*, 2014; Stocker *et al.*, 2020). Assuming that female vervet monkeys prefer grooming with bonded partners, our results hence suggest that a dominant's change in attitude and predisposition for future reciprocity may be based on other factors beyond possible cortisol reduction, oxytocin increases, or at least not be solely founded on such.

Importantly, the dominant having additional grooming partners did not affect its tolerance levels towards the initial grooming partner. Therefore, female vervets do not appear to experience cognitive constraints on upregulating tolerance levels with several grooming partners in parallel, similarly to rats tested on food-cooperation tests (Schweinfurth and Taborsky, 2020). As a result, it seems that subordinates might not necessarily have to monitor a dominant's additional social interactions to assess whether their window of opportunity is closed, which could exclude the possibility of additional grooming interactions inducing memory interferences. Given the negative slope of tolerance levels as a function of time-lapse from a grooming event (Fig. 1-a, Fig. 2), the results are best described in the following way: a grooming interaction triggers the start of an individualised sand-clock, where the amount of sand in the upper part represents the extra level of tolerance that a dominant is willing to give. With time, this gradually becomes less and less, until tolerance levels are back to baseline. Our results suggest that dominants may be able to keep several simultaneous individual-based sand-clocks, although we are not aware of a cognitive or physiological process that may facilitate such processes akin to sand-clocks' regulation. Although we did not specifically test for this, we could observe that within our dataset, the dominants' tolerance toward subordinates was very similar between 'additional grooming partners' and 'no additional grooming partners' (71.92% VS 75.29% tolerance). Our results differ from laboratory experiments on reciprocity in rats, where it was found that the amount of helping a subject had received during their last interaction influenced their level of helping independently of a time delay up to three days (Schweinfurth and Taborsky, 2020). Why rats would show levels of cooperation that are unaffected over days while the vervets' tolerance returns to baseline levels within hours is currently unclear. A potential explanation could be that by conducting experimental tests in the same cages, rats may find it easier to remember specific past interactions. Comparative studies on captive and wild populations of the same species may help to elucidate whether conditions in captivity promote the use of more sophisticated reciprocation rules.

Of the two parameters describing the grooming patterns during an interaction, the surplus grooming received did not affect tolerance, while the time duration that the subordinate groomed the dominant associated positively with tolerance. For a better understanding of these diverging results, we ran two simple correlations. First, we confirmed that the two variables are correlated with each other (spearman, r= 0.79; p <0.001). Second, we correlated grooming given by the subordinate with grooming given by the dominant, which yielded a positive result (spearman, r= 0.55; p <0.001). With these additional results, we can first conclude that dominants seem not to assess their debt towards subordinates after a grooming interaction (our surplus grooming received factor) to decide how much they should upregulate tolerance levels, as would have been expected if there was an aspect of precise counting or scorekeeping in their attitudinal reciprocity. Instead, dominants seem to upregulate tolerance either to the time that they received grooming or the correlated total duration of a grooming interaction, independently of how much they had contributed themselves. Because the two variables are correlated, it is currently impossible to distinguish between various underlying mechanisms. One possibility is that dominants are constrained in their assessment and therefore the more they are being groomed the more grateful they become (Trivers, 1971), irrespective of other interaction details. Another possibility is that longer interactions correlate with a dominant's current need to receive grooming. In this scenario, the dominant grooms to increase the amount of grooming received, and the resulting higher positive valence of the interaction triggers higher levels of tolerance despite the dominant possibly having already reciprocated in kind to a certain extent. Anyhow, the debt-related condition in which a dominant may sink after a grooming interaction may be, after all, something rather common given that subordinates are interested in higher-ranking grooming partners (Seyfarth, 1977; Tiddi, Aureli and Schino, 2012). Finally, long interactions might have a high positive valence because the prolonged affiliative interaction also involves being in proximity, independently of how much each partner contributes to the grooming. Such positive interactions might be key to improve the long-term dyadic bond or relationship quality between grooming partners (Majolo, Schino, & Aureli, 2012; Schino, Di Giuseppe, & Visalberghi, 2009; Schino & Pellegrini, 2009; Schino & Aureli, 2009; Seyfarth et al., 2010), which would contrast to short-term tolerance as a symmetric measure.

In conclusion, our study revealed in unprecedented detail the mechanisms underlying the exchange of grooming for tolerance in vervet monkeys. Subordinates have a time window of several hours to cash in their grooming service, due to attitudinal reciprocity by the dominant. This contrasts with the results from lab-based human-subject exchange tasks, which led to the conclusion that non-human animals are constrained in their ability to reciprocate because they strongly discount the value of future benefits over current ones: in this paradigm, subjects often wait seconds to minutes when doing so increases their reward (Stevens and Hauser, 2004; Ramseyer *et al.*, 2006; Dufour *et al.*, 2007). Our investigation of female dyads shows that attitudinal reciprocity mechanisms may well allow getting around the cognitive challenges that delayed rewards could otherwise impose, possibly by the way of an interplay of psychological-emotional states. Furthermore, our data do not support the notion that the general concept of subordinates trading grooming for tolerance applies to the course of single interactions (Seyfarth, 1977) but instead hints to more entangled multi-layered reciprocity dynamics. In line with previous studies demonstrating the benefits of grooming (Keverne, Martensz and Tuite, 1989; Dunbar, 1991; Aureli, Preston and de Waal, 2005), our results suggest that dominants giving grooming also increases short-term tolerance, either directly or by causing subordinates to groom longer in return. Our study thus highlights the need to understand the explicit mechanisms underlying decision-making, like how the reward system functions (Glimcher, 2011; Sutton and Barto, 2018; Wubs, Bshary and Lehmann, 2018), rather than measuring correlates of material payoffs, to better predict cooperation based on reciprocity.

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1.6. References

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1.7. Figures and tables

Model	Dependent variable	Predictor	$X^2_{df = 1}$	P-Value (>Chi-Square)	Estimate	Std. Error
Confirmatory	outcome	Sample type condition (control VS experiment)	83.671	*<0.001*	3.530	0.3860
Full model	outcome	Time lapse	5.439	0.019	-1.169	0.500
		Bond	0.199	0.655	-0.268	0.602
		Additional grooming partners	0.008	0.928	-0.044	0.498
		Surplus grooming received	2.22	0.136	-0.387	0.260
		Time grooming received	4.732	*0.029*	*0.499*	*0.229*

Table 1. GLMM summary of statistical results for the confirmatory question model and full time-questions model. The variables additional grooming partners, surplus grooming received and time grooming received are all from the perspective of the dominant subject that was focal followed. Statistically significant results shown in bold.

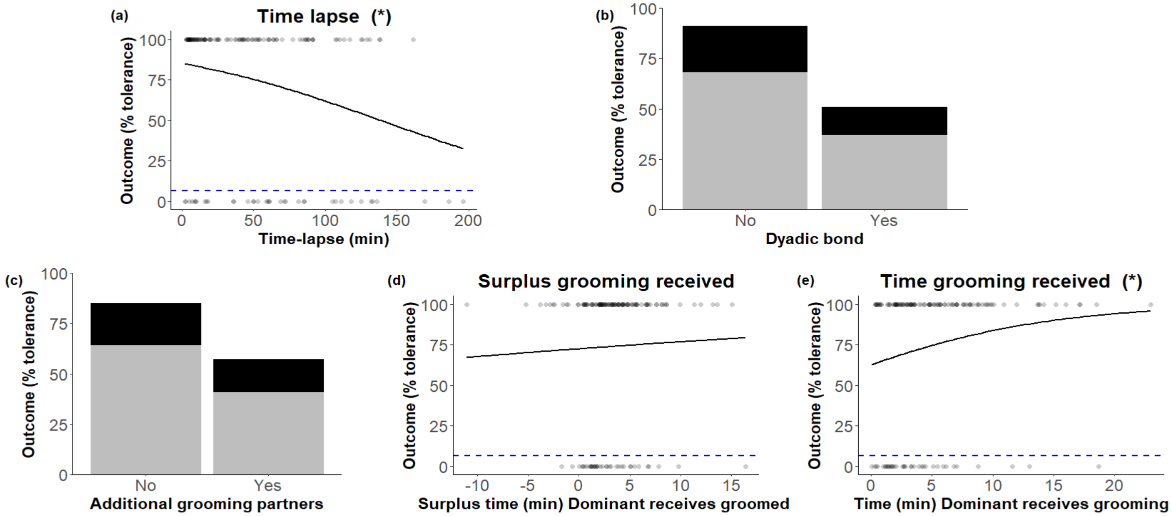

Figure 1. Graphs showing the dynamics of tolerance with the different factors of study measuring the output as the probability of dominants' tolerance towards her subordinate partner at the boxes experiment. Letter codes (a-e) of each graph correspond to the questions outlined in the introduction. Shown on top, left to right: a) time-lapse (with significance asterisk), and b) dyadic bond. Second row: c) additional grooming partners by the dominant; d) surplus grooming received by the dominant, and e) time duration of the grooming received by the dominant from the subordinate (with significance asterisk). Probability of tolerance by the dominant toward the subordinate displayed along the y-axis as a percentage from all samples (tolerance is binary and each dot represents one sample). In (a) and (c) graphs time is represented in minutes along the x-axis, where the different grooming samples collected are shown as grey circles indicating the binary outcome of tolerance or aggression and tolerance baseline levels are shown as dotted line at the 9.6% (from control experiments). In (b) and (c) graphs the x-axis represents the binary condition (yes, no) of each factor and bars are colour-coded in black for aggression and grey for tolerance.

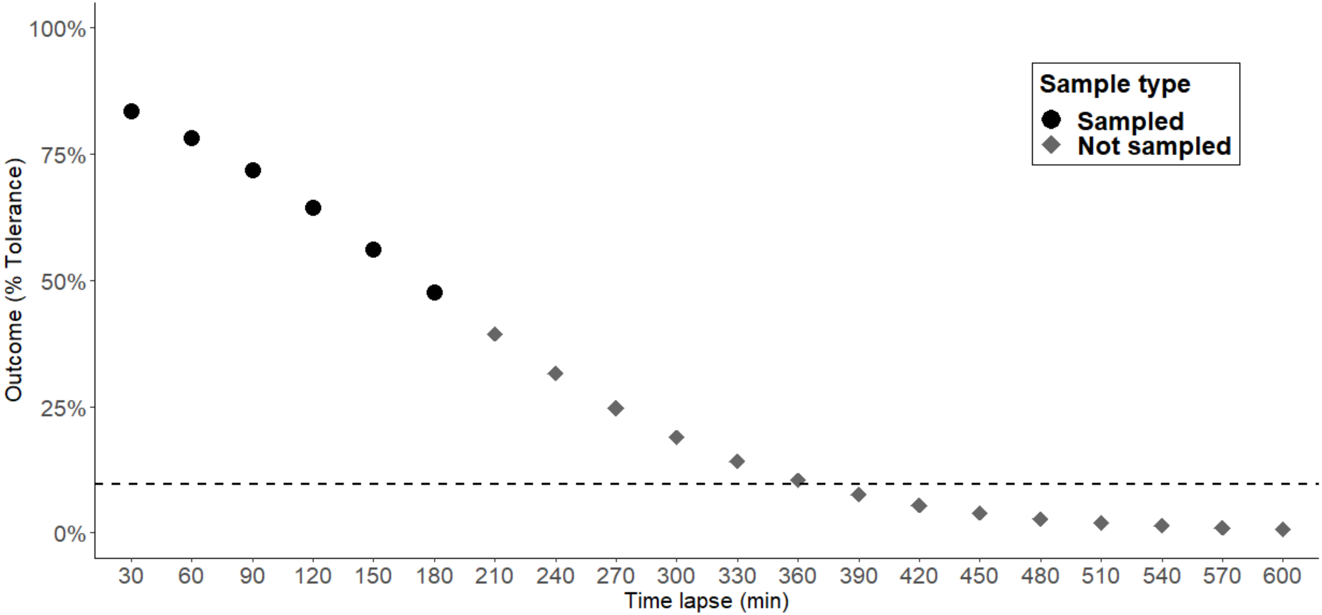

Figure 2. Prediction based on the GLMM model. Prediction using the average condition for the different continuous predictors (time duration dominant gets groomed, surplus time dominant gets groomed) and the most widely represented of the remaining (binary) variables (bond, additional partners dominant gets groomed). Black circles represent grooming samples we collected and grey diamonds represent samples that are predicted. The dotted line shows tolerance baseline levels from control conditions.

1.8. Appendix

Figure A.1. Two subjects from the NH group having access to their boxes. Photo by David Lemieux.

Methods details-Reference distance calculation

The calculation of the reference distance was a prerequisite that enabled us to conduct experiments that tested how tolerance evolved with regards to how much time passed from the original grooming interaction to the boxes setup. Thus, having all the female dyad combinations on same conditions (tolerance levels 10-20%) allowed the evaluation of time and other factors (bond, additional partners beyond the original grooming partner, surplus time that the dominant received grooming and the time duration that the dominant received grooming from the subordinate). Although the reference distance is a prerequisite to test which factors affected possible changes in tolerance levels, we evaluated its possible correlation with other factors in order to better understand it. The reference distance was not correlated with other variables that we calculated for all dyads like rate nearest neighbours or relationship tenor (affiliative interactions divided by agonistic interactions, Silk & Seyfarth, 2013). Alternatively, the reference distance was correlated with other factors that we calculated like social bond (r= 0.27, P=0.0014) as in Borgeaud and Bshary (Borgeaud and Bshary, 2015), rank difference (r=0.22, P=0.0072) and grooming reciprocity index (grooming that ego individual gives to her partner divided by grooming that ego individual receives by the partner, Newton-Fisher & Lee, 2011) (r=-0.19, P=0.027).

Group	Adult females trained to boxes experiments
BD	Oulik, Asis, Hippie, Heerlik, Pannekoekie, Siele, Enge, Rissiepit, Mieles
NH	Geneva, Gaya, Uppsala, Xian, Pretoria

Table A1. Identity of the adult females (subjects) of the experiment

Group	Dominant individual	Subordinate indivdual	Nº controls	Nº exps.	Rank Dom.	Rank Sub.	Dyad	Reference distance	Social index
NH	Gaya	Pretoria	8	2	24.533	18.0611	Gaya-Pretoria	1.75	5.61051
NH	Gaya	Uppsala	16	10	24.533	23.1466	Gaya-Uppsala	1.75	2.18186
NH	Gaya	Xian	19	18	24.533	21.4070	Gaya-Xian	1.5	4.37374
NH	Geneva	Gaya	14	18	25.142	24.5332	Geneva-Gaya	3	8.41576
NH	Geneva	Pretoria	3	2	25.142	18.0611	Geneva-Pretoria	4	0.46754
NH	Geneva	Uppsala	6	5	25.142	23.1466	Geneva-Uppsala	3	2.03066
NH	Geneva	Xian	5	1	25.142	21.4070	Geneva-Xian	4	1.40584
NH	Uppsala	Pretoria	6	1	23.146	18.0611	Uppsala-Pretoria	3	5.5977
NH	Uppsala	Xian	4	2	23.146	21.4070	Uppsala-Xian	3.25	6.24819
NH	Xian	Pretoria	3	2	21.407	18.0611	Xian-Pretoria	3.5	6.2339
BD	*Asis*	*Pannekoekie*	*0*	*1*	*27.547*	*21.310*	*Asis-Pannekoekie*	*4*	*0*
BD	Engel	Mieles	7	2	25.080	18.9172	Engel-Mielies	2.3	2.94632
BD	*Engel*	*Pannekoekie*	*5*	*1*	*25.080*	*21.3105*	*Engel-Pannekoekie*	*3*	*2.04343*
BD	Engel	Siele	2	3	25.080	21.8546	Engel-Siele	1.5	4.83215
BD	Heerlik	Engel	12	16	25.299	25.0805	Heerlik-Engel	2.5	12.2289
BD	Heerlik	Mieles	14	12	25.299	18.9712	Heerlik-Mielies	3	4.58248
BD	Heerlik	Pannekoekie	5	2	25.299	21.310	Heerlik-Pannekoekie	2	5.7987
BD	Heerlik	Rissiepit	4	1	25.299	19.3171	Heerlik-Rissiepit	2.5	2.46548

BD	Heerlik	Siele	6	6	25.299	21.8546	Heerlik-Siele	3	3.91577
BD	Hippie	Engel	3	11	26.4155	25.0805	Hippie-Engel	2	12.9115
BD	Hippie	Mieles	2	8	26.415	18.9712	Hippie-Mielies	2.5	5.88975
BD	Hippie	Pannekoekie	6	1	26.415	21.310	Hippie-Pannekoekie	3	2.43285
BD	Hippie	Rissiepit	1	1	26.415	19.3171	Hippie-Rissiepit	3.5	2.6914
BD	Hippie	Siele	3	2	26.415	21.8546	Hippie-Siele	2.5	7.19154
BD	Oulik	Engel	7	3	30.441	25.0805	Oulik-Engel	2.5	4.95248
BD	Oulik	Heerlik	5	1	30.441	25.2994	Oulik-Heerlik	2	5.47759
BD	Oulik	Mieles	1	1	30.441	18.9712	Oulik-Mielies	3.5	5.78058
BD	Oulik	Siele	2	2	30.441	21.8546	Oulik-Siele	3	1.72153
BD	Pannekoekie	Mieles	3	6	21.310	18.9712	Pannekoekie-Mielies	2	3.07713
BD	Rissiepit	Mieles	3	1	19.317	18.9712	Rissipiet-Mielies	2	1.67143
BD	Siele	Pannekoekie	3	2	21.854	21.310	Siele-Pannekoekie	0.7	3.83442

Table A2. Data collected on different subjects. From left to right: group, identities of the dominant and subordinate adult female subjects that composed the different dyads, number of experiments per dyad, rank of dominant and subordinate subjects, reference distance and social index of the dyad. The dyad Asis-Pann (in italic) was excluded for the analysis as it lacked control samples. The dyad Enge-Pann was excluded from the analysis because the only experiment sample was direction grooming groomer (direction excluded from analysis due to sample size limitations.

Grooming interaction	Data collected
Original grooming interaction dyad	Identity of the subjects, time start and end of each grooming interaction, duration of interaction, who resumes/stop grooming and timing, who is the dominant
Additional grooming interactions by the dominant between original grooming and experimental set up)	Social interactions on the dominant individual, information with similar detail to the original grooming interactions, number of additional grooming partners, the rank of the subjects, kinship (are they kin or not) and bond
Experimental set-up	Time, reference distance, outcome (tolerance/aggression), remarks (description of different behaviours displayed)

Table A3. Data collection at the different stages of the experiment.

Subjects	Group	David Score (DS)	Normalized David Score (normDS)
Ouli	BD	365.295	30.441
Asis*	BD	232.171	27.547
Hipp	BD	180.114	26.416
Heer	BD	128.770	25.299
Enge	BD	118.704	25.081
Siel	BD	-29.689	21.855
Pann	BD	- 54.718	21.310
Snor*	BD	-67.739	21.027
Gese*	BD	-73.323	20.906
Numb*	BD	-75.414	20.861
Riss	BD	- 146.414	19.317
Miel	BD	-162.323	18.971
LBlind*	BD	-206.837	18.003
Gene	BD	301.707	25.143
Gaya	NH	281.594	24.533
Upps	NH	235.838	23.147
Xian	NH	178.433	21.407
Pret	NH	68.0167	18.061
Roma	NH	-120.207	12.357
Reva	NH	-122.036	12.302

Table A4. Rank scores of the different female subjects of BD and NH groups. Individuals with * were not part of any dyad we studied.

Slot	Time (minutes)	Tolerance
1	30	0.835
2	60	0.782
3	90	0.718
4	120	0.718
5	150	0.562
6	180	0.477
7	210	0.394
8	240	0.316
9	270	0.247
10	300	0.189
11	330	0.142
12	390	0.104
13	420	0.076
14	420	0.055
15	450	0.040
16	480	0.030
17	510	0.020
18	540	0.014
19	570	0.010
20	600	0.007

Table A5. Model prediction for the decline of tolerance with the time-lapse of samples collected and beyond (predicted).

CHAPTER 2. Wild female vervet monkeys change grooming patterns and partners when freed from feeding constraints

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RB and MGG conceived the idea, MGG, CB, CB collected the data, MGG analysed the data, MGG run the analysis, MGG wrote the manuscript with DF and RB

2.1. Abstract

Social animals face daily challenges to fulfil feeding, resting and social needs. In vervet monkeys (*Chlorocebus pygerythrus*), females are the core of the social group, with relationships mainly established and maintained through grooming. However, social relationships are not necessarily mutual or driven by the same interests. In a complex and diverse social environment, individuals may benefit from the ability to adapt their manoeuvring to different pressures. We experimentally manipulated the activity budget of two adult females (fed subjects) per group in four wild groups to investigate activity budgets, grooming behaviour variation, and the implications on possible social interactions' changes. Specifically, we provisioned food to one fed subject at a time during two weeks (treatment) and evaluated changes in their grooming behaviour before, during and after the subjects were fed, and compared these patterns with the remaining adult females in the group (non-fed subjects) over the same period. In the provisioning phase, fed subjects decreased their allocation of feeding, but increased resting and social time. Using null models, we found that the increased grooming activity by fed subjects increased those females' grooming strength and reciprocity index. Fed subjects also showed preferences to groom bonded, kin, and adult female individuals. Moreover, when evaluating the continuity of the provisioning effects on grooming strength, we found no carryover effect after the treatment terminated. Our results demonstrate rapid social behaviour plasticity following manipulation of ecological conditions on specific female individuals, allowing for flexible shifts in grooming patterns that hint at Machiavellian-like adjustments that may help achieve social benefits through, at least partially, restructuring their social network when experimentally released from daily feeding obligations.

Keywords: activity budget, behaviour plasticity, fed subjects, grooming, non-fed subjects, null models, vervet monkeys *(Chlorocebus pygerythrus)*

2.2. Introduction

While living in social groups allows individuals to reduce predation risks and to keep neighbouring groups at bay, it also causes within-group competition for resources (Beauchamp, 2014; Cheney & Seyfarth, 1987; Rubenstein, 1978; van Schaik & van Hooff, 1983). Within-group competition leads to selection on individuals to show behaviours that minimise the costs of conflicts, like showing submissive behaviour to dominants and building alliances for mutual support (Mesterton-Gibbons and Dugatkin, 1995; Forkman and Haskell, 2004; Broom, Koenig and Borries, 2009). It has been proposed that cooperation and conflict between members of the same group was a major selective force for the evolution of complex cognitive processes and more complex brains. The Machiavellian Intelligence Hypothesis (MIH), initially developed to understand primate social behaviour, focuses on the cognitive processes (Bshary, Di Lascio, Pinto, & van de Waal, 2011; Humphrey, 1976; Whiten & Byrne, 1988; Whiten & Schaik, 2007). Early empirical efforts related primatological observations with tactical deception, i.e. the production of a signal out of its context to induce recipients to show context-related behaviour (to own disadvantage and the signaller's advantage), to the presence of theory-of-mind, i.e. the ability to perceive other individuals as agents with their own goals and beliefs (Harcourt, 1988; Byrne and Whiten, 1992). However, tactical deception has been observed in various species that have small brains relative to monkeys and apes, including forest birds, domestic chicken, drongos, ravens, wolves and cleaner fish (Munn, 1986; Byrne and Whitten, 1997a; Bshary, Wickler and Fricke, 2002; Bugnyar and Kotrschal, 2002; Packard, 2012; Flower, Gribble and Ridley, 2014). Such examples show that according to the general proposal of MIH, behavioural data should be interpreted 'daringly' concerning underlying cognitive processes (Barrett & Henzi, 2005).

A more modest approach to the MIH is to focus first on the extent to which animals show strategic sophistication in their social interactions, as a basis for the potential development of experimental paradigms that allow testing whether or not the underlying cognitive processes are complex. An estimate of strategic sophistication can be how flexible animals are in their ability to respond to social and environmental information. Behavioural flexibility or plasticity helps avoid rigid adherence to certain behavioural options and instead permits the adoption of flexible behavioural possibilities (Lehmann, Korstjens, & Dunbar, 2007; Oliveira, 2012; Snell-Rood, 2013; Stamps & Groothuis, 2010; Taborsky & Oliveira, 2012). Flexibility can potentially operate on different time scales, i.e. within a day, between seasons or even years (Henzi *et al.*, 2009; Sick *et al.*, 2014).

One potential way to test for behavioural flexibility in the context of social manoeuvring is to alter time budget constraints. Given that time is a finite resource, it is important to consider that the time individuals devote to social interactions must be traded off against other relevant activities like feeding or resting (Dunbar, 1992). Meta-analyses show that the high demand for foraging and resting limits the time individuals have to socially interact with group peers (Dunbar, Korstjens, & Lehmann, 2009; Lehmann, Korstjens, & Dunbar, 2007). Under natural conditions, all members of a group face similar time budget constraints, which may mask individual competition over access to the most profitable partners within a group. For example, all group members may prefer to interact, cultivate and potentially establish social bonds with the most dominant individuals, as those may provide protection and/or tolerance (Seyfarth 1977; Wubs et al. 2018). As long as all group members are time-limited to invest in establishing social bonds, the competitive nature of social interactions may be difficult to investigate. However, reducing time budget constraints of preselected subjects may reveal if they use the extra time for social manoeuvring or whether they simply rest more.

Here, we experimentally subsidized individual female vervet monkeys with high-quality food to test how that manipulation would affect their time budget, and to what extent they would use the reduced need for foraging to improve their social relationships and with whom. We focused on changes in their grooming activities as a key social behaviour. Grooming serves to remove a partner's ectoparasites from areas that are difficult to access for oneself, and beyond, to build social relationships and to repair them (termed reconciliation; (de Waal and van Roosmalen, 1979) not only in primates (Bonnie & de Waal, 2004; Burkett et al., 2016; Dunbar & Shultz, 2010; Engelmann & Herrmann, 2016; Fedurek, Dunbar, & Academy, 2009; Preston & de Waal, 2002) but also in a variety of mammals (Feh and de Mazierès, 1993; Mooring, Mckenzie and Hart, 1996; Stieger, Schweinfurth and Taborsky, 2017), birds (where it is called preening; Emery, Seed, Von Bayern, & Clayton, 2007; Fraser & Bugnyar, 2012; Morales Picard et al., 2020) and even in fish (referred to as tactile stimulation; Bshary & Würth, 2001; Soares, Oliveira, Ros, Grutter, & Bshary, 2011). Grooming has relaxing effects due to a variety of physiological responses, including the release of beta-endorphins (Dunbar, 2010; Keverne, Martensz, & Tuite, 1989; Machin & Dunbar, 2011) and has been also related to oxytocin levels (Benítez, Sosnowski, Tomeo, & Brosnan, 2018; Carter & Wilkinson, 2015; Crockford et al., 2013; Snowdon et al., 2010) as well as a reduction on stress hormones (Brent, Semple, Dubuc, Heistermann, & Maclarnon, 2011; Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Seyfarth & Cheney, 2012; Soares, Bshary, Mendonça, Grutter, & Oliveira, 2012; Wittig et al., 2008). Regular grooming partners are more likely to form coalitions during conflicts (Schino & Aureli, 2008; Seyfarth et al., 2010; van Schaik, Pandit, & Vogel, 2006; Young, Majolo, Schülke, & Ostner, 2014), to exchange commodities like tolerance or support in conflicts (Borgeaud & Bshary, 2015; Schino, 2007; Schino & Aureli, 2008; Tiddi, Aureli, Polizzi Di Sorrentino, Janson, & Schino, 2011), and to share food (Carter, 2013; Fruteau, Voelkl, van Damme, & Noë, 2009; Ventura, Majolo, Koyama, Hardie, & Schino, 2006; von Bayern, de Kort, Clayton, & Emery, 2014; Wittig et al., 2014). Having stable strong bonds appears to have measurable positive fitness consequences in terms of life expectancy and infant survival (Riehl, Strong, & Riehl, 2018; Silk, Alberts, & Altmann, 2003; Silk et al., 2010). Based on this literature, we expected that a reduction in foraging time may reveal changes in our vervet monkey subjects' grooming behaviours that could indicate strategizing, understood as predilection or selective affinity towards certain group members (van Schaik, 2016).

In four study groups, one high-ranking and one low-ranking adult female subsequently received daily extra food during a treatment phase of two weeks. Thus, we focused our study on two different categories of female individuals: the experimental individuals we fed during the treatment phase (fed subjects) and the rest of adult females (denoted as non-fed subjects hereafter). We selected adult females as study subjects because vervet monkeys live in female-bonded groups where females are the philopatric sex (Isbell, Cheney and Seyfarth, 1991). Robust female-female associations can enable them to override the potential costs of male aggression (Barrett & Henzi, 2002; Sterck, Watts, & van Schaik, 1997) and help coordinate and solve collective action problems while defending territories and the food sources within them (Willems *et al.*, 2015). Females' hierarchy is rigid and linear whereby dominants have priority of access to food sources, and individuals have precise third party-rank relationship knowledge (Borgeaud, Alvino, van Leeuwen, Townsend, & Bshary, 2015; Renevey, Bshary, & van de Waal, 2013). We conducted our experiment during the dry season when there is low food abundance, so we expected vervet monkeys across age-sex classes to be experiencing time-budget restrictions. Because social interactions determine group structure and the nature of the connections within (Hinde, 1976; Whitehead, Bejder and Ottensmeyer, 1999), we used a social network analysis approach for the quantitative analysis of the interactions (edges) between individuals (nodes) (Whitehead, 2008) and its underlying causes and consequences (Cantor *et al.*, 2020). Social network analysis allows the assessment of social interactions dynamically by linking social behaviours to time slots, thus permitting the comparison of time intervals and accurately pinpoint changes (Waters and Fewell, 2012; Hobson, Avery and Wright, 2013; Pinter-Wollman *et al.*, 2014; Farine, 2018).

First, we needed to confirm that activity budgets varied during experimental feeding treatment (confirmatory activity budgets). We predicted that by experimentally inducing a reduction in the need for the fed subjects to allocate time to foraging, our experimental manipulation should lower time-budget constraints on resting, which we predicted would increase. If the time allocated to social interactions is normally limited (Dunbar et al., 2009; Lehmann et al., 2007), we also expected fed subjects to spend more time socializing, in particular, to spend more time giving grooming to other individuals. Such a result would yield several follow-up questions: A) Do fed subjects' grooming changes differ from non-fed subjects when freed from feeding restrictions, and do fed subjects change their grooming partners differently depending on how much they groom before the treatment? B) Does having extra time improve the fed subjects' standing in the group, i.e. does their position in the social network become more central through an increase in their number of grooming partners (B1) and/or the frequency of interactions (B2)? C) Do other group members reciprocate or give fed subjects more grooming in return (grooming reciprocity balance)? D) How do fed subjects distribute their extra grooming relative to their partners' attributes; do they focus on social bonds (D1), on high-ranking individuals (D2), on relatives (D3), on other adult females (D4)? E) In the case that the fed subjects increase their grooming given as part of the activity budget while fed, do they maintain it after the food provisioning is finished (E)? And finally, do dominant and subordinate female fed subjects adjust grooming in similar ways (increase in grooming given) (F1)? Moreover, do they differ in their grooming reciprocity balance (F2)? Changes in grooming patterns, including grooming with more partners, should, in turn, affect key social network parameters (Brent, Maclarnon, Platt, & Semple, 2013; Crofoot, Rubenstein, Maiya, & Berger-Wolf, 2011; Henzi et al., 2009). We used grooming interaction data to calculate the rate of accumulation of grooming partners and the number of interactions over time, which constitute informative measures of the individuals' social investment in the group (Krause and James, 2010; Sueur *et al.*, 2011; Farine and Whitehead, 2015). If vervet monkey females strategically compete with other group members over access to profitable partners and/or over central positions within the group's social network, we expected that fed subjects would have more rapidly expanding grooming networks compared to non-fed subjects. Furthermore, we predicted that fed subjects should opt to preferentially groom adult females and high-ranking individuals because of the benefits that can be gained from socializing with them (Seyfarth, 1977).

2.3. Methods

2.3.1. Study site and subjects of study

We carried out our experiment at the Inkawu Vervet Project (IVP) research site, in Mawana Game Reserve (28°00.327S, 031°12.348E, Kwazulu Natal, South Africa). The study was conducted in four groups: Kubu (4 adult females and 12 total individuals); Ankhase (3 adult females and 22 total individuals); Noha (6 adult females and 29 total individuals); and Baie Dankie (10 adult females and 44 total individuals), making a total of 23 adult female individuals that are key in their societies (see more details in the Appendix) (Isbell, Cheney and Seyfarth, 1991). Among all adult females of each group, we selected one dominant and one subordinate as experimental fed subjects (subjects hereafter) based on their rank (more details in the Appendix). We chose the highest-ranking female as the dominant fed subject in each group and the lowest or closest to the lowest-ranking female as the subordinate fed subject (habituation state allowing for feeding sessions). The rest of the adult females compose the category of non-fed subjects. All individuals were recognised through identifiable physical traits and observers were apt for data collection after 80% of Cohen's Kappa agreement.

2.3.2. Experimental design and data collection

Primates living in seasonal environments undergo food availability fluctuation periods and adapt their activity budget flexibly (Barrett et al., 2003; Canteloup, Borgeaud, Wubs, & van de Waal, 2019; McFarland, Barrett, Boner, Freeman, & Henzi, 2014). When food is scarce primates intensify feeding efforts on lower-quality resources while keeping low foraging efficiency (Miller *et al.*, 2020) and regulate resting time to endure harsh environmental conditions (Dunbar, 1992; Korstjens, Lehmann, & Dunbar, 2010). This experiment was carried out during the dry season (July-October) as low food availability favours the monkeys' motivation to participate. We structured the experiment as follows: *i)* 2 weeks to 1 month of non-feeding phase (control-before), *ii)* 4 weeks of treatment—comprised of 2 weeks feeding the dominant subject, and 2 weeks feeding the subordinate subject (not simultaneously), and *iii)* 2 weeks to 1 month of non-feeding phase (control-after, see Fig. 1. Appendix). Food provisioning consisted of two feeding sessions per day: the first, early in the morning as the monkeys woke up, consisting of two apples with 40 grains of corn inserted (around 280 kcal); the second, three hours after, consisting of two apples (around 200 kcal) (see more details in Appendix). Food provisioning constituted approximately half to a third of the daily caloric intake depending on females' reproductive state (Hess, Hendrickx and Stabenfeldt, 1979; Seier *et al.*, 2000).

We collected systematic focal animal sampling data (Altmann, 1974) on all experimental females—fed subjects and non-fed subjects— throughout the day, to register their activity across study phases: *1)* control-before, *2 & 3)* treatment: dominant fed, subordinate fed, and *4)* control-after. The main activities were feeding, resting, moving, and social (broad social encompassing sitting in contact, mouth-to-mouth, grooming given, grooming received; more details in the Appendix). Because moving activity is influenced by group behavioural patterns (Montiglio, McGlothlin and Farine, 2018), especially during the dry season when food is sparsely distributed (Janson and van Schaik, 1988), we did not draw conclusions from this activity, since our focus lay on behavioural performance at the individual level. Our focal data consisted of 20 minutes follows collected over three time periods (on alternate days) to cover the entire spectrum of activities, as vervets often nap for long stretches during the hottest period of the day (personal observation) whereby behaviours were entered every two minutes. Altogether, we collected over 17000 data points during 283 hrs of focal follows across the 23 experimental females (average 6.21 ± 0.1 hrs per individual per study phase). The same data was used to calculate the grooming derived parameters for each experimental female ego network.

While our focals were focused only on experimental females, grooming partners could extend beyond the females' subset. Given that it was not always possible to ensure an individual full observation during the focal-which caused the loss of some data points, we converted our grooming measurements to rates (Leu *et al.*, 2016; Davis, Crofoot and Farine, 2018). Our first measure was an equivalent of degree—or the number of grooming partners—which we calculated as the accumulation of grooming partners (i.e. degree divided by observation time) to account for differences in observation time. The second was strength (Farine, 2015), which was calculated as the number of grooming interactions detected over the individuals' focal follows, divided by the time that individual was observed. We calculated social bonds using proximity data collected from focal animal sampling (Altmann, 1974) following Fedurek's method as an indicator of social affinity between female dyads (Borgeaud & Bshary, 2015, 2018; Fedurek et al., 2013; Machanda, Gilby, & Wrangham, 2014) that was highest when two individuals were mutual social partners (see rank and social bond details in Appendix). Accordingly, we will refer to bonded partners or social bonds when they fulfilled the requirements of being mutual social partners. We used agonistic interactions' data from ad-libitum data to calculate rank scores using the Elo-rating package (Neumann, Duboscq, Dubuc, Ginting, *et al.*, 2011; Sánchez-Tójar, Schroeder and Farine, 2018) in R (R Core Team, 2008). We included dyadic agonistic interactions that had a clear aggressive (chase, bite, hit, take place, hand on top of the head, stare-attack); and submissive behaviour (retreat, flee, scream, crawl). Finally, we used our ten-year life history database to extract mother-offspring and siblings' affiliations as a measure of kinship.

2.3.3. Confirmatory activity budget questions: effects of the food supplementation

As a first step, we investigated whether the treatment phase or supplementary feeding induced changes in the activity budgets (feeding, resting, moving and broad social) of the fed subjects. For that, we analysed each activity separately-feeding, resting, broad social (social henceforth), and grooming given. We conducted a series of generalized linear mixed models (GLMMs) (Bolker *et al.*, 2009; Zuur, Ieno and Elphick, 2010) to evaluate the effect of the treatment measured as the phase of the study (treatment-dominant fed and treatment-subordinate fed) on the different activities. The response variable in the models is represented by the proportion of times the fed subjects displayed any activity in each study phase. Thus, we studied the variation of i) feeding, ii) resting, iii) social behaviours, from which we extracted iv) grooming given, and v) moving behaviours and we performed GLMMs for each activity as the response variable and study phase as the explanatory variable and the category of individual (fed and non-fed) as another explanatory variable with an interaction of the two. We analysed the change of activities over two study phases: (1) control–before versus treatment (effect of treatment), or 2) treatment versus control–after (carryover effects) separately for fed subjects and non-fed subjects as only fed subjects were exposed to experimental conditions during the treatment phase. Individual identity, group, and time period of the day were set as random factors in the models. All analyses were performed using the lme4 package (Bates *et al.*, 2020) in R (R Core Team, 2008).

2.3.4. Change in social behaviour question: grooming given network measures

To test the impact of food supplementation on grooming behaviours (questions A-E), we calculated grooming measurements of rate of accumulation of grooming partners, grooming strength and grooming reciprocity during each study phase from the focal data, including all age and sex class possible grooming partners the females had. The number of grooming partners reflects the number of edges—or relationships—a given individual accumulated over their observation time, while grooming strength refers to the number of grooming interactions over the observation time (Clayton, 2017; Farine & Whitehead, 2015; Krause, Croft, & James, 2007; Kurvers, Krause, Croft,Wilson, & Wolf, 2014; Whitehead, 2008; Wilson et al., 2014). Both measurements are suitable indicators of the social connectivity of the individual within the mesh of the group and bear meaning about the individuals' social standing (Krause, Croft and James, 2007; Whitehead, 2008). We used grooming given to measure the number of grooming partners and out-strength (strength hereafter) as grooming network measures to capture the focal individuals giving the grooming service to social partners (any individual of the group). The grooming reciprocity balance (grooming balance hereafter) was calculated as a dyadic concept of each female (fed subjects and non-fed subjects) by dividing each female's grooming given and received with each social partner, thus functioning as a proxy of grooming reciprocity (Kaburu and Newton-Fisher, 2015).

We studied grooming change across study phases to address different questions. Specifically, we tested the following:

A) We assessed the change in grooming partners when individuals were freed from feeding restrictions by comparing the grooming given to partners (strength) during the treatment divided by the grooming given to partners (grooming strength) in the control-before. This was done by dividing grooming given during the treatment by the grooming given during the control-before (at the dyadic level). This permitted us to see whether fed subjects and non-fed subject individuals changed differently and if individuals whose grooming strength was most limited initially expressed a larger increase in grooming given compared to those whose grooming strength was higher.

B) We investigated if the supposed extra time that the fed subjects gained thanks to the supplementary feeding influenced their standing in the network by studying their accumulation of grooming partners (B1) and grooming strength (B2) between the control-before and treatment phase (both measures based on grooming given).

C) We examined to what extent the grooming balance might shift between the control-before and the treatment phases. A positive balance translates into a subject's grooming given bias, while a negative one reflects a subject's inclination toward receiving. Balances close to zero reflect evenness in grooming given and received.

D) We studied if the "extra grooming"—in the form of grooming strength—that we expected fed subjects to perform during the treatment phase preferentially targeted specific individuals as grooming partners relative to the following attributes (all binary): social bond (D1), high-rank (D2), relatives (D3), or adult females (D4). A variation in the preferences could indicate tactical selectivity to filter the social partners to engage in grooming interactions with.

E) Because the feeding conditions ended with the treatment, we investigated the maintenance of the fed subjects' expected grooming increase during the treatment—in the form of grooming strength—in the study phase that followed (control-after). This would imply the existence of carryover effects.

F) We evaluated if dominant and subordinate fed subjects adjusted their grooming given similarly by looking at their grooming given as part of a measure of grooming strength (F1). Finally, we looked at their grooming balance as an estimate of the reciprocated grooming dominant and subordinate fed subjects received (F2).

To calculate the significance of the change for the different grooming questions (A-F2), we used null model hypothesis testing (Croft *et al.*, 2011; Farine and Whitehead, 2015; Farine, 2017). Since we were interested in understanding the role of the experiment and the effect of food provisioning on our observed focal data (how fed subjects and non-fed subjects changed their grooming rates) and possible tactical preferences to direct grooming efforts to specific partner' attributes and grooming reciprocity, we designed a permutation test in which we randomized the study phase variable within each individual. This test is similar to node permutations, where instead of randomizing identity we randomized the study phase corresponding to each individuals' social metric (social network measures of accumulation of grooming partners, strength, grooming balance). We calculated the observed effect by subtracting the mean change in the category subjects from the mean change in the category non-subjects, obtaining the test-statistic representing the difference in the response among individuals according to treatments. We repeated this calculation on the permuted data, repeating this procedure 1000 times. We evaluated the significance of the differences by comparing the observed test statistic to the distribution of the randomized test statistic values, where an observed value is significantly different if it is greater or smaller than 95% of the randomized data (Farine, 2017). Therefore, we interpret both upper and lower significance thresholds following the ensuing criterion: "*the result is significant at Prand= 0.05 if 2.5% of the random values are greater than or equal to the observed value, or if more than 97.5% of the random values are greater than or equal to the observed value*" (Farine, 2017), here we refer to *Prand* as the proportion of randomly generated values (scheme of the study in Fig. 1. of the Appendix).

2.3.5. Ethical note

Ethical permission for the study was granted by the Ezemvelo Wildlife Board (KwaZulu-Natal, South Africa), the University of Cape Town, and the van der Walt family, owners of Mawana Game Reserve. The study adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research (Buchanan *et al.*, 2012). All individuals were habituated to the feeding boxes without direct human-monkey interaction. We attracted fed subject adult females to the boxes set-up by clicking the tongue, a sound they learned to associate with the boxes feeding sessions. Fed subjects approached their boxes voluntarily and had no dependent infants during the study. The experimental set-up did not cause dominant females to physically aggress subordinate counterparts, and hence no wounds were caused by our experiments. Corn and apples were cleaned beforehand and handled with gloves to avoid the possible transmission of diseases.

2.4. Results

2.4.1. Confirmatory activity budget questions: effects of the food supplementation

We found that the fed subjects decreased their feeding from control-before to the treatment phase significantly, around 22% and subsequently increased by approximately 16% their feeding from the treatment phase to control-after (β= -0.97, SE= 0.08, P <0.001; β= 0.72, SE= 0.08, P <0.001); (see Tables 1 and 2, Figure 1). In contrast, the category non-fed subjects increased feeding time by about 6 % during the treatment phase relative to control-before, and decreased their feeding allocation 14% during control-after (β= 0.28, SE= 0.05, P <0.001; β= -0.62, SE= 0.05, P <0.001). The category fed subjects significantly increased their resting during the treatment, almost 16%, compared to the control-before, and decreased their resting again after the food supplementation was over during the control-after by almost 8% (β= 0.88, SE= 0.1, P <0.001; β= -0.42, SE= 0.9, P <0.001). Non-fed subjects maintained their resting levels from control-before to treatment unchanged but increased their resting levels by almost twofold during the control-after compared to treatment around 8% (β= -0.09, SE= 0.09, P =0.29; β= 0.66, SE= 0.07, P <0.001).

Regarding broad social behaviours, the fed subjects significantly increased these, by almost 10% from control-before to treatment and decreased it again in the control-after around 11% (β= 0.66, SE= 0.1, P <0.001; β= -0.84, SE= 0.11, P <0.001). Non-fed subjects maintained their broad social behaviours stable from control-before to treatment, and from this phase to control-after (β= -0.1, SE= 0.08, P =0.39; β= 0.05, SE= 0.07, P =0.76), therefore not changing their sociality significantly (as a consequence, sublevel of social activity grooming given remained unchanged too). Fed subjects significantly changed their allocation to grooming given across study phases as during the treatment phase or supplementary feeding conditions they increased almost 7% their grooming given compared to control-before, and reduced their grooming allocation afterwards by 6.5% (β= 0.94, SE= 0.16, P <0.001.; β= -0.84, SE= 0.15, P <0.001). Here grooming given is encompassed within social behaviours and serves as a measure of grooming effort that we can relate to strength in a grooming network (Fig 5.A. in Appendix). Non-subjects decreased their grooming given from control-before to treatment, with a non-significant increase in control-after relative to treatment (β= -0.27, SE= 0.10, P =0.02.; β= 0.18, SE= 0.10, P =0.17).

For completeness, we found that the fed-subjects did not significantly change their moving from control-before to treatment but they did change from the treatment to the phase control-after (β= -0.26, SE= 0.13, P =0.10.; β= 0.32, SE= 0.12, P *= 0.02*). Non-fed subjects significantly changed their allocation to moving activity between those phases by decreasing by 4% between control-before and treatment and increasing it by almost 6% between treatment and control (β= -0.49, SE= 0.09, P <0.001.; β= 0.65, SE= 0.09, P <0.001).

2.4.2. Change of grooming partners

The permutation analysis revealed that the fed-subjects (N= 8 individuals) changed their grooming partners differently than non-fed subjects (N= 15 individuals) between control-before and treatment phase (Table 3, Test A), as they increased their network more than non-fed subjects (mean difference subjects VS mean difference non-subjects) that did not undergo a relevant change (slope Figure 9A in Appendix). Moreover, the fed subjects' negative slope suggests that those that had lower grooming in the control-before phase increased more (larger ratio of treatment and control-before). Thus, individuals that groomed least during the control-before (left side of x-axis, Figure 9A, Appendix) added more grooming partners to their network (per unit of observation time) during the treatment phase, as the grooming in the treatment phase is disproportionately larger than the grooming in control-before.

2.4.3. Grooming given changes: social network measures

All analyses involving comparisons between fed-subjects and non-subjects compared a sample size of 8 individuals and 15 individuals across all groups of study. Permutation tests revealed that fed subjects increased the rate of accumulation of grooming partners (Table 3, Test B1; Figure 2 all measures) increased 1.21 times from the one registered by non-fed subjects between control-before and treatment that increased 0.57 times. Moreover, subjects increased significantly their grooming strength compared to non-subjects (Table 3, Test B2), as they more than doubled their grooming strength from control-before, increasing it 2.43 times in treatment compared to control-before contrary to non-fed subjects that experienced a small decrease (treatment 0.79 smaller than control-before). Fed subjects increased proportionately more their grooming given compared to the grooming they received from other group members, as their grooming balance significantly changed between control-before and treatment from unskewed grooming balance during control-before to being more biased toward giving grooming (Table 3, Test C), increasing 3.7 times their grooming balance (grooming given divided by grooming received), while non-subjects decreased it 0.19 times in the treatment compared to control-before.

Concerning the attributes of the grooming partners, fed subjects increased significantly their grooming strength to their social bonds (fed subjects increased 4.3 times and non-fed subjects decreased it 0.66), their kin (fed subjects increase 1.51 times and non-fed subjects decreased it 0.68), and to other adult females (fed subjects increase 5.5 times and non-fed subjects decreased it 0.83), (Table 3, Test D1, D3, D4), while their increase in grooming strength to high-ranked individuals was pronounced and close to significance levels (Table 3, Test D2) (fed subjects increase 1.66 times and non-fed subjects decreased it 0.86 times). Regarding a possible carryover effect, fed subjects significantly changed their grooming strength after the feeding treatment (decreased 0.49 times) and did not maintain the increase registered from control-before to treatment when control-after and treatment phase were compared (Table 3, Test E) while non-fed subjects decreased it on 0.91 times. Summarizing, the category fed subjects changed their grooming measures positively more than non-fed subjects, except in the carryover of strength where the comparison is set between control-after and treatment.

Regarding the adjustment of grooming given as part of the activity budget of the two subject sub-categories, there was no significant difference between dominants (N=4 individuals, one per group) and subordinates (N=4 individuals, one per group) in how much they upgraded their grooming efforts between control-before and treatment phase (Table 3, Test F1; Fig 3-Test F1), as dominant subjects increased their grooming given 2.33 times during the treatment compared to control-before and subordinate subjects similarly increased 2.46 times. Regarding the grooming reciprocity balance, dominants and subordinates gave more than they received at the dyadic level (Table 3, Test F2; Fig 3- Test F2) although both dominant and subordinate subjects groomed more while fed, notably dominants increasing from negative balance-more grooming received than given- to a positive balance, while subordinates simply increased their positive grooming balance.

2.5. Discussion

In this experiment, we investigated if provisioning food to selected adult female vervet monkey subjects for two weeks would change their activity budget, grooming behaviour, and resulting social connectivity in the network. In comparison to the other adult females, experimental subjects adopted significant changes in their activity budget, and notably decreased feeding and increased resting, social, and grooming behaviours while being fed (treatment phase) compared to the preceding phase of control-before and the following phase the control-after. The subjects significantly increased allocation to social behaviours and grooming given during the treatment phase, independently of their hierarchy status. Finally, subjects not only groomed more but also increasing the rate at which they accumulated grooming partners over time (close to significance) and their grooming strength. Importantly, the subjects' increase in grooming activities during treatment was not distributed equally among other group members but targeted at specific individuals with the following non-mutually exclusive attributes: kin, bonded, high-ranking and adult females. Thus, both high- and low-ranking subjects used the period of reduced time budget constraints to improve their social standing with key group members. In the absence of knowledge of the underlying mechanisms, we consider these strategic adjustments in their social behaviour 'Machiavellian-like'. Nevertheless, the fact that subjects used more of their freed time for resting than for social activities warrants further investigation. Only the collection of similar data on other species may reveal whether our results should be interpreted as 'vervets are not particularly Machiavellian in the social behaviour' or whether being the only one with spare time often prevented subjects to find interaction partners, making resting the default alternative.

Our experimental manipulation worked as expected, with fed subjects freeing 22% of their feeding time even if supplementary feeding ended around 10 to 11 am each day while data collection continued until sunset hours (around 6 pm). Dominant and subordinate individuals adjusted their time budgets in remarkably similar ways, suggesting that individuals experience time budget trade-offs rather independently of their rank. Although these changes were elicited via food provisioning, our results support that animals under stark seasonality contrasts can behave flexibly to adjust time budgets to the resulting challenges (Barrett et al., 2003; Canteloup, Borgeaud, Wubs et al., 2019; Dunbar et al., 2009; Herbers, 1981; McFarland et al., 2014; Pollard & Blumstein, 2008).

Despite grooming serving important hygienic purposes (Hutchins and Barash, 1976) we interpret the subjects' increase in grooming given during the treatment as evidence of social responsiveness to a motivation to interact more socially and with more partners, which brought a rewiring in their social networks (Kurvers *et al.*, 2014; Farine, 2019) that may as well promote cooperation (Ohtsuki *et al.*, 2006; Fehl, van der Post and Semmann, 2011; Rand, Arbesman and Christakis, 2011; Wang, Suri and Watts, 2012). We highlight that the dominant subjects increased their grooming balance slightly above zero, which contrasts with their grooming balance before the treatment when they received more than they gave. Indeed, dominants are normally perceived as high-quality grooming partners by the rest of the group and hence receive more grooming than they give, partly in exchange for tolerance and coalitionary support (Borgeaud & Bshary, 2015; Renevey et al., 2013; Schino, 2001; Seyfarth, 1977; Snyder-Mackler et al., 2016; Wrangham, 1980; Wubs, Bshary, & Lehmann, 2018). Our results demonstrate that even dominants may shift their social priorities when given spare time, increasing their grooming efforts and their social network.

If an increase in grooming effort had prospects of null return, subjects may have been better off by dedicating the surplus time gained from decreasing foraging exclusively to resting (Korstjens, Lehmann and Dunbar, 2010), which did not happen. The Machiavellian Intelligence Hypothesis presupposes that sophisticated tactical behaviours evolved due to the daily challenges of social life (Harcourt, 1988; Byrne and Whitten, 1997b; Bshary *et al.*, 2011). Two results are in line with the hypothesis that subjects were indeed strategic in their grooming adjustments: the characteristics of the targets of increased grooming and the increase in the grooming network. Regarding the targets, a selective increase in grooming kin is likely to yield indirect fitness benefits (Hamilton, 1964a, 1964b), while selectively increasing the grooming between strong social bonds should yield direct fitness benefits due to interdependency (Roberts 2005). The selective increase in grooming high-ranking individuals fits the concept of trading services for increased tolerance and support (Seyfarth, 1977; Wubs, Bshary and Lehmann, 2018). Finally, adult females form the core of vervet monkey groups due to female philopatry (Isbell, Cheney and Seyfarth, 1990; Sterck, Watts and van Schaik, 1997; Renevey, Bshary and van de Waal, 2013), and intensifying female-female grooming networks may yield benefits against male aggression (Barrett & Henzi, 2002; Sterck et al., 1997) or enemy groups (Willems *et al.*, 2015). Therefore, while our study did not quantify any potential benefits of the subjects' increased grooming activities, the changes in grooming patterns fit predictions based on well-established concepts of altruism and cooperation. It is known that vervet monkeys can distinguish other individuals' ranks, matrilines and relationships accurately (Borgeaud et al., 2015; Cheney, 2011), and our results indicate the applied value of having such knowledge. Also, the increase in the grooming network suggests that animals living in complex societies can behave tactically, and re-structure their networks consequently (Farine, 2019; Flack, Girvan, de Waal, & Krakauer, 2006). Such tactical displays could enable the fulfilment of personal gains by promoting the integration in the social network, perhaps by enhancing the bonding (the emotional closeness) with their grooming partners, which requires substantial time and effort (Chang, Brent, Adams, Klein, Pearson, Watson, Platt, 2013; Roberts, Dunbar, Pollet, & Kuppens, 2009; Sutcliffe, Dunbar, Binder, & Arrow, 2012). Such bonding can be adaptive as it can favour help during conflicts (Hemelrijk, 1994; Schino, Polizzi di Sorrentino, & Tiddi, 2007; Seyfarth, 1977), conflict resolution (de Waal and van Roosmalen, 1979; McFarland and Majolo, 2011), or pave the road for future cooperative interactions (Bhagavatula *et al.*, 2010; Berghänel *et al.*, 2011; Cheney, 2011). In conclusion, there are many potential benefits of unilaterally 'raising the stakes' (Roberts & Sherratt 1998) when supplemented even if the grooming is not reciprocated in kind.

Overall, our experimental manipulation of subjects' feeding conditions offers insights into animals' capacity to exhibit grooming plasticity and network rewiring in interesting ways. Subjects varied several grooming metrics within relatively short time frames, revealing that network structures are not static entities but the outcomes of individuals making tactical decisions according to the specifics of their situation (Sih, Hanser, & Mchugh, 2009; Wilson et al., 2014). This flexibility is a key aspect of the Machiavellian intelligence hypothesis, which proposes that primates evolved complex cognitive abilities to cope with a complex social environment (Harcourt, 1988; Byrne and Whitten, 1997b). However, we note that our study only identified strategic behaviour in vervet monkeys, without identifying the underlying cognitive machinery. The identification of Machiavellian-like strategic social behaviour in vervet monkeys opens at least the possibility that advanced cognitive processes, like components of a theory of mind (Premack and Woodruff, 1978; Seyfarth and Cheney, 2013), are at play. A second major challenge for future research is to identify the potential benefits of a unilateral increase in grooming. While most potential benefits are likely to be direct, like the recipient being more tolerant or supportive, there is also the possibility that individual decision rules have cascading effects on group interaction patterns and as a consequence group performance, which would affect the fitness of all group members.

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2.7 Figures and tables

Model	**Dependent variable**	**Category individual**	**Explanatory variable: Study Phase**	**Estimate**	**SE**	**P-value**
Activity budget model	**Feeding**	Fed subjects	Treatment VS Control-before	-0.972	0.081	*<0.001*
			Control-after VS Treatment	0.720	0.078	*<0.001*
		Non-fed subjects	Treatment VS Control-before	0.278	0.055	*<0.001*
			Control-after VS Treatment	-0.621	0.053	*<0.001*
	Resting	Fed subjects	Treatment VS Control-before	0.884	0.098	*<0.001*
			Control-after VS Treatment	-0.423	0.087	*<0.001*
		Non-fed subjects	Treatment VS Control-before	-0.088	0.085	0.294
			Control-after VS Treatment	0.661	0.071	*<0.001*
	Social	Fed subjects	Treatment VS Control-before	0.662	0.107	*<0.001*
			Control-after VS Treatment	-0.839	0.110	*<0.001*
		Non-fed subjects	Treatment VS Control-before	-0.100	0.076	0.387

		Control-after VS Treatment	0.053	0.075	0.763
Grooming given	Fed subjects	Treatment VS Control-before	0.942	0.158	*<0.001*
		Control-after VS Treatment	-0.843	0.149	*<0.001*
	Non-fed subjects	Treatment VS Control-before	-0.275	0.102	*0.019*
		Control-after VS Treatment	0.184	0.103	0.172
Moving	Fed subjects	Treatment VS Control-before	-0.259	0.127	0.102
		Control-after VS Treatment	0.319	0.122	*0.025*
	Non-fed subjects	Treatment VS Control-before	-0.490	0.087	*<0.001*
		Control-after VS Treatment	0.647	0.081	*<0.001*

Table 1. Summary of GLMMs models showing the effect of study phases on the activities of feeding, resting, social, and grooming given. Study phases are compared between i) control-before and treatment, and ii) treatment and control-after for the two categories of individuals: fed-subjects and non-fed subjects.

Model	**Dependent variable**	**Explanatory variables**	**Chisq.**	**Df**	**P-value**
Activity budget model	Feeding	Study phase	38.650	2	*<0.001*
		Category individual	40.767	1	*<0.001*
		Study Phase * Category individual	214.167	2	*<0.001*
	Resting	Study phase	55.339	2	*<0.001*
		Category individual	38.411	1	*<0.001*
		Study Phase * Category individual	119.583	2	*<0.001*
	Social	Study phase	16.003	2	*<0.001*
		Category individual	7.660	1	0.0056
		Study Phase * Category individual	63.717	2	*<0.001*
	Grooming given	Study phase	3.705	2	0.157
		Category individual	6.042	1	0.014
		Study Phase * Category individual	61.512	2	*<0.001*
	Moving	Study phase	79.337	2	*<0.001*
		Category individual	0.247	1	0.619
		Study Phase * Category individual	5.609	2	0.061

Table 2. Summary of the activity budget GLMMs for the different activities. Shown: explanatory variables of study phase (control-before, treatment, control-after), category of individual (fed subjects, non-fed subjects) and interaction of study phase with category of individuals.

Test	Grooming variable	Fed subjects		Non-fed subjects		Observed value	Permutation quantiles		Prand
		Mean difference	change	Mean difference	change		2.5% thresold	97.5% thresold	
A	Change in grooming partners	-209.6	NA	-84.53	NA	-125.07	-141.8	31.79	0.055
B1	Accumm. grooming partners	0.005	1.21	-0.011	0.57	0.016	-0.0071	0.018	0.958
B_2	Strength	0.006	2.43	-0.001	0.79	0.007	-0.001	0.003	*1**
C	Grooming reciprocity balance	0.0038	-3.7	-0.0017	0.19	0.006	-0.001	0.004	*0.992**
D1	Strength to bond	0.035	4.36	-0.011	0.66	0.046	-0.015	0.035	*1**
D2	Strength to rank	0.02	1.66	-0.004	0.86	0.024	-0.012	0.027	0.951
D3	Strength to kinship	0.008	1.51	-0.008	0.68	0.016	-0.008	0.016	*0.981**
D4	Strength to adult females	0.027	5.5	-0.004	0.83	0.031	-0.009	0.025	*0.988**
E	Carryover effect (strength)	-0.004	0.49	-0.001	0.91	-0.003	-0.001	0.003	*0.014**

F_1	Grooming given (activity budget)	6.06	2.33	8.38	2.46	-2.32	-4.50	11.93	0.366
F_2	Grooming reciprocity balance	30.50	-0.11	22.21	3.66	8.28	-21.47	55.53	0.586

Table 3. Results summary of null model analysis for the different grooming measures (A-E). Mean difference illustrates the difference between fed-subjects and non-fed subjects between study phases treatment and control-before (except for carryover, that is calculated between control-after and treatment). Change calculates the variation that fed subjects and non-fed subjects experienced between study phases by dividing the treatment values by the control-before values (except in carryover, dividing control-after by treatment), so values below 1 represent decreases, and values higher than 1 represent a positive increase. Observed and Prand are based on the difference of the means of fed subjects and non-fed subjects between study phases. In test A the calculation of % of change is not possible due to the calculation of this variable involving the two study phases (grooming partners during treatment/grooming partners during control-before). Test B1 corresponds to the accumulation of grooming partners (Accumm. Grooming partners). Tests A-E compare fed subjects and non-fed subjects. Tests F1 and F2 compare the two fed subject subcategories (dominants and subordinates). Permutation quantiles represent the upper and lower thresholds for significance, corresponding to the upper 97.5% and lower 2.5% quantiles of the test statistics estimated from the permuted data. Prand values (proportion of randomly generated values) are significant ($P>0.975$ or $P<0.025$) and shown with * when random values are less than or equal to, and greater than or equal to the observed value. Negative results in C and F_2 are not result of a decrease, but instead from a negative value in control-before (see Table 11A in Appendix).

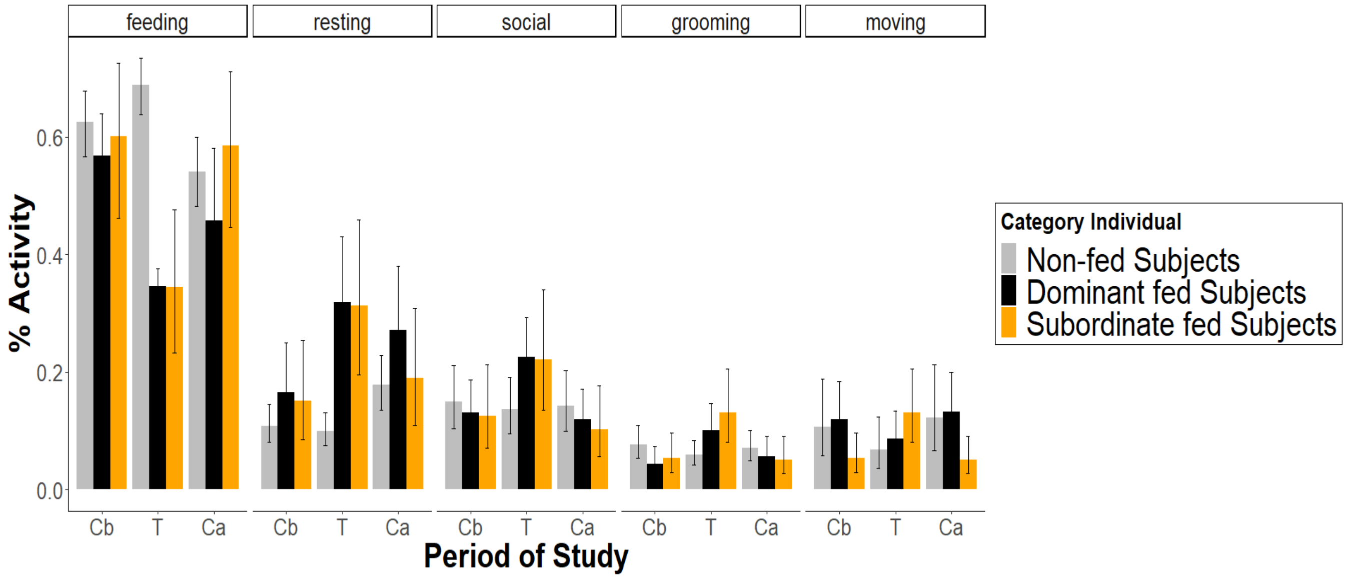

Figure 1. Activity budget change across study phases. Starting from left to right: feeding, resting, (broad) social behaviours, grooming given and moving. Each activity is represented as a percentage from the total focal points collected along the y-axis for the different study phases, displayed along the x-axis (Cb for control-before, T for treatment or supplementary feeding and Ca for control-after). The different categories of subjects represented in different colours: grey or non-fed subjects and the category fed-subjects divided into two sub-levels: black for dominants and orange for subordinates. Confidence intervals show the upper and lower limits of the means for each activity. More statistical output details are provided in tables 2 and 3 of the Appendix.

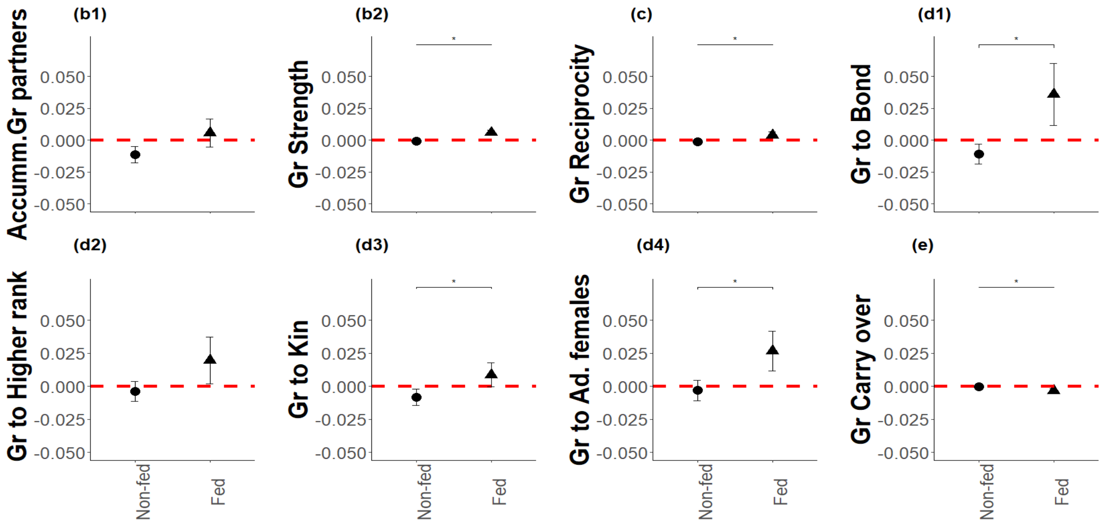

Figure 2. Grooming measures of non-fed subjects and fed subjects across study phases (along the x-axis as "Non-fed" and "Fed"). Differences (y-axis) represent changes in grooming behaviour (Gr) between control-before and treatment phase except in carryover—treatment and control-after. From left to right, first row shows: **b1)** difference in accumulation of grooming partners; **b2)** difference in grooming strength; **c)** difference in grooming reciprocity balance, d**1)** difference in grooming strength to bonded partners. Second row: **d2)** difference in grooming strength to high-rank partners; d**3)** difference in grooming strength to kin partners; **d4)** difference in grooming strength to adult females; **e)** grooming strength carryover. Error bars show the 95% quantiles of the differences. As each value was calculated accounting for the time of observation as the exact time each individual was observed in each study phase, the changes in values are all close to the 0 value, even though effect sizes can be large (see text). Histograms showing permuted and observed values are shown in Figure 7A and 8A in Appendix.

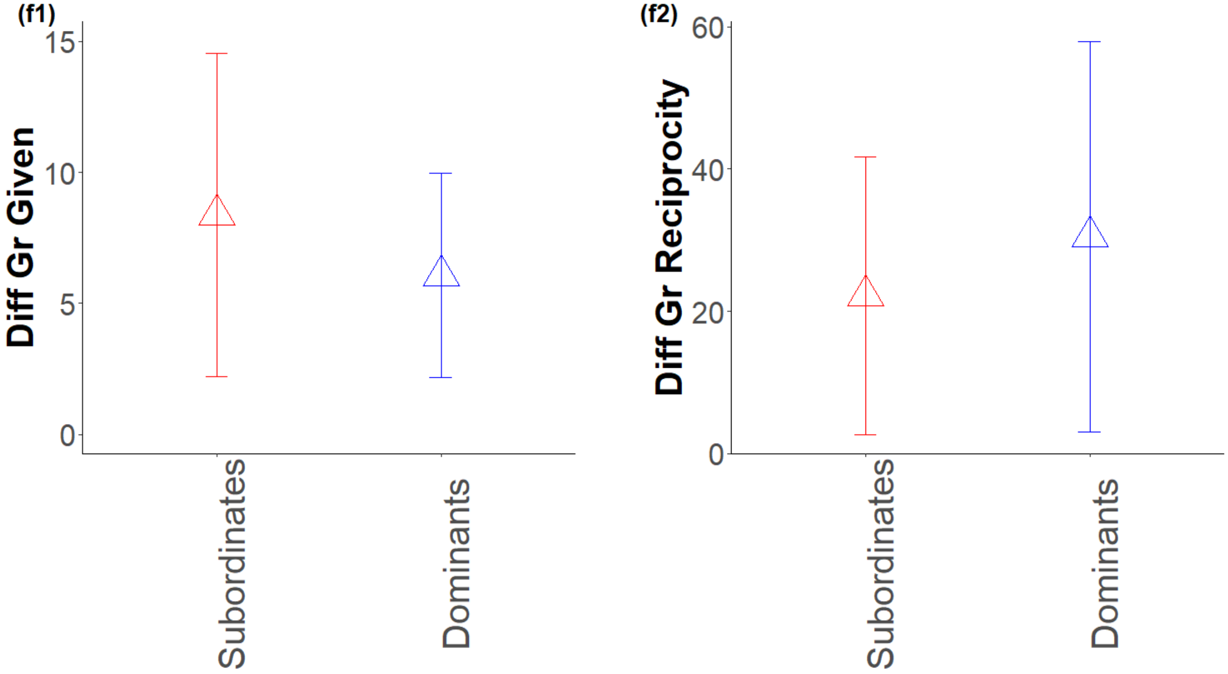

Figure 3. Observed values for the two subcategories of fed subjects. Subordinates (empty red triangles) and dominants (empty blue triangles)**.** Differences (y-axis) represent changes in grooming behaviour (Gr) between control-before and treatment phase. Graph f1 shows differences in grooming given and graph f2 shows the difference in grooming reciprocity balance calculated from grooming strengths between control-before and treatment phase, both showing differences of percentages of grooming given as part of the activity budgets (f1) and as part of grooming allocation (grooming given and grooming received, f2).

2.8 Appendix

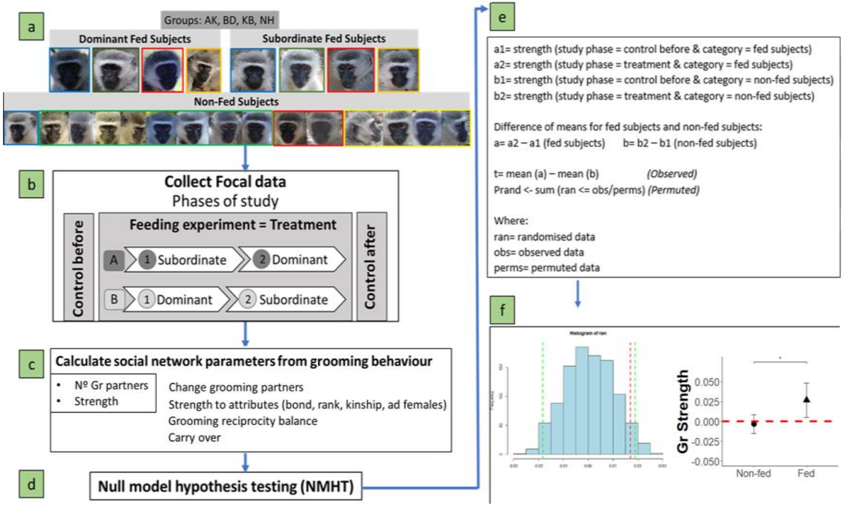

Figure 1A. Scheme representing the main steps of the study, from data collection to data analysis. a) Different fed-subjects (dominants and subordinates) and non-fed subject females that were part of the focal data collection. Individuals framed in blue, green, red and yellow correspond to the different study groups of AK, BD, KB and NH. **b)** Data collection based on focal animal sampling across the different study phases 1) control-before, 2 & 3) treatment organized in (A) first subordinate fed, dominant fed later, or (B) first dominant fed, subordinate fed later (B), and 4) control-after. **c)** Social network measures object of study based on the subjects and non-subjects' grooming behaviour that were calculated from focal data that accounted time of observation (focal data), therefore having grooming rates. **d)** Null model hypothesis testing (NMHT) following (Farine, 2017). **e)** Example of the permutation code for the NMHT where observed and permuted data was calculated using the different social network measures (here case example of grooming partners; more details below and in Appendix). **f)** Graphical representations from permutation calculations. On the left, histogram with dotted green lines representing the range of permuted data and dotted red line representing the observed data. Frequency of the permuted data represented along the y-axis. Graphical representation to the right shows the comparison of the two different categories, fed subjects (as Fed) and non-fed subjects (Non-fed). The scale of the difference of the grooming measure represented along the y-axis.

Details of Material and Methods

Elo-rating

Condition for agonistic behaviours to be included in the Elo-rating calculation: only agonistic interactions when the two individuals involved displayed one of the behaviours mentioned in the methods section were considered. Therefore, interactions where only one individual performing a winner or a loser behaviour was not sufficient and was excluded from our data. We only included agonistic interactions involving two individuals, therefore excluding any data that had third parties (coalitions, redirection of aggression). Hierarchy calculation based on ad libitum data of 6 months before the onset of the experiment using the Elo-Rating package developed by Dr. Neumann (Neumann, Duboscq, Dubuc and Ginting, 2011). After the values were calculated, they were adapted into binary (0,1). In the permutation analysis, we studied if the dominant and subordinate subjects groomed more with high-ranking individuals than the category of individuals non-subjects. High-ranking individuals were those with the value of 1, while lower-ranking ones than higher-ranking were assigned values of 0.

Bond

Bond index calculations using ad libitum data of 6 months before the onset of the experiment following Fedurek method (Fedurek, 2013). This method determines whether two individuals are preferred social partners using different types of data like individuals being in the same party, individuals being within 5 metres, and individuals being nearest neighbours. Once values were calculated, the outcome of the calculations was: mutual-social partners, uni-social partners and no social partners. Of these, bonds that were bidirectional are expected to form stronger social bonds and we assigned them the value of 1 and we assigned the value of 0 to all remaining dyad combinations so in our analysis social bonds were a binary factor. As a clarification note, the fact that two individuals are mutual social partners does not imply that one individual cannot have more than one. This method is therefore concentrating in proximities between individuals while they are performing different activities like feeding and moving, as monkeys can fill their check-pouches with food that they eat as they travel (Smith, Link and Cords, 2008).

Kinship

Bond index calculations using ad libitum data of 6 months before the onset of the experiment following Fedurek method (Fedurek, 2013). This method determines whether two individuals are preferred social partners using different types of data like individuals being in the same party, individuals being within 5 metres, and individuals being nearest neighbours. Once values were calculated, the outcome of the calculations was: mutual-social partners, uni-social partners and no social partners. Of these, bonds that were bidirectional are expected to form stronger social bonds and we assigned them the value of 1 and we assigned the value of 0 to all remaining dyad combinations so in our analysis social bonds were a binary factor. As a clarification note, the fact that two individuals are mutual social partners does not imply that one individual cannot have more than one. This method is therefore concentrating in proximities between individuals while they are performing different activities like feeding and moving, as monkeys can fill their check-pouches with food that they eat as they travel (Smith, Link and Cords, 2008).

Adult female individuals in each group

We focussed the data collection on adult females because they are the core of the social group and we were interested in studying if they would be strategic in the way they use the “extra time” by grooming more. We collected data on adult females in four wild groups of vervet monkeys. Here the list of the names of each adult female belonging to the three different categories of individuals. Dominant and subordinate individuals compose the broader category of individuals “fed subjects” and non-fed subjects are the rest of the adult females in the group. We selected one top-dominant and one top-subordinate in each group.

Training phase before the onset of the study

The food provisioning was dispatched using personalised wooden boxes that we opened with a remote control when the fed subjects touched the box. Individual boxes personalisation consists of wooden flag covers with unique colour patterns that individuals learnt to recognise when presented two separated boxes separated two metres from each other. We considered the different fed subjects’ success in choosing the right box when they performed their right choice above 75% of the times during training sessions. All this was required for the conduction of the experiment (2 feeding sessions per day).

Similar training was conducted on vervet monkeys previously by other researchers at the IVP study site not provoking any perturbation of the wellbeing of the individuals (Borgeaud and Bshary, 2015; Arseneau-Robar *et al.*, 2016; Borgeaud *et al.*, 2017; Bono *et al.*, 2018; Canteloup, Hoppitt and van de Waal, 2020).

Food provisioning

The mix of food aimed to offer fast-burning energy through the apple, and slower burning carbohydrate-based energy of the corn. The timing an individual needed to ingest apple with corn was much higher than apple alone, so we avoided inserting corn in the second feeding to avoid other individuals interfering with the fed subject due to a more elevated group activity. This was because during the training phases we realised that the first feeding session offered more time for feeding sessions since the monkeys were either still awakening or grooming at the sleeping site, which contrasted with the second feeding session (about 3 hours after the termination of the first feeding session), as at these hours general the group was actively foraging and moving. Each session was carried out swiftly (10-15 minutes) to avoid the fed subjects' isolation from the rest of the group. By isolation, we mean that the subject being fed could not catch up with the rest of the group once the feeding session had terminated. This was not the case because the experiment was conducted during the dry season when group spread of the groups is maximum (personal observation) and this created ample opportunity to proceed with the feeding sessions discretely so the subject could eat the food swiftly and neighbours would not bother (as this could elicit attention and even chases to steal the food). We ensured the absence of neighbours as an audience to avoid provoking/eliciting undesired behaviour reactions of third parties.

Phases of study

The mix of food aimed to offer fast-burning energy through the apple, and slower burning carbohydrate-based energy of the corn. The timing an individual needed to ingest apple with corn was much higher than apple alone, so we avoided inserting corn in the second feeding to avoid other individuals interfering with the fed subject due to a more elevated group activity. This was because during the training phases we realised that the first feeding session offered more time for feeding sessions since the monkeys were either still awakening or grooming at the sleeping site, which contrasted with the second feeding session (about 3 hours after the termination of the first feeding

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Data collection

We collected data on all female individuals (of all categories: fed subjects and non-fed subjects) during all study phases. We considered a minimum of 40 minutes gap for consecutive focal collection on a given individual to avoid individuals' over-representation of behaviours. When the dominant and subordinate fed subjects were not fed during a treatment phase (for the dominant, when the subordinate was fed; for the subordinate, when the dominant was fed), their grooming behaviour counted when they were giving grooming to another female that incorporated that grooming in the focal data as grooming received. If, on the contrary, fed subjects that were not being fed received grooming from any other adult female in the group, it was their partner who has incorporated as grooming behaviour as grooming given. Likewise, any behavioural data that was collected on the fed subjects while they were not fed was not used for activity budgets except in the cases above mentioned. Because the category of individuals non-fed subjects was never fed, the data that was collected during the treatment phases of dominant and subordinate fed were merged into one single phase for the analysis (treatment phase). We collected data on all female individuals (of all categories: fed subjects and non-fed subjects) during all study phases. We considered a minimum of 40 minutes gap for consecutive focal collection on a given individual to avoid individuals' over-representation of behaviours. When the dominant and subordinate fed subjects were not fed during a treatment phase (for the dominant, when the subordinate was fed; for the subordinate, when the dominant was fed), their grooming behaviour counted when they were giving grooming to another female that incorporated that grooming in the focal data as grooming received. If, on the contrary, fed subjects that were not

being fed received grooming from any other adult female in the group, it was their partner who has incorporated as grooming behaviour as grooming given. Likewise, any behavioural data that was collected on the fed subjects while they were not fed was not used for activity budgets except in the cases above mentioned. Because the category of individuals non-fed subjects was never fed, the data that was collected during the treatment phases of dominant and subordinate fed were merged into one single phase for the analysis (treatment phase). Focals consisted of a sequence of 10 data points collected every 2 minutes while following an individual and are collected in three different time zones (TZ), each one with an approximated duration of 4 hours. Time zones were adapted to the length of the days depending on sunrise-sunset hours. Focals were only included in the models when at least 8 points of the possible 10 were collected. Focal collection was organised to have all individuals sampled evenly across different time zones, in all study phases.

Group	KB	AK	BD	NH
Adult females	5	4	11	6
Total individuals	12	23	46	33

Table 1A. Number of adult females and total individuals in each study group.

Group	Dominants Fed Subjects	Subordinates Fed Subjects	Non-Fed subjects
AK	Gugu	Nkosikasi	Ndonsa, Mamoobi*
KB	Yenissei	Nessie	Aare, Amur, Mara*
BD	Oulik	Mielies	Asis, Engel, Gesels, Heerlik, Numbies, Pannekoekie, Prinses, Rissiepit, Snorretjie*
NH	Geneva	Pretoria	Gaya, Reva, Roma, Uppsala

Table 2A. List of names for the selected dominant and subordinate female fed subjects in each group. The individuals with an asterisk correspond to adult females on which we could not collect data due to injuries or shyness. Despite that, whenever our focal individuals engaged in an interaction with them, they still counted as adult females in our grooming analysis.

Group	Discarded individual	Reason
KB	Mara*	Too shy and peripheral for focal collection (focal data has never been collected on this individual)
AK	Mamoobi*	Badly injured (possibly due to predation) during the study period, she did not manage to keep up with the group during most of the time that the study period lasted
BD	Snorretjie*	Too shy and peripheral for focal collection

Table 3A. Females on which focal data collection was unfeasible

Group	Individual	Rank (Elo Score)
AK	**Gugu**	**0.688**
	Nkos	0.433
	Ndon	**0.221**
	Mamo*	0.037
BD	**Ouli**	**0.844**
	Asis	0.671
	Prin	0.475
	Heer	0.392
	Snor*	0.378
	Gese	0.349
	Enge	0.326
	Numb	0.270
	Pann	0.033
	Miel	**0.009**
	Riss	0.000
KB	**Yeni**	**0.600**
	Amur	0.436
	Aare	0.327
	Mara*	0.305
	Ness	**0.216**
NH	**Gene**	**1.000**
	Gaya	0.875
	Upps	0.729
	Pret	**0.466**
	Reva	0.125
	Roma	0.117

Table 4A. Elo-rating scores of all adult females (fed subjects and non-fed subjects in bold).

Group	Name	Age	Sex
BD	Neuchâtel	adult	male
BD	Chernobyl	adult	male
BD	Madagascar	adult	male
BD	Mvula	adult	male
BD	Hwahwa	adult	male
BD	Ububhibhi	adult	male
BD	Oulik	adult	female
BD	Prinses	adult	female
BD	Pannekoekie	adult	female
BD	Asis	adult	female
BD	Heerlik	adult	female
BD	Mieles	adult	female
BD	Snorretjie	adult	female
BD	Gesels	adult	female
BD	Numbies	adult	female
BD	Rissiepit	adult	female
BD	Engel	adult	female
BD	Little blind	juvenile	female
BD	Rooikat	juvenile	male
BD	Vakie	juvenile	male
BD	Pieperig	juvenile	female
BD	Hippie	juvenile	female
BD	Siele	juvenile	female
BD	Nurks	juvenile	female
BD	Rakker	juvenile	male
BD	Wurm	juvenile	male
BD	Bullebak	juvenile	male
BD	Vulkaan	juvenile	male
BD	Aapie	juvenile	female
BD	Potjie	juvenile	female
BD	Obelisk	juvenile	male
BD	Asseblief	juvenile	female
BD	Heilweis	juvenile	male
BD	Meerkat	juvenile	male
BD	Safari	juvenile	female
BD	Gaaf	juvenile	male
BD	Nooiens	juvenile	female
BD	Redelik	juvenile	female
BD	Eina	juvenile	female
BD	Ooetjies	baby	female
BD	Adder	baby	male
BD	Hasie	baby	female
BD	Ratel	baby	male
BD	Puolka	baby	female
AK	Hlokoloza	juvenile	male
AK	Heyi	juvenile	male
AK	Nyoni	juvenile	male
AK	Ginqika	juvenile	female
AK	Ghida	juvenile	female
AK	Gubha	juvenile	female
AK	Humusha	juvenile	male
AK	Hluhluwe	juvenile	male
AK	Nyanga	juvenile	female
AK	Ndiza	juvenile	male
AK	Mathimula	juvenile	male
AK	Ndawonya	baby	female
KB	Liffey	adult	male
KB	Yenessei	adult	female
KB	Mara	adult	female
KB	Amur	adult	female
KB	Nessie	adult	female
KB	Aare	adult	female
KB	Yalu	juvenile	female
KB	Yangtze	juvenile	male
KB	Avon	juvenile	male
KB	Mississippi	juvenile	male
KB	Arno	juvenile	male
KB	Malawi	juvenile	male
NH	Govu	adult	male
NH	Tweed	adult	male
NH	Uppsala	adult	female
NH	Geneva	adult	female
NH	Gaya	adult	female
NH	Pretoria	adult	female
NH	Roma	adult	female
NH	Reva	adult	female
NH	Xian	juvenile	female
NH	Tirroan	juvenile	male
NH	Rheban	juvenile	male
NH	Uji	juvenile	male
NH	Glastonberry	juvenile	male
NH	Xalapa	juvenile	female
NH	Praia	juvenile	female
NH	Zanzibar	juvenile	male
NH	Boston	juvenile	male
NH	Jixi	juvenile	male
NH	Rennes	juvenile	female
NH	Umtata	juvenile	male

AK	Cancun	adult	male	NH	Granada	juvenile	male
AK	Wolfie	adult	male	NH	Propiano	juvenile	male
AK	Atitlan	adult	male	NH	Bela-Bela	juvenile	female
AK	Gugu	adult	female	NH	Jeddah	juvenile	male
AK	Nkosikasi	adult	female	NH	Lima	juvenile	female
AK	Ndonsa	adult	female	NH	Ulaanbaatar	baby	male
AK	Mamoobi	adult	female	NH	Pruszkow	baby	male
AK	Geleza	juvenile	female	NH	Roslin	baby	male
AK	Unwabo	juvenile	male	NH	Reykjavik	baby	male
AK	Hola	juvenile	male				

Table 5A. Group composition including all individuals (any age-sex class) in all group of study.

Figure 2A. Remote-opening box with the personal flag of dominant adult female individual Yeni from Kubu group (KB) before provisioning the food.

Figure3A. Example of feeding sessions. Subordinate adult fed subject females during a feeding session having access to their box that contains the high-quality food supply. Mieles from BD group (left), and Nessie from KB group (right).

Figure 4A. Training period. Photo of the dominant fed subject female in NH group, Geneva, at the different stages of training, first with one box, and posteriorly presented with two boxes.

Activity	Behaviour
Feeding	Reaching, bite-chewing, searching, lick, drink
Resting	Sleeping, resting, self-scratching, auto-grooming, vigilant
Social	*Affiliative behaviours:* Grooming, being groomed, mouth to mouth, lip-smacking, infant handling, play, nurse infant *Agonistic behaviours:* stare-attack, take place, steal food, chase, grab, bite, steal baby, hand on top of the head *Sexual behaviours*: present, inspect sexual parts, mounting, masturbating, homosexual mounting
Moving	Walking, jumping, hopping, galloping, climbing, descending

Table 6A. Representation of the main behaviours that were collected in the focal data.

Group	Control-before	Treatment phase - Dominant fed	Treatment phase - Subordinate fed	Control-after
AK	2-28 July	1-12 August	16-26 August	6-29 September
KB	1-28 July	16-26 August	2-13 August	6-30 September
BD	1-18 August	29 August-10 September	12-24 September	5-27 October
NH	1-26 August	12-24 September	29 August-10 September	4-25 August

Table 7A. Schedule of the different study phases for each fed subject individual (dominants and subordinates) for each study group (AK, KB, BD, NH).

Phases of Study	Nº of focals per individual per TZ	Total nº focals (focals collected in 3 TZ)	Time observed (min)
Control before	4	12	120
Treatment dominant subject fed	8	24	240
Treatment subordinate subject fed	8	24	240
Control after	4	12	120
TOTAL	24	72	720

Table 8A. Sampling effort: data gathered during the different study phases. Note that these were the focals collected and a focal could range from 8 to 10 focal points, thus the resulting focal points for each individual were not exact as explained in the manuscript (also visible in the raw data file).

Group	Individual	Category individual 1	Category individual 2	Control before	Treatment	Control after
AK	**Gugu**	**Fed Subject_Dominant**	**Fed Subject**	**122**	**257**	**146**
AK	Ndon	Non-subject	Non-fed subject	118	495	149
AK	**Nkos**	**Fed Subject_Subordinate**	**Fed Subject**	**142**	**236**	**148**
KB	Aare	Non-subject	Non-fed subject	107	502	150
KB	Amur	Non-subject	Non-fed subject	124	475	135
KB	**Ness**	**Fed Subject_Subordinate**	**Fed Subject**	**127**	**287**	**156**
KB	**Yeni**	**Fed Subject_Dominant**	**Fed Subject**	127	287	156
NH	Gaya	Non-subject	Non-fed subject	114	499	116
NH	**Gene**	**Fed Subject_Dominant**	**Fed Subject**	**118**	**235**	**118**
NH	**Pret**	**Fed Subject_Subordinate**	**Fed Subject**	**117**	**236**	**120**
NH	Reva	Non-subject	Non-fed subject	129	489	115
NH	Roma	Non-subject	Non-fed subject	110	472	108
NH	Upps	Non-subject	Non-fed subject	120	488	128
BD	Asis	Non-subject	Non-fed subject	110	539	120
BD	Enge	Non-subject	Non-fed subject	127	503	127
BD	Gese	Non-subject	Non-fed subject	117	522	120
BD	Heer	Non-subject	Non-fed subject	128	500	130
BD	**Miel**	**Fed Subject_Subordinate**	**Fed Subject**	**129**	**249**	**119**
BD	Numb	Non-subject	Non-fed subject	113	512	120
BD	**Ouli**	**Fed Subject_Dominant**	**Fed Subject**	**120**	**247**	**118**

BD	Pann	Non-subject	Non-fed subject	107	478	119
BD	Prin	Non-subject	Non-fed subject	112	482	119
BD	Riss	Non-subject	Non-fed subject	125	496	130

Table 9A. Data collection (data points) during the different study phases on each adult female individual that formed part of the study.

			Activity			
Category	**Individuals**	**Study Phase**	**feeding**	**moving**	**resting**	**social**
Dom (fed subjects)	4	control-before	575	102	160	107
	4	treatment	354	95	339	234
	4	control-after	571	147	225	92
Sub (fed subjects)	4	control-before	619	117	127	143
	4	treatment	352	90	334	232
	4	control-after	674	65	170	106
Other (non-fed subjects)	15	control-before	1098	208	198	257
	15	treatment	5102	575	774	1001
	15	control-after	1020	258	345	263

Table 10A. Data that was available for the activity budget's analysis.

Activity budget model: feeding, resting, social, grooming given and moving

We provide here with an example of the model structure that we used for the different activity budgets.
feeding <- glmer(feed ~ PhaseNew*Category + (1|individual)+ (1|Group)+ (1|TZ), family=binomial, data=act1)

-*PhaseNew*: Phase of study (control-before, treatment, control-after).

-*Category*: Category of individuals: Fed and non-fed (within fed there are two sub-categories of individuals: dominants and subordinates).

-*Individual*: identity of each individual of study, subjects and non-subjects.

-*Group*: Identity of four groups where we conducted the experiments: AK, BD, KB, and NH.

-*TZ*: what we refer along the text as time period. Days were split in three even time slices containing all hours of daylight when data collection was conducted.

*The same model structure was used to evaluate activities of resting, social, grooming given, and moving.

Null model hypothesis testing: randomisation algorithm

We used a series of null model hypothesis approach and generated datasets based on randomisations to evaluate if the difference in grooming behaviours between the fed subjects and non-fed subjects phases was different in the observed dataset in comparison to randomisations (Croft *et al.*, 2011; Farine and Whitehead, 2015) based on the observed data. Observed data for each grooming parameter were obtained by subtracting the grooming during the treatment phase and the control before phase for the two different categories of individuals, subjects and non-subjects. We proceeded following these calculations, applied to the grooming parameter of accumulation of grooming partners (accumm. gr partners):

a1= accumm. gr partners *(study phase= control before & category = fed subjects)*
a2= accumm. gr partners *(study phase= treatment & category = fed subjects)*
b1= accumm. gr partners *(study phase= control before & category = non-fed subjets)*
b2= accumm. gr partners *(study phase= treatment & category = non fed-subjects)*

Following, we calculated the difference of the means of t observed data of each grooming parameter for the two categories of individuals (fed subjects and non-fed subjects):

$a = a2 - a1$ (fed subjects) $b = b2 - b1$ (non-fed subjects)

$t = \mathrm{mean}(a) - \mathrm{mean}(b)$ *(Observed)* *(`Prand <- sum(ran <= obs)/perms`)* *(Permuted)*

Where:
ran = randomised data
obs= observed data
perms= permuted data

We evaluated the significance of the differences by comparing the observed test statistic to the distribution of the randomized test statistic values, where an observed value is significantly different if it is greater or smaller than 95% of the randomized data (Farine, 2017). Therefore, we interpret both upper and lower significance thresholds following the ensuing criterion: "*the result is significant at Prand= 0.05 if 2.5% of the random values are greater than or equal to the observed value, or if more than 97.5% of the random values are greater than or equal to the observed value*" (Farine, 2017). We refer to Prand as the proportion of randomly generated values.

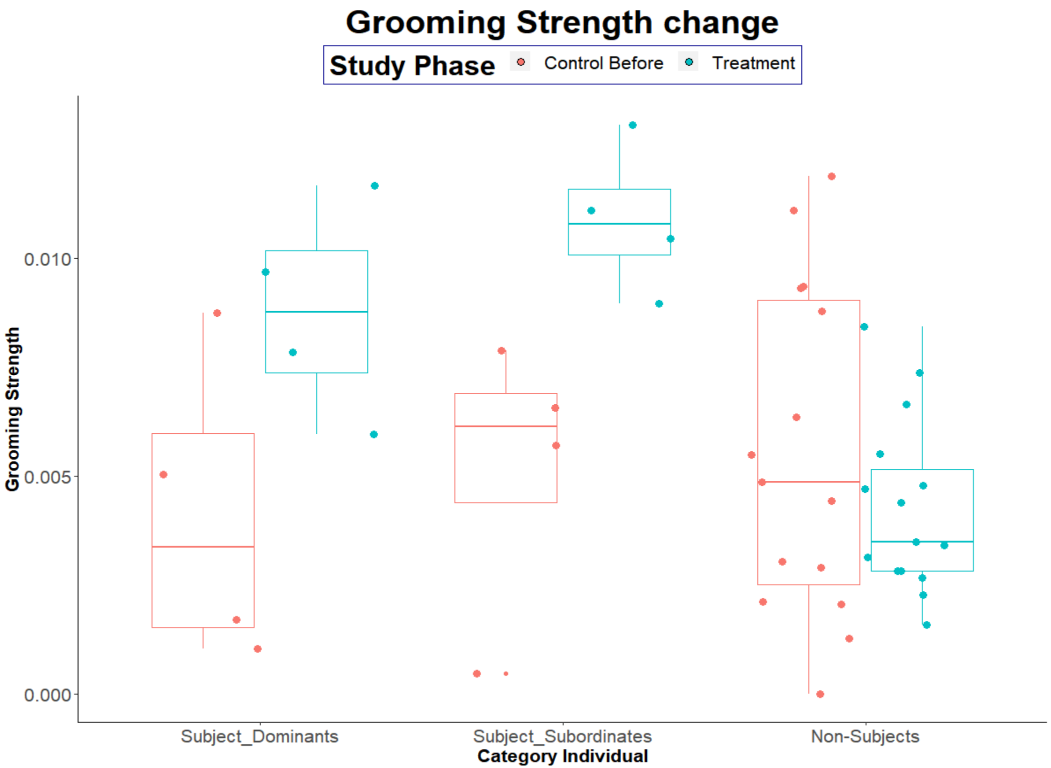

Figure 5A. Grooming strength for the different categories of individuals. Along with the x-axis, from left to right: dominant fed subjects (as Subject_Dominants), subordinate fed subjects (as Subjects_Subordinates) and non-subjects (as Non-Subjects). Along the y-axis, grooming strength. Plots in red colour correspond to the phase of study control-before and in blue colour to the treatment phase. Each dot represents the average for each individual within each category of individual.

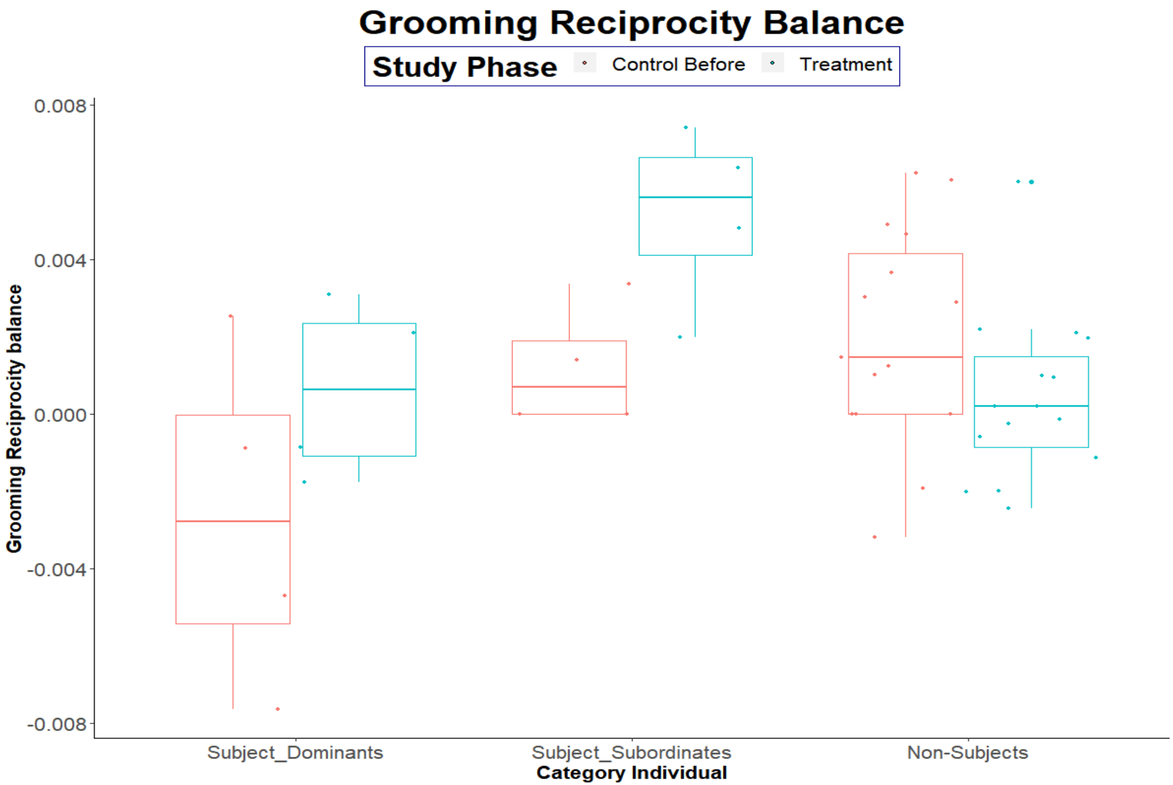

Figure 6A. Grooming reciprocity balance for the different categories of individuals. Along with the x-axis, from left to right: dominant subjects (as Subject_Dominants), subordinate subjects (as Subject_Subordinates) and non-subjects (as Non-Subjects). Along the y-axis, grooming reciprocity balance. Plots in red correspond to the phase of study control-before and in blue colour to the treatment phase. Each dot represents the average for each individual within each category of individual.

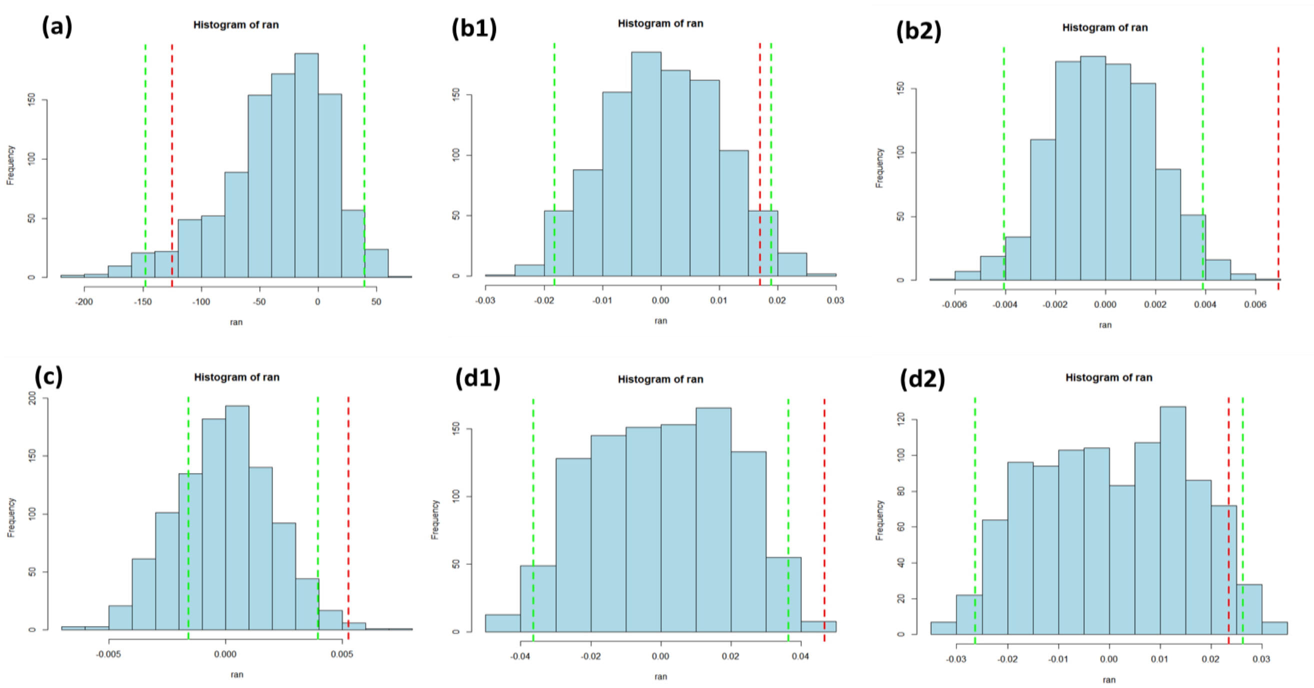

Figure 7A. Observed and randomised data: histograms (I). Starting from right to left, first row: a) Change in grooming partners, b1) Accumulation of grooming partners, b2) Grooming strength, and second row: c) Grooming reciprocity balance, d1) Grooming to bonded partners, d2) Grooming to high-rank partners. Dashed red line corresponds to observed data, and two dashed green lines to permuted data from observed data using the algorithm shown on page 5 and 6 between fed subjects and non-fed subjects. Discontinuous green lines contain the range of the permuted values, and discontinuous red line show the observed value (difference of the means of fed subjects minus difference of the means of non-fed subjects, each one of these differences calculates the difference for that category of individuals between treatment and control-before).

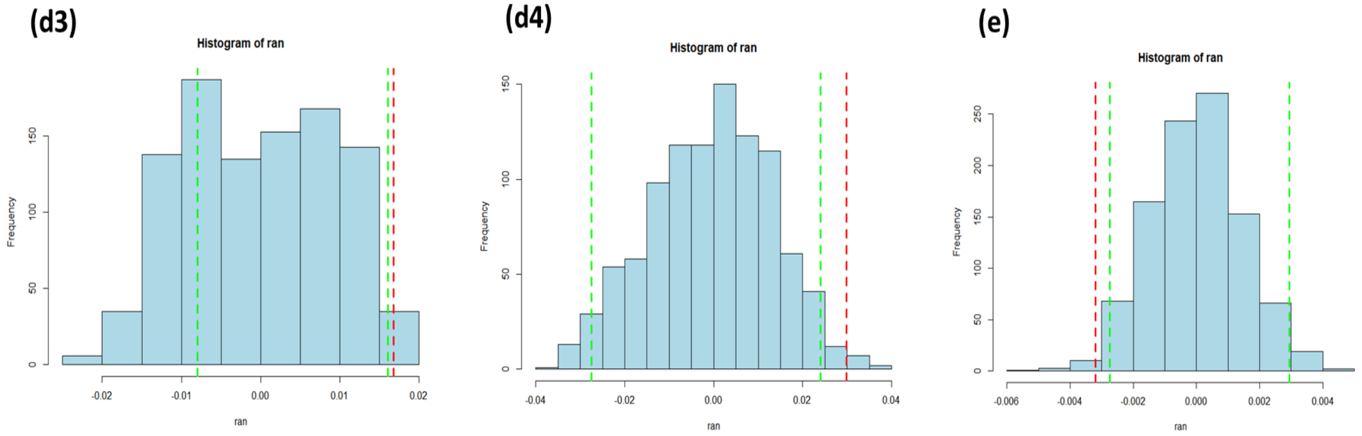

Figure 8A. **Observed and randomised data: histograms (II).** Starting from left to right, first row: d3) Grooming to kin partners; d4) Grooming to adult females; e) Carryover strength. Dashed red line corresponds to observed data, and two dashed green lines to permuted data from observed data using the algorithm shown in page 5 and 6 between fed subjects and non-fed subjects. Discontinuous green lines contain the range of the permuted values, and discontinuous red line show the observed value (difference of the means of fed subjects minus difference of the means of non-fed subjects, each one of these differences calculates the difference for that category of individuals between treatment and control-before, except in the carryover graph, that calculates the difference between control-after and treatment).

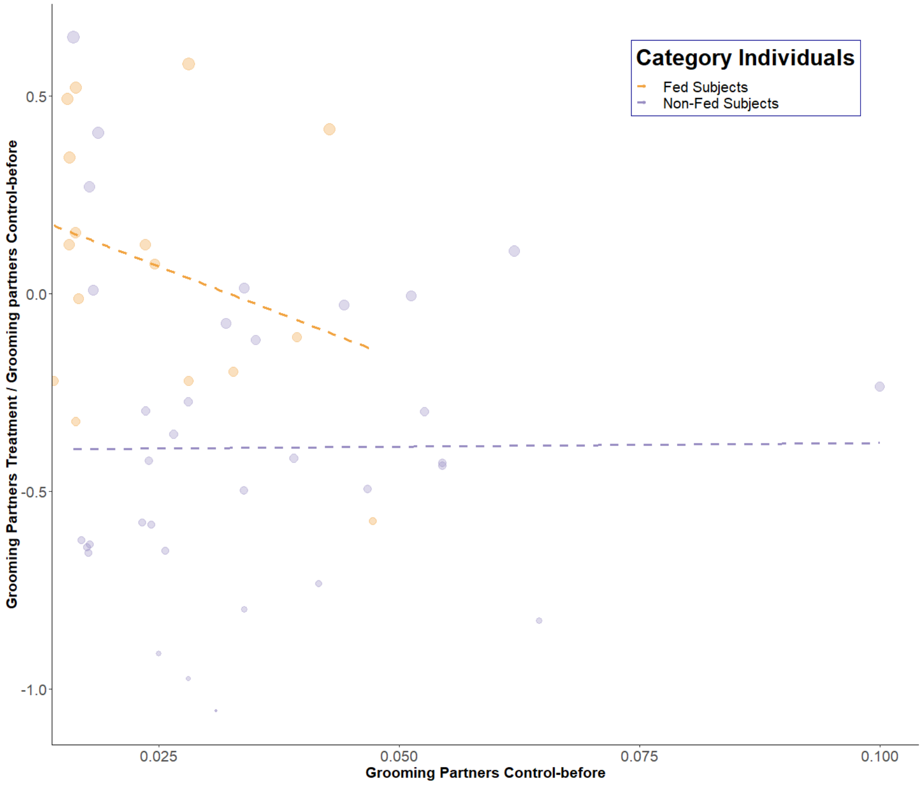

Figure 9A. Change in grooming social network of fed subjects and non-fed subjects between treatment phase and control-before. The y-axis is the log ratio of grooming given to partners during treatment and the control-before study phases. The x-axis is the grooming given during the phase control-before. The size of the circles represents the grooming given strength. The slope and dots showing the category fed subjects appear in yellow and the category non-fed subjects in purple.

Test	**Grooming variable**	**Cb**		**Treatment**	
		Subjects	**Non-subjects**	**Subjects**	**Non-subjects**
A	Change in grooming partners	NA	NA	NA	NA
B$_1$	Accumm. grooming partners	0.02682	0.02649	0.03236	0.01509
B$_2$	Strength	0.00411	0.00495	0.00998	0.00391
C	Grooming reciprocity balance	-0.0008	0.00170	0.00304	0.00032
D$_1$	Strength to bond	0.01065	0.03237	0.04649	0.02147
D$_2$	Strength to rank	0.02969	0.02790	0.04924	0.02403
D$_3$	Strength to kinship	0.01678	0.02596	0.02532	0.01774
D$_4$	Strength to adult females	0.00592	0.01868	0.03257	0.01543
E	Carryover effect (strength)	0.00694	0.00360	0.00341	0.00327
F$_1$	Grooming given (activity budget)	4.56307	5.74594	10.6214	14.12580
F$_2$	Grooming reciprocity balance	-27.472	8.34759	3.02379	30.56143

Table 11A. Control-before and Treatment average observed values for the category of subjects and non-subjects. Average observed values were computed by dividing the treatment value by the control-before value of each category of the individual to reflect the values of change in Table 3. Here we can see that in C and F_2 the values are negative because control-before phase registered negative values.

CHAPTER 3. Drivers and outcomes in territory disputes: from ecological characteristics to numerical asymmetry in vervet monkeys

Manuscript in preparation for the invitation of a theme issue of Philosophical Transactions B on "Intergroup conflict: origins, dynamics and consequences across taxa" edited by Carsten K.W. De Dreu and Zegni Triki

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MGG conceived the idea, MGG and MdG prepared and analysed the data,
MGG wrote the manuscript with the help of MdG, RB, and EvdW

3.1. Abstract

Neighbouring groups compete over access to resources and territories in intergroup encounters. These encounters constitute public goods and collective action problems that primarily evolved due to the fitness benefits of safeguarding their territories regardless of individual free-riding. Factors like seasonality, spatial location or idiosyncratic value can shape the benefits and costs of contesting resources and the defensibility of attitudes, ultimately defining encounters' dynamics and outputs. We collected the location and outcome of intergroup encounters in four groups of wild vervet monkeys (n >

500). Subsequently, we evaluated the probability of encounter occurrence and outcome throughout the study area using a spatiotemporal approach by interpolating ecological measures based on vegetation availability (i.e., NDVI at 10 m^2 resolution, extracted from Sentinel 2) and core and overlapping areas. Our findings revealed that the probability of encountering a neighbouring group increased at locations with high relative values of vegetation availability, particularly within core areas. Although encounter outcomes were not influenced by ecological measures that integrated both groups' perspective, nor by the proximity to the group's core area, we found that smaller groups systematically won bigger groups. This suggests that more defection took place in bigger groups that did not manage to put together enough workforce of volunteers and resolve the social dilemma to cooperatively fight against the rival group. This study highlights the complexity of territorial disputes in non-human primates and the need to tackle them holistically.

Keywords: intergroup encounter, vervet monkey (*Chlorocebus pygerythrus*), Normalized difference vegetation index (NDVI), game theory, group size

3.2. Introduction

Group-living has evolved across the animal kingdom to lower predation risks while increasing the defensibility of food sources against competitors (Janson & van Schaik, 1988; Janson & Goldsmith, 1995; Markham & Gesquiere, 2017). Despite these benefits, animal groups experience intergroup competition with neighbouring groups to gain access to specific food resources and also with members of their group (Christensen & Radford, 2018; Willems, Arseneau-Robar, Schleuning, & van Schaik, 2015). Territorial disputes are widespread in group-living animals ranging from aggressive, lethal fights to tolerant and even cooperative encounters (termites, Thompson et al., 2020; lions, Mosser & Packer, 2009; banded mongooses, Furrer, Kyabulima, Willems, Cant, & Manser, 2011; meerkats, Dyble, Houslay, Manser, & Clutton-Brock, 2019; green wood hoopoe, Radford, 2008, 2011; bonobos, Lucchesi, Cheng, Janmaat, Mundry, & Pisor, 2020; Western lowland gorilla, Morrison et al., 2020). Hence, conflict management is an essential aspect of group-living animals, where strategic decision making appears key to balance the detrimental effects of losing an encounter and the potential benefits of winning (review of factors; Beehner & Kitchen, 2007).

Territories typically emerge from animals' space use and ranging patterns associated with ecological and social conditions (i.e., food resources distribution, presence of predators and mates, proximity to competitors; Börger et al., 2006; Campos et al., 2014; Hamilton, Milne, Walker, & Brown, 2007; Mitchell & Powell, 2004; Seiler, Boesch, Mundry, Stephens, & Robbins, 2017) that have fitness implications like safety from predators and protection of food sources (Mitchell and Powell, 2012; Forrester, Casady and Wittmer, 2015). For instance, female chimpanzees (*Pan troglodytes*) exposed to high neighbouring pressure experienced low offspring survival and long interbirth intervals due to reduced access to nutritionally valuable food resources after conflicts (Lemoine et al., 2020). Similarly, both wild baboons (*Papio cynocephalus*) and capuchin monkeys (*Cebus capucinus*) limited their access to food resources after losing aggressive intergroup encounters (Markham & Altmann, 2012; Crofoot et al., 2008). The group's decision to engage in a territorial dispute will vary as a function of its relative fighting ability against the contestant (i.e., resource-holding potential or asymmetry in fighting ability between the two parties involved in the dispute, Maynard-Smith & Parker, 1976) and its ability to cohesively react against rivals (Batchelor & Briffa, 2010; Crofoot, Gilby, Wikelski, & Kays, 2007; Harris, 2010; Van Belle & Scarry, 2015). By gauging information on weaponry and numerical superiority animal groups likely ponder their capacity to out-power any rival (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Dyble et al., 2019; Mosser & Packer, 2009; Roth & Cords, 2016; Scarry, 2013; Scarry & Tujague, 2012). Further, groups' predisposition to fight hinges on resource distribution, population density information (Jolly *et al.*, 1993; Kitchen, Cheney and Seyfarth, 2004; Thompson *et al.*, 2017), territory use and the geographical location, e.g. frequency of home range use, centre, core-area or overlapping (Crofoot et al., 2007; Furrer et al., 2011; Koch, Signer, Kappeler, & Fichtel, 2016; Markham et al., 2012; Markham, Guttal, Alberts, & Altmann, 2013; Willems et al., 2013). If group living animals adapt travelling routes to resources' abundance (Janmaat et al., 2006; Janson & Byrne, 2007a; Pochron, 2005) one could assume such challenges to lie on cognitive abilities that touch on memory and preference values (Rosati, 2017). In that view, animals may be able to integrate a gradient of preference values in the perception of different areas (Barrett, 2006) based on how relevant are these areas to them.

Hence groups may make use of their territories in idiosyncratic ways, i.e. core-areas that are frequently used and harbour highly valued resources may elicit intense defensiveness adjustment against rival groups (Asensio, Schaffner, & Aureli, 2015; Brown, 2013; Kaufmann, 1983; Samuel, Pierce, & Garton, 1985; Scarry, 2013; Vander Wal & Rodgers, 2012). The importance that a group may attribute to a given area might, to some extent, rely on the energy intake it offers (Chapman, Wrangham and Chapman, 1995), which has important fitness connotations (Morales *et al.*, 2010). Beyond the sheer net energy retrieval potential, territories might be worthy concerning how efficient and safe from predators foraging can be (Schoener, 1971; Stephens and Krebs, 1986), or how suitable the development of important activities like resting and socializing is (Lehmann, Korstjens and Dunbar, 2007; Dunbar, Korstjens and Lehmann, 2009). Accordingly, group-living animals have spatial memory abilities that integrate resources' information and develop familiarity to home range areas (Di Fiore & Suarez, 2007; Janson & Byrne, 2007; Koch, Signer, Kappeler, & Fichtel, 2016a; Noser & Byrne, 2007; Sigg & Stolba, 1981; Vlasak, 2006). Therefore, territoriality is adaptive because it warrants benefits that greatly outweigh the costs of maintaining it (Brown & Orians, 1970; Brown, 1964; Cheney, 1992).

Generally, overlapping areas constitute buffer zones that help to establish boundaries and protect core areas (Bonadonna et al., 2017; Di Fiore & Suarez, 2007; Eckardt, Stoinski, Rosenbaum, & Santymire, 2019; Mech & Harper, 2002; Wartmann, Juárez, & Fernandez-Duque, 2014; Wrangham, Crofoot, Lundy, & Gilby, 2007) and can concentrate encounters between neighbouring groups (Mech, 1994; Tórrez-Herrera, Davis, & Crofoot, 2020). Also, animal movement is in synchrony with the resources that territories hold (Janmaat, Byrne, & Zuberbühler, 2006; Janson & Byrne, 2007; Pochron, 2005) evidencing cognitive capacities that allow adaptation of territory usage to ecological variation (Janmaat et al., 2006; Janson, 1998). Because territories elicit disputes between groups, this posits a social dilemma that could be interpreted as an N-players game (n-PG) (Archetti & Scheuring, 2010; Nunn & Lewis, 2010; Olson, 1965). This dilemma is a type of collective action problem (CAPs) as the members of the group are challenged to safeguard their territory from intruders (Willems et al., 2015). One possible avenue of n-PG is the volunteer's dilemma (Archetti, 2009; Diekmann, 1985) in which a public good is produced if, and only if, at least some individuals of the group volunteer to assume the costs of cooperating. Consequently, intergroup encounters between neighbouring groups are a CAP where group members can volunteer and play the strategy of defending the territory to repel rival groups while assuming potential fitness costs like injuries (Kingma, Santema, Taborsky, & Komdeur, 2014; Langergraber et al., 2017; Willems & van Schaik, 2015). Winning contests renders obvious direct benefits like staying and maintaining an area and its resources (Crofoot *et al.*, 2007; Thompson *et al.*, 2017) and indirect ones through reproductive success enhancement thanks to out-competing rivals (Bowles & Gintis, 2011; Choi & Bowles, 2007; Wrangham, 1999). Alternatively, losing contests and access to geographical ranges is burdensome and can impose longer travelling distances to forage (Batchelor & Briffa, 2011; Crofoot, 2013; Markham et al., 2012; Scarry & Tujague, 2012; Wrangham, Wilson, & Muller, 2006). This form of cooperation between group members may have facilitated the evolution of parochial altruism, group cohesion and joint-action (Choi & Bowles, 2007; Willems et al., 2013; Willems & van Schaik, 2015). On the other hand, assuming its potential risks may have contributed to the evolution of communication, peaceful coexistence and tolerance, permitting intergroup conflict prevention (Bowles, 2006, 2009; Choi & Bowles, 2007; Ham, Hedwig, Lappan, & Choe, 2016; Lemoine et al., 2020; Pisor & Surbeck, 2019; Radford, 2011; Robinson, 1979; Rusch, 2014). Altogether, the array of behavioural signatures around CAP portrays an interesting mix of n-PG that involves cooperation and perception values (Enquist & Leimar, 1987; Maynard Smith, 1979).

Because different individuals' motivation –due to age, sex, rank, etc.- to participate may vary among all group members, free-riding happens (Crofoot & Gilby, 2012; Dugatkin, 1990; Nunn & Deaner, 2004; Nunn & Lewis, 2010; Willems, Hellriegel, & van Schaik, 2013; Willems & van Schaik, 2015) and create payoff asymmetries (Furrer et al., 2011; Maynard Smith, 1974; Maynard Smith & Parker, 1976). And yet, intergroup encounters involving collectives constitutes a form of group cooperation (Archetti, 2009; Archetti et al., 2011; Willems et al., 2013; Willems & van Schaik, 2015). Since territories have the potential of warranting fitness, one could expect that some areas to be more important than the average because the overall group perception of resource value is higher, because of strategic interests lay, the accumulated knowledge or territory use habits attribute special significance (Enquist & Leimar, 1987; Janmaat, Byrne, & Zuberbühler, 2006; Janson & Byrne, 2007; Pochron, 2005).

In that frame, cognitive-based subjective perception of resources' value is built on past experiences and learning feed memory systems which shape decision-making and affect intergroup conflict dynamics (Arseneau-Robar et al., 2018; Enquist & Leimar, 1987; Langergraber et al., 2017; Trivers, 1972; Willems et al., 2015; Wrangham, 1980; Wright, 2007).

Vervet monkeys (*Chlorocebus pygerythrus*) live in female-bonded societies where the preservation of ones' territory- and its patchily-distributed resources- are key to females' fitness and therefore worth defending in encounters (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017; Arseneau-Robar et al., 2016; Cheney & Seyfarth, 1987; Cheney, 1992; Jolly et al., 1993; Kinnaird, 1992; Perry, 1996; Wrangham, 1980). Alternatively, males' fitness is contingent on access to mating partners although their defence of territories may have been coopted as hired guns (Fashing, 2001; Hill, 1994; Kinnaird, 1992; van Schaik et al., 1992; Wrangham, 1986) or as a case of intersexual cooperation (Arseneau-Robar, Müller, Taucher, van Schaik, & Willems, 2016). As we know, behavioural outputs can illustrate intergroup dynamics and shed light on the interplay of ecological and territorial factors of economic value. Here, we aim to disentangle the role of territorial and ecological factors in the spatial occurrence and winning-losing dynamics of intergroup encounters of four wild groups of vervet monkeys from 2016 to 2019. To better comprehend intergroup encounters we address two concrete questions: where do encounters happen concerning ecological (A) and ownership aspects (B)? In addition, which factors are determinant for groups to win the contests? To investigate the *where question*, we use NDVI (Normalized Differentiation Vegetation Index) as a proxy of food availability (Arseneau-Robar et al., 2017; Willems, Barton, & Hill, 2009; Willems & Hill, 2009) and establish three ecological variables to evaluate their weight on the spatial occurrence of intergroup encounters. NDVI is a measure of photosynthetic activity that has been used to study vegetation quality, phenology and primary productivity in savannahs (Willems et al., 2009), littoral forests (Donati et al., 2020) and tropical forests (Pettorelli et al., 2011), being a valuable proxy of food availability (Blersch, Bonnell, Barrett, & Henzi, 2021; Willems, 2007; Willems & Hill, 2009).

First, we calculate the NDVI value of the intergroup encounter location relative to the average of a groups' territory to see if vervet monkeys integrate the wholeness of their territory into the value of a specific area in what would be a *relative value perception here and now* (A1), and expect higher frequencies of encounters in zones of higher value. Second, we study the influence of the encounters' location current NDVI as the average value for a year as a *wider time scale perception* (A2). If groups' perception value relies on a longer time scale quality of an area, this would suggest additional layers to the *here and now* occurrence of encounters' occurrence (*average quality across time perception*). Third, we calculate the maximum NDVI of an encounter area and maintain that measurement across time independently of when the encounter occurs (A3). All these calculations are done from the perspective of the focal group and the perspective of the encounter group is integrated by dividing the focal by the encounter groups' values for each measurement. If vervet monkeys base their perception of value on the maximum potential an area can hold at any time, these areas would be worth defending. These aspects (A1-3) could inform about vervet monkeys' territory processing abilities as primates possess large-scale spatial knowledge (Boesch & Boesch, 1984; Janmaat et al., 2006; Janson, 1998; Noser & Byrne, 2007; Sigg & Stolba, 1981) and how they affect territoriality. This would likely influence decision-making processes and suggest cognitive abilities in the integration of information sources, and at different time scales (Janmaat, Byrne and Zuberbühler, 2006). Further, we assess the spatial occurrence of encounters relative to ownership (B). For that, we study overlapping zones (B1) (Bermejo, 2004; Caillaud et al., 2014; Willems & van Schaik, 2015), which we expect to concentrate more encounters based on field observations and their importance as buffer zones (Mech, 1994), and core-areas (B2), that are those that are more frequently used.

Finally, we investigate which factors may influence who wins the encounters and we consider a mix of ecological and territorial variables likely to play a role in conditioning groups' motivation to outcompete their rivals and win the contests. For that, we consider the ecological variable A1 and measure the relative value of an encounter area from the perspective of the focal group and compare it to that of the encounter group. Again, each measurement involves the two groups' perspectives on a given area relative to their territories, and a more positive value would indicate that the encounter area is of more relative importance to the focal group (A1). As a second ecological variable, we use the maximum NDVI of the year on a given encounter area and calculate the relative value for each group by dividing the focal groups' value by that of the encounter group (A3). We hypothesize that these two variables are influential for groups' value perception so that they tip the balance toward winning outcomes. As territorial variables, we consider the following: category of area (core, not core; B2.1), relative distance to the core (minimum distance to the core of focal group divided by that of the encounter group; B2.2), and relative intensity of use (scaling of how much the focal group uses the area of the encounter divided by that of the encounters' group;(B3) (Table 1.A. in Appendix with ecological and ownership terms defined). We expect to find a residence effect (Haley, 1994; Koch, Signer, Kappeler, & Fichtel, 2016b) bearing an influence so that groups win more "at home", or closer to core-areas (shorter distance to the core) and proximity to highly-used areas. These concepts may allow us to assess how value perceptions might vary with the geographical and territory space dimension. Furthermore, if vervet monkeys won more at home this could illustrate a sort of Bourgeois effect whereby vervets would be keener Hawk strategy player when being territory owners, and Dove strategy players when being away (Maynard Smith, 1982). At last, we consider group size as the number of adult females in a group as a likely factor helping bigger groups to win smaller ones (Beehner and Kitchen, 2007; Harris, 2010). Altogether, we bring in ecology and territory-use aspects to peel off the layers that shape groups' perception values on intergroup conflicts' occurrence and some important factors that may allow claiming victories.

3.3. Methods

3.3.1. Study site and study subjects

Data were collected at the Inkawu Vervet Project, in Mawana Game Reserve (KwaZulu-Natal, South Africa, S 28° 00'; E 031° 12') from January 2016 to October 2019. The habitat type of the study area is primarily savannah interspersed with occasional woodland patches. The diversity and richness of plant species increase near the seasonal Swart-Mfolozi River that crosses some groups' territories creating *dongas* or *gullies* (steep-sided ravines formed by water erosion; Podwojewski, Janeau, Caquineau, & Hughes, 2020). We studied four neighbouring groups of habituated wild vervet monkeys: Ankhase (AK), Baie Dankie (BD), Crossing (CR) and Noha (NH). Group sizes ranged between 17 –67 individuals of all age-classes (average ± s.d= 38.3 ± 5.7 total), of which between 4 – 21 were adult females (average ± s.d= 10.5 ± 2.5). All individuals were individually identified with facial and body features. Of all groups, we selected intergroup encounters between four dyadic group combinations based on shared territory overlap and availability of data: i) AK-BD, ii) AK-NH, iii) BD-NH, and iv) BD-CR (N_{total}= 540 IGE, average ± s.d per group dyad=135 ± 52.6 IGE).

3.3.2. Behavioural observations and intergroup encounters

The data was collected from February 2016 through October 2019 on all habituated groups using handheld devices (Palm Zire 22 and HP Travel Companion iPAQ rx5935) and Pendragon 5.1 software. We considered intergroup encounter context whenever two groups approached within 100 meters and both became aware and reacted to each other's presence (Arseneau-Robar et al., 2018; Arseneau-Robar et al., 2017). Whenever encounters started, we recorded the GPS location of the focal group, time and identities of the focal and encountered groups. Since encounters in vervet monkeys can involve a wide range of aggressive and antagonistic behaviours (Arseneau-Robar et al., 2016), we collected the behaviour of all visible individuals from the focal group on an all-occurrence basis during encounters (i.e., vigilance, vocalisations, the distance between groups, affiliative-grooming, mouth to mouth, agonistic interactions- chases, attacks, face-offs, bites, and mating-between and within groups, Altmann, 1974). We determined the end of an encounter when one of the groups stayed in the area and the other one abandoned it (i.e., the former group was displaced by the first one, Arseneau-Robar et al., 2017; Majolo et al., 2020). Thus, we considered the group that stayed in the encounter's location as the *winner* and the group that was displaced as *looser* (Arseneau-Robar et al., 2017). Occasionally, we could not determine a clear outcome of the encounter because both groups tolerated each other and one or both took different directions without being displaced so we classified these encounters as draws (Arseneau-Robar et al., 2016). All animals in the different study groups were individually recognized and observers that collected the data (research assistants, PhDs, and postdocs) after a minimum inter-observer reliability agreement of 80% Cohen's Kappa (Cohen, 1960).

3.3.3. Ethical note

All individuals of all groups were fully habituated when the data was collected not involving any direct human-monkey interaction. Ezemvelo Wildlife Board (Kwazulu-Natal, South Africa), the University of Cape Town, and the van der Walt family that own Mawana Game Reserve where the IVP is located granted ethical permission for the collection of any data that adheres to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research (Buchanan *et al.*, 2012).

3.3.4. Satellite imagery

We extracted remotely sensed information on plant phenology from Copernicus Sentinel-2, a satellite launched by the European Space Agency in 2015, that takes global snapshots of the Earth at 14-day intervals with a resolution of 10 m^2 (Skidmore *et al.*, 2015). Since remote sensing images were not recorded on the exact date of the encounters, we estimated the availability of vegetation of each quadrat using the closest remote sensing record to the date in which each IGE was observed. On average, the time frame between the encounters' occurrence and its associated satellite image was 8.97 ± 7.45 days. We selected satellite images with a cloud cover below 15% to enhance the accuracy of our estimations on vegetation availability (Pettorelli *et al.*, 2011).

3.3.5. Data analysis

We estimated the study groups' home ranges using the R package *adehabitatHR* 0.4.15 and the Kernel Density Estimation (hereafter "KDE") method with the first GPS location of each focal sample (i.e., 30 min intervals between GPS locations; Calenge, 2006). We defined a group's home range as the 95% KDE isopleth and core area as the 50% KDE isopleth (Willems et al., 2009). Thus, we considered that an encounter took place within the core area of one of the study groups if it fell within the 50% isopleth of their KDE. Additionally, we calculated the distance of each encounter location to the core area of each group involved in such encounter and divided the former by the first one as an indicator of relative proximity to the focal group's core area (hereafter "relative proximity to the core"). Similarly, if an encounter fell within the 95% KDE isopleth of two or more groups we considered that encounter to take place within an overlapping area. If the encounter fell within the 95% KDE isopleth of only one group we considered that encounter to take place within a non-overlapping area. Subsequently, we generated a grid cell of 50x50-m^2 covering the home ranges of the study groups. We used the satellite images abovementioned to calculate the mean Normalized Diversity Vegetation Index (hereafter NDVI) for each quadrat and each recorded date as the resultant coefficient between earth surface reflectance patterns in the red and near-infrared regions of the electromagnetic spectrum (Tucker et al., 2005; Willems, Barton, & Hill, 2009). We estimated the ecological value of each quadrat by calculating three metrics derived from mean NDVI measurements: (1) absolute maximum NDVI per year (hereafter "maximum annual NDVI") as the maximum NDVI recorded for each year in each quadrat; (2) relative NDVI per year (hereafter "relative annual NDVI") as the mean NDVI recorded in a given quadrat during an encounter day divided by the mean annual NDVI of the group's home range; and, (3) relative NDVI per day (hereafter "relative daily NDVI") as the mean NDVI recorded in a given quadrat during an encounter day divided by the mean NDVI of the group's home range during the day of the encounter (Fig. 1). Thus, we estimated the maximum ecological value of a quadrat, the long-term ecological value and the short-term ecological value of each quadrat of the study area. In addition, we calculated the relative ecological value of a given quadrat for the focal group concerning the encounter group by dividing the relative annual and daily NDVI of that quadrat for the focal group by the relative annual and daily NDVI of that quadrat for the encounter group (hereafter "annual ecological value between groups" and "daily ecological value between groups" respectively). We calculated all metrics using QGIS 3.12.2.

We calculated the intensity of use of a given quadrat as the proportional number of GPS locations collected within such quadrat concerning the number of GPS locations collected across the home range of the study group (similar to the "marginality index", Lucchesi et al., 2020), and the "familiarity index"; Jang, Boesch, Mundry, Ban, & Janmaat, 2019). Subsequently, we divided the focal group's intensity of use of a given quadrat by the encounter group's intensity of use of such quadrat to infer its "relative intensity of use". Lastly, we differentiated between mating and birth season in order to assess the influence of female reproductive status in the occurrence and outcome of encounters. First, during mating season, which ranges from February to August (Struhsaker, 1967), access to fertile females could be influencing tensions between groups (Kitchen, Cheney and Seyfarth, 2004). Second, during the birth season, which ranges from September to January (Seier *et al.*, 2000), the presence of newborns could increase the group's motivation to defend and protect their territory (Garber, Pruetz and Isaacson, 1993). (see Scheme NDVI and quadrats in Figure 1.).

3.3.6. Statistical analysis

We examined the dynamics of intergroup encounters in vervet monkeys by constructing and implementing statistical models with a binomial error structure and a logit link function using the function "*glmer*" of the *lme4* package 1.1–21 in R 3.6.1 (R Core Team, 2020; Bates, Maechler, Bolker, & Walker, 2014). First, we designed three generalized linear mixed models (hereafter "GLMMs"; Bolker et al., 2009) to determine the probability that an intergroup encounter occurred within a given cell. We used the presence/absence of encounters in quadrats as a binary response variable for the models. For each date in which we had recorded at least one encounter, we randomly selected 50 quadrats across the home range of the focal group to compare the characteristics of the quadrat where the encounter took place against the characteristics of the quadrats where encounters were not recorded for that day. Thus, we minimized issues derived from spatial autocorrelation in our dataset (i.e., adjacent quadrats can lead to convergence issues and Type I errors, Kissling & Carl, 2007) by randomly sampling quadrats. For each of these models, we used a different variable related to the ecological value of the quadrat where encounters were recorded (i.e., maximum NDVI, relative annual NDVI and relative daily NDVI) since these ecological variables happened to be correlated among them. In addition, we included a fixed set of predictors in the three models that indicated whether such quadrat: 1) fell within or outside the core area of the group; 2) fell within or outside overlapping areas between neighbouring groups; and, 3) the date when the encounter took place concurred with mating or breeding season. Each model included three two-way interactions between the variable accounting for the ecological value of the quadrat and each of the three transversal predictors. We included group ID and date ID as random effect variables, and random slopes for all predictors to keep Type I error rates at a nominal level of 5% (Schielzeth and Forstmeier, 2009; Barr *et al.*, 2013).

We accounted for two types of the season in our dataset, the mating season that ranges from February to August (Struhsaker, 1967), and access to fertile females may influence tensions between groups (Kitchen, Cheney and Seyfarth, 2004). We also considered the birth season, which spans from September to January (Seier *et al.*, 2000), and represent a moment of utmost vulnerability for babies, therefore constituting a possible motivational aspect to defend ones' territory (Garber, Pruetz and Isaacson, 1993). All animals in the different study groups were individually recognized and observers collected data after minimum inter-observer reliability agreement of 80% Cohen's Kappa (Cohen, 1960).

Second, we designed a GLMM to test the influence of a set of predictors in the outcome of encounters among neighbouring groups of vervet monkeys. We used winning/losing of encounters in quadrats as the binary response variable for the model. All the predictor variables included in this model aimed to incorporate the perspective of both groups regarding a given area. Thus, we included both the annual and daily ecological value proportional between groups (as explained above). Concretely, the predictors are an interaction of the distance to the core area with the annual NDVI value and the interaction of the distance to the core with the NDVI at the moment of the encounter, the relative intensity of use of the quadrat where the encounter happened, the season (mating, birth) and the number of adult females (highly correlated with adult males or total number of adults in the group, see Fig 2.A. in Appendix). We selected group ID as a random effect.

For all models, quantitative predictors were z-transformed to a mean of 0 and standard deviation of 1 before fitting the models. We visually checked that the distribution of the residuals was normal and homogenous (i.e., qq-plots were plotted against fitted values). To rule out collinearity between variables, we examined the variance inflation factor of the models using the function "vif" from the *car* packages (all the vif values in the models were below 1.3; Fox & Weisberg, 2011). We evaluated the stability of the GLMMs by comparing the estimates derived from a model based on all data with those obtained from models based on subsets that excluded levels of the random effects one at a time. We did not find that model assumptions were violated. In all cases, we compared the full model to a corresponding null model (with only random and control variables) using likelihood-ratio tests (i.e., "anova" function set to Chisq). When an interaction term had no significant effect, we ran a reduced model including only the main effects. Finally, if the likelihood ratio test for full and null model comparison was significant, we inspected the significance of each predictor variable using likelihood ratio tests comparing full models with reduced models without that variable, using the "drop1" function (Barr *et al.*, 2013).

3.4. Results

3.4.1. Models predicting the occurrence of encounters (A)

In our analysis of the first ecological variable (A1), we found that intergroup encounters concentrated more in areas with higher NDVI relative to that of the home range (full model VS null model: $\chi^2 = 15.054$, df = 7, p-value = 0.0035). This analysis also shows a trend in which overlapping areas concentrated more encounters (Est. ± SE= 1.402 ± 0.667, p-value=0.074), and of these areas an interaction with the relative NDVI variable (Est. ± SE= -0.245 ± 0.128, p-value=0.069). This model revealed the significance of the interaction of the core areas with the relative NDVI variable (Est. ± SE= 0.404 ± 0.118, p-value=0.009, see more details about all variables in Table 1). The model that addressed the current NDVI value to the average annual value (A2) disclosed that intergroup encounters were more frequent in areas of higher relative value (full model VS null model: $\chi^2 = 20.989$, df = 7, p-value = 0.0038) (see Fig. 2). In this model, the overlap area remains an almost significant trend that increases the encounter occurrence (Est. ± SE= 1.492 ± 0.661, p-value=0.056). Here, the NDVI variable of study (a2) and the interaction with core area significantly influenced the encounter occurrence (Est. ± SE= 0.339 ± 0.201, p-value=0.009, Est. ± SE= 0.429 ± 0.161, p-value=0.025). In the third model, we found that the ecological variable (A3) that considered the maximum NDVI value that a given area could express in a year did not influence the occurrence of intergroup encounters (full model VS null model: $\chi^2 = 11.386$, df = 7, p-value = 0.115). The only variable that marked a trend was the overlap area (Est. ± SE= 1.416± 0.685, p-value=0.077), indicating the encounters were more likely in these territories (see Table 1, Fig.2).

3.4.2. Outcome model (B)

This model was used with a smaller subset of the data because a significant proportion of the encounters did not register a clear outcome ($N_{clear\text{-}winner}=314$, $N_{No\text{-}clear\text{-}winner}=335$*).* This model was significantly different from the null model ($\chi^2 = 22.63$, df = 8, p-value = 0.003). The first ecological variable considered, the relative NDVI value indicative of the value here and now (A1), did not affect the outcome likelihood (Est. ± SE= 0.2 ± 0.21, p-value=0.26). The second ecological variable considered, the annual NDVI variable (A2) was a non-significant trend showing that groups were more likely to win when annual NDVI values were higher (Est. ± SE= 0.08 ± 0.16, p-value=0.58, see all results in Table 2). Of the different territorial variables (core area, distance to the core, and intensity of use: B2.1, B2.2, B3), none influenced the dynamics of winning, but group size, measured through the number of adult females was significant. As it turns out, the number of adult females influenced the winning output in an unpredicted fashion, so smaller groups were more likely to win (Est. ± SE= -1.2 ± 0.2, p-value=4.9e-5). Of all the interactions between the different predictors, none had a significant effect on the likelihood of winning (see Table 2).

3.5. Discussion

Territory defence in animal groups (including humans) links with food resources availability and access to areas for the development of relevant activities that permit animals to optimise their situation within their socio-ecologies (Bates, 1970; Burt, 1949; Campos et al., 2014; Hamilton et al., 2007; Maher & Lott, 2000). Although some studies have exposed that home ranges' use can vary across time (Janmaat et al., 2006; Janson & Byrne, 2007; Pochron, 2005), it is not clear how such fluidity could associate with the spatial likelihood of conflict occurrence and how winning outcomes may reflect groups' perception values. Here, we delved into different ecological aspects related to the vegetation abundance (using NDVI measurements) that serve as proxies of food abundance for vervet monkeys and found that an interplay of ecological and ownership factors underlie intergroup encounters' spatial occurrence. Specifically, relative NDVI home range values in core areas and annual NDVI (alone and in interaction with core areas) concentrate encounter locations in vervet monkeys in what may constitute a sort of "hot spots" where access to these areas is under dispute between neighbouring groups. In our investigation of the possible influential factors regulating the balance of outcomes, we demonstrate that the different ecological variables we selected, to which we applied a perspective that included that of the focal group relative to that of the encounter group, did not tip the balance towards winning or losing. Neither ownership factors did, although groups' capacity to win encounter seemed to be based on differences of group size accounted here as the number of females. Strikingly, differently than it would have been predicted, that is, that group size would help win contests as found in banded mongooses (Furrer *et al.*, 2011), we found that smaller groups were more likely to win intergroup encounters, similarly to the results shown by Lewis et al. in

Verreaux's Sifakas where group size negatively influenced individual participation (Lewis *et al.*, 2020) (group size as the number of adult females and outcome in Fig.1.A in App.).

While many studies provide important insights about interaction location between groups (Crofoot et al., 2007; Furrer et al., 2011; Tórrez-Herrera et al., 2020), our examination of four dyadic group relationships across four years provides important insights to discern which factors are pivotal for intergroup conflicts to occur on the spatial scale and for groups to win the contests. Our approach to encounters using three different measures of ecological value aimed to unwrap which factors are key to vervet monkeys by studying their effect on conflict occurrence. Concretely, we aimed at contributing to the understanding of how animals show preferences for certain territory areas relying on memory abilities (Di Fiore & Suarez, 2007; Janson & Byrne, 2007; Koch, Signer, Kappeler, & Fichtel, 2016b). In that context, it seemed appropriate the conception of ecological variables that had, each one, similar but also distinct subtleties, such as the value of a given area relative to that of the overall home range, relative to the annual value of a given specific location, and relative to the maximum possible in a year.

Using an ample record of the encounter, our analysis of the where question showed that vervet monkeys are more willing to fight to defend a territory in areas that can have important NDVI values relative to the annual value of the entire home range. This finding hints at a perspective of value that goes beyond here and now. This reveals that the perspective of value, therefore, resides in two components that represent building blocks of territory value recognition: value and territory (as ownership). Accordingly, a specific area that renders high productivity may be deemed in terms of goodness by integrating the entire home range into that evaluation. This kind of perspective likely rests on territory recognition capacities that stem from spatial cognitive capacities (Rosati, 2017) and make for decision-making and strategizing about territories beyond the short-term sightedness of here and now. Beyond, core areas interact positively with these variable constituting areas worth being fought for vervet monkeys. Additionally, we found that the relative ecological value of here and now did not elicit more defensibility alone, although these areas influenced encounter occurrence when in interaction with areas that were more frequently used (or core areas). If these areas alone had influenced encounter occurrence it would have not been all too surprising, since resource availability and energy intake can adjust defensiveness (Asensio et al., 2015; Brown, 2013; Scarry, 2013). Instead, it seems that the current value of an area did not represent enough stimuli.

This is interesting, although it would be interesting to evaluate further aspects related to the actual resources that exist at a given location such as the variance in the abundance of resources across blocks of time (month, year), the proximity to water, or the way they are distributes as has obvious connotations that condition access options so resources can be more or less monopolise by dominant individuals. Ultimately, it could be interesting to study the possible link between highly-frequented foraging areas with areas in which resting and social activities are concentrated most, which could suggest a preeminent role of females' knowledge or habits of territory use in general. If this was the case, this could indirectly point at the females' influence on the overall group behavioural dynamics in female bonded societies (Wrangham, 1980) as giving relevance to resources beyond the here and now may be crucial for survival. The interaction with core areas reveals that high current ecological values are particularly worthy if these occur in frequently used areas, which could be related to a higher sense of ownership or the knowledge of the territory modulating perception value and trigger defensibility.

Our study of the maximum ecological value of an area offers alternative interpretations. One could infer that areas' maximum potential if interpreted isolated do not raise perception values enough perhaps because these maximums are not long-lasting enough for groups' to significantly benefit. Perhaps these areas of high value deserve to be studied more deeply to better grasp which specific resources they consist of and how big a role can they play for vervet monkeys' fitness. It could be that those maximums consist of ephemeral resources that vervet profit from and exploit, without this, necessarily transcending into the configuration of perception value through attachment or valence (Enquist and Leimar, 1987; Barrett, 2006). Experimental studies could address this particular issue using playbacks and simulating neighbouring groups' presence (Furrer *et al.*, 2011; Kurihara and Muto, 2021) as a focal group approaches an area of outstanding maximums. An alternative interpretation could be that while beneficial, areas that offer important production peaks, if ephemeral, may be of less pronounced fitness relevance for vervet monkeys than the allocation of fallback foods that are key when resources are more stable across the territory (Marshall and Wrangham, 2007). The lack of relevance of areas with maximums is further supported if considered in combination with the fact that an interaction of core area or overlap areas did not elicit more encounters either, contrary to what we found in the other two ecological variables. This finding, although depicting a lack of significance deserves more attention as there may be interesting cognitive-based resource value perception-attribution underpinnings involved. These aspects could also have ramifications associated with certain cognitive limits that establish the need to prioritize certain zones and its associated behavioural relevance (some areas more used to rest, socialise, forage, forage at different times of the year, etc.). This would suggest that territories may be dynamic and perhaps worth defending for specific reasons.

Contrary to our predictions, our analysis of the potential factors modulating winning outcomes manifested a lack of influence of the two relative ecological variables that we measured concerning the focal group but also taking into account the encounter group perspective. The question of which factors drive groups to win more did not rely either on what we considered ownership aspects of the territory such as the core area and the relative distance to the core area. The idea of how cognition systems work about the perspectives of value begs for more studies on intergroup encounters to better understand investment and payoffs. One reason, again, may have to do with cognitive optimisation mechanisms that allowed or limited animals to computerize only certain inputs, of which, ecology-based ones may be more subject to variation due to seasonality, rather than possible alternatives that rely more based on group habits and tradition.

We propose that perception value over ecological or ownership aspects of the territory are manifested through encounter occurrence and outcome balances. Beyond the specifics of what these two distinct analysis reported, we highlight that these materialise during cooperative group behaviour (Beehner & Kitchen, 2007; Pisor & Surbeck, 2019). Independent of the potential for cheating that the defence of a public good represents (Willems et al., 2015), the encounter context serves as a platform to study n-PGs and volunteer's dilemma (Archetti & Scheuring, 2010; Diekmann, 1985; Dugatkin & Reeve, 1998; Nunn & Lewis, 2010). We interpret this in the light of group consensus or quorum (Furrer, 2009; Pyritz, 2011; Cronin, 2016) where we speculate that females are key players. Thus, it is here where the strong influence that smaller group sizes were remarkably more likely to win the contests. Again, which are the specific processes that permit collectives to display cooperative behaviours in relative synchrony (assuming that there are full-time and occasional defectors) represent unchartered waters. A way to gain a grip on these specific issues would be to evaluate individual performance to pinpoint with accuracy which individuals incur more constantly in the cost of volunteering and symbolically hold up the flag of the group during n-PG such as encounters where group coordination is crucial (Archetti, 2009; Arseneau-Robar et al., 2016; Noë, 1990; Nunn & Lewis, 2010). Here, subtle communication forms may have evolved for individual collectives to engage in fighting or not as a group.

Intergroup encounters characterize archetypical n-PG cooperative behaviours that allow group animals to preserve territories that warrant fitness, although less is known about how effective displays of cooperative behaviours coexist with defection when two groups' weaponry or resource holding potentials differ. This striking result opens relevant questions about how strategies may develop not only about winning but also around a lack of will or intent to win as a form of cheating or not enough volunteers joining in the volunteer's dilemma to gather momentum and defeat the opponent. We assume that either bigger groups suffer more the volunteer's dilemma conundrum and are therefore exposed to higher rates of defection (Olson, 1965) and therefore are worse off to resolve social dilemmas that require collective action and coordination. Notwithstanding, sophisticated communication strategies may underlie groups' decision-making, perhaps lead by some influential individuals that result in the group as a whole not engaging enough to outcompete a rival during an encounter. This latter idea opens interesting research avenues that could specifically target individuals in spatially prominent positions of the group while facing a rival to study possible subtle communication signals. These signals could be expected from cognitive machinery that permits value discrimination and is possibly linked to quorum consensus reaching and other forms of intelligence, as adaptive cognitive capacities are more likely to come in blocks (Maille and Schradin, 2016; Thornton and Boogert, 2019; Henke-von der Malsburg, Kappeler and Fichtel, 2020). If such behaviours exist or not is something not known at the moment, although this would be in line with the evolution of tolerance and sophisticated ways to avoid confrontation (Pisor & Surbeck, 2019). Another aspect that would merit attention is the differential importance that encounters may have, as although they are traditionally seen and accounted equally our study revealed some interesting insights and the opening of more questions worth pursuing, i.e. intensity or duration of the encounter. Finally, a long-term investigation of how dyadic groups co-evolve core and overlapping areas concerning the accumulated score-sheet of victories and defeats would shed light on the relevance of winning (and where wins take place). On the other hand, the concept of nagging behaviour (Stamps and Krishnan, 2001) could amplify the understanding of defeats and their implicit benefits in group dyadic relationships not necessarily driven by losing per se, but by persisting in not giving up.

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3.6. References

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3.7. Figures and tables

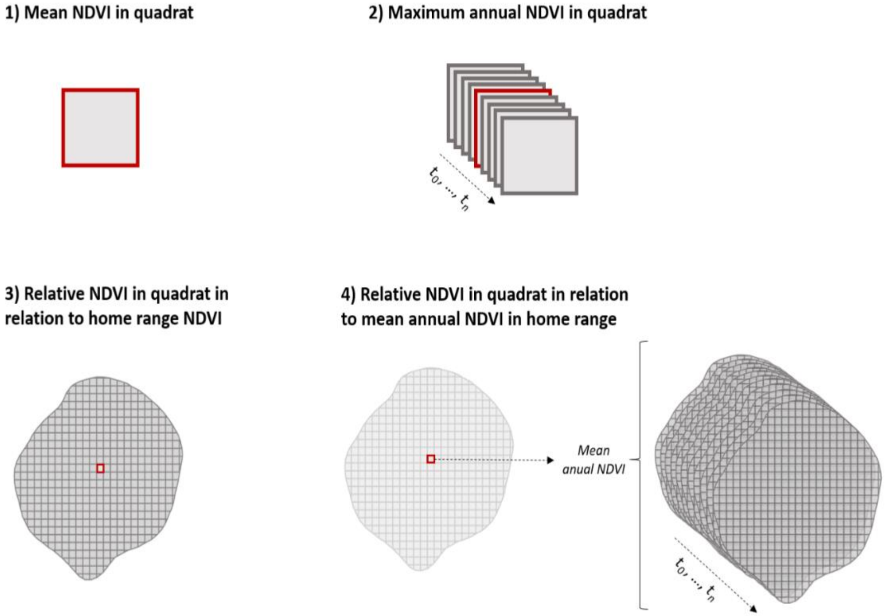

Figure 1. Scheme of how NDVI values were calculated. For each quadrat in the study area, we calculated: 1) the mean NDVI per recorded date; 2) the maximum annual NDVI; 3) the relative daily NDVI during encounter days; and, 4) the relative annual NDVI during encounter days.

	model *where* 1: ecological variable A1 χ^2 = 15.054, df = 7, *p*-value = 0.0035 **Relative daily NDVI* at quadrat in relation to NDVI in home range during IGE**			**model *where* 2: *ecological variable A2*** χ^2 =20.989, df = 7, *p*-value = 0.038 **Relative annual NDVI* at quadrat in relation to annual NDVI in home range**			**model *where* 3: ecological variable A3** χ^2 = 11.386, df = 7, *p*-value = 0.115 **Maximum annual NDVI* at quadrat**		
Predictor	**Est. ± SE**	**CI_{lower} – CI_{upper}**	***p*-value**	**Est. ± SE**	**CI_{lower} – CI_{upper}**	***p*-value**	**Est. ± SE**	**CI_{lower} – CI_{upper}**	***p*-value**
(Intercept)	- 3.029 ± 0.947	-5.076 – - 0.978		-2.816± 0.952	-4.923 – - 0.820		-3.119 ± 0.999	-5.014 – - 0.958	
NDVI variable*	0.137 ± 0.127	-0.204 – 0.245	0.130	0.339± 0.201	0.083– 0.689	**0.009**	0.030 ± 0.172	-0.177 – 0.566	0.169
Reproductive status	0.065 ± 0.256	-0.451 – 0.4383	0.848	-0.202 ± 0.257	-0.582– 0.224	0.373	0.046 ± 0.268	-0.495 – 0.451	0.922
Core area	0.620 ± 0.398	-0.276 – 1.636	0.229	0.708 ± 0.431	-0.280 – 1.646	0.189	0.611 ± 0.443	-0.381 – 1.477	0.188
Overlap area	1.402 ± 0.667	0.086 – 2.850	0.074	1.492 ± 0.661	0.296 – 3.077	0.056	1.416 ± 0.685	0.020 – 2.718	0.077
NDVI variable : Reproduc	0.015 ± 0.154	-0.232 – 0.261	0.923	-0.236 ± 0.243	-0.695 – 0.267	0.396	0.317 ± 0.204	-0.233 – 0.399	0.131

tive status									
NDVI variable : Core area	0.404 ± 0.118	-0.110 – 0.541	**0.009**	0.429 ± 0.161	0.049 – 0.618	**0.025**	0.306 ± 0.144	-0.458 – 0.588	0.149
NDVI variable : Overlap area	-0.245 ± 0.128	-0.237 – 0.226	0.069	0.207 ± 0.219	-0.071– 0.642	0.116	-0.095 ± 0.152	-0.274 – 0.326	0.541

Table 1. Summary of the results of the model examining the probability of encounter occurrence across the study area. Significant p-values are highlighted in blue and bold, and almost significant trends highlighted in grey. The predictor NDVI variable is different for each model as it the header of each one of the results' boxes show.

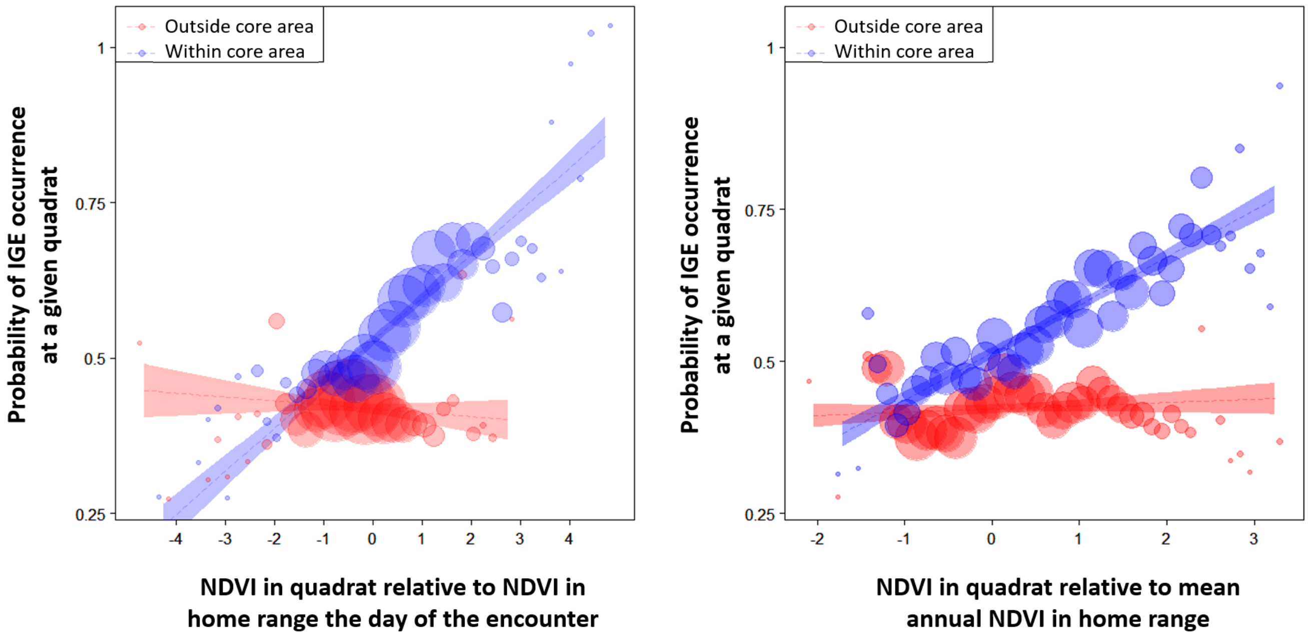

Figure 2. Graphical visualisation of the where model. Differences in the probability of encountering a group in a given quadrat as subject to the: (A) mean NDVI in quadrat relative to the mean NDVI in home range during the encounter day; and (B) mean NDVI in quadrat relative to the mean annual NDVI in the home range. The dashed lines represent the fitted model (with all other predictors being centred), dots represent the averaged probability of having an encounter, and their area corresponds to the number of encounters in the respective bin (N = 1 to 25 per bin). Shaded areas represent 95% confidence intervals of the fitted models.

Model outcome (winning/losing): χ^2 = 22.63, df = 8, *p*-value = 0.0038			
Predictor	**Estimate ± SE**	**$CI_{lower} – CI_{upper}$**	***p*-value**
(Intercept)	-0.503± 0.256	-1.00- -0.001	0.049
Relative NDVI	0.237±0.213	-0.180–0.654	0.266
Annual NDVI	0.088±0.160	0.226–0.401	0.584
Distance to core	0.223±0.171	-0.111–0.557	0.191
Intensity of use	0.033±0.141	-0.242–0.309	0.814
Season	0.208±0.280	-0.339-0.756	0.456
Group size	-1.214±0.281	-1.765– -0.662	**4.9e-5**
Relative NDVI : Distance core	0.364±0.238	-0.101–0.829	0.125
Annual NDVI : Distance core	-0.037±0.198	-0.425–0.351	0.851

Table 2. Summary of the model outcome results. Highlighted in blue and bold significant p-values. The model estimates reflect the probability of winning. Estimates here are relative as the different variables (relative and annual NDVI, distance to core, and intensity of use and core area) are measured from the perspective of the focal group. Accordingly, if estimates are positive they show that a group’s relative NDVI at the encounter location is higher than that of the encounter or rival group, and likewise for all other variables.

3.8. Appendix

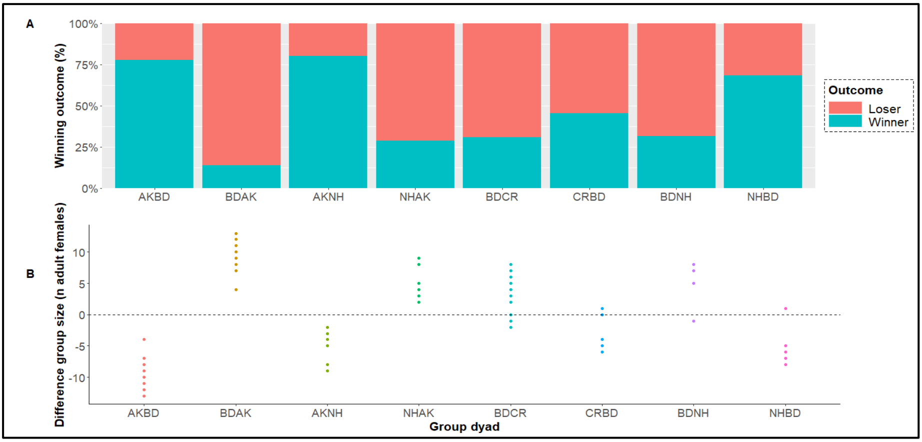

Figure 1A. Graphical visualisation of the winning (outcome) model. The figure above (A) reflects the winning outcome for each dyad. Dyads along the x-axis are named in order so the focal group comes first followed by the encounter group (i.e. AKBD, AK as a focal group, BD as encounter group). Winning appears calculated as a percentage of the total, whereby the winner is coloured in blue and the loser in red. The figure below (B) shows the number of adult females of each dyad, calculated by discounting to the focal group the number of females of the encounter group. Different points appear for a given dyad group combination as they reflect the changes of demography that occurred during the four years of data. The number of adult females was considered because it is highly correlated to the number of total individuals of the group (Figure 2 below), and because adult females are the philopatric sex and therefore key to the society of vervet monkeys. Note that dyadic group size superiority relationships were maintained throughout the entire period of study, so if one group was bigger in 2013 relative to another, that difference persisted across time, and until 2019. The IVP experienced a shortage of manpower during the four months of 2019 due to a lion incident that forced us to concentrate research on all groups except CR, a reason that did not allow us to have exact data on that group’s demography. However, given that we have a long record of female demography evolution in the other groups, and we can conclude that the numbers of adult females rarely vary greatly in the space of a few months, we assumed that CR’s number of adult females stayed stable in that period.

Glossary of terms	
Ecological variables	*Relative home range NDVI* NDVI of the grid relative to the average of the home range of the group
	Relative annual NDVI during the intergroup encounter NDVI of the grid relative to the average of the year of the home range of the group
	Maximum annual NDVI Maximum NDVI value of the grid in a year
Ownership variables	*Core area* Areas that are most frequently used calculated using Kernels. Core areas can overlap in our study groups.
	Overlapping area Areas that are less frequently used, and can be used by several groups Overlapping areas can be also core areas
	Distance to core Minimum distance of a group to its closer core area Calculated from the perspective of the focal group, that integrates the encounter group, so positive values indicate that the focal group is less far from its core than the encounter group
	Intensity of use Calculated using focals of the four years, this value incorporates how much a group used a given area relative to how much the opponent used the same area Positive values indicate that the focal group used the area more often than the encounter group

Table 1A. Ecological and territorial terms for the variables that were used across the manuscript and that were investigated.

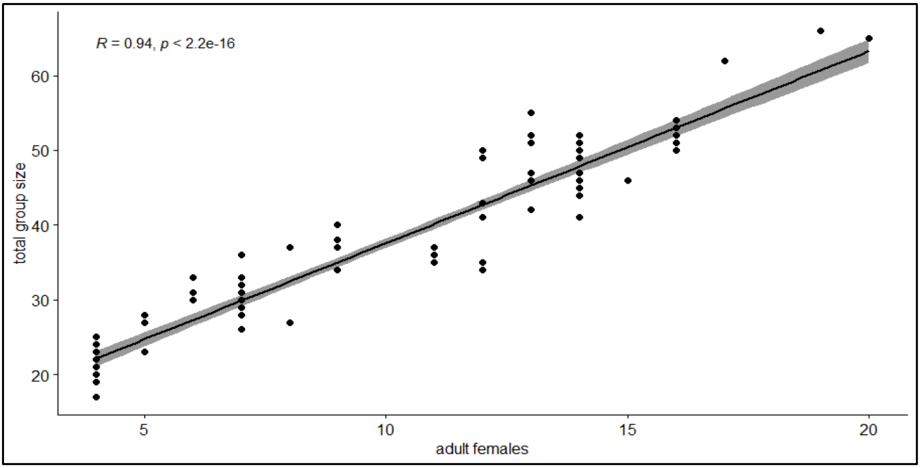

Figure 2A. Correlation of the number of females with the number of total individuals in the group (including adult males, adult females, juveniles, and infants) for all groups' four years of data. This correlation allows us to use the number of adult females in the group as a proxy of group size, given that they are the core of the social group and have more fitness interest in keeping their territories, as they spend their entire lifespans in the groups where they are born.

CHAPTER 4. A multi-level approach to fissions in wild vervet monkeys: causal factors and strategies shaping decision-making

Manuscript in preparation

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MGG conceived the idea and RB, AC, and EvdW help refine the project, MGG collected and prepared the data that was analysed by MGG with the assistance of AQ, MW, and CC, MGG wrote the first version of the manuscript that was further edited in a collaborative effort between MGG, CC, EvdW, and RB

4.1. Abstract

Group living is beneficial for animals because it aids them to cope with important challenges. However, an important trade-off is that if competition for food sources increases, individuals can find constraints to socialise. Food shortage can intensify when groups increase or under extreme climatic events. These conditions may impose a torrent of cascading effects on the individuals, affecting group movement, spatial cohesion and synchrony, or elicit agonistic interactions between members. In some instances, groups fission and the philopatric sex disbands with other individuals establishing a new founder group. Here we investigated if identifiable changes on activity budgets, group dispersion, and grooming-based network metrics at the individual and group-level take place near the fission time by studying two years of data in 3-month time windows in three groups of wild primates. We focussed on adult females as a subset of the population because they are the core of their societies and are the philopatric sex. Finally, we evaluated the strategies that adult females may have followed when facing crucial decision-making that involves staying or leaving in the original group's territory, and assortment around the decision of with whom to stay using pairwise correlation analysis based on grooming, kinship and proximity that we compared with the final group composition of the two daughter groups. Moreover, we assessed three potential fitness-related factors that may have influenced the females' strategies to be more or less risk-prone (stay or leave). All fission processes took place amid a severe drought in South Africa. Our mixed approach revealed that contrary to our predictions, activity budgets changed differently in the three groups, and some grooming-based individual network metrics increased closer to the fission. Groups did not appear to recur to increasing spatial dispersion around the fission time, suggesting that predation pressure may have influenced, even under harsh environmental conditions. Interestingly, females that did not experience the death of a close kin member seem to have adopted risk-prone behaviours and adventured leaving their original group and territory, while those that suffered it appear to play the risk-averse strategy of staying in the territory.

Keywords: Activity budgets, adult females, decision-making, grooming, fission, network metrics, risk, strategies.

4.2. Introduction

Group-living is widespread among the animal kingdom (Krause and Ruxton, 2002). Most notably, by living in groups, individuals gain access to food sources against out-group competitors (Sterck, Watts and van Schaik, 1997; Koenig, 2002), reduce their risk of predation and defend better their territories (Richard, 1974; Krause & Ruxton, 2002; van Schaik & van Hooff, 1983). Food competition can take the form of contest competition if the resources are clumped and some individuals can monopolise them or scramble competition when the resources are limited, highly dispersed and of little value, which makes monopolisation unfeasible (Janson & van Schaik, 1988; Sterck et al., 1997; van Schaik, 1989). Moreover, group size can increase group competition (Alexander, 1974; Chapman, Wrangham, & Chapman, 1995; Isbell, 1991; van Schaik & van Hooff, 1983; Wrangham, 1980) and impose constraints on the capacity to exploit habitat optimums (VanderWaal, Mosser and Packer, 2009) conditioning travelling distances (Grove, 2012) and complicating individuals' ability to maintain large social networks (Maldonado-Chaparro, Hubbard, & Blumstein, 2015). Hence, animals experience defying challenges to maintain their activity budgets in balance (Dunbar, 1992; Dunbar, Korstjens, & Lehmann, 2009; Pollard & Blumstein, 2008) which may condition elevated stress levels if conditions are not favourable (Pride, 2005; Markham *et al.*, 2015).

One extreme response to stress is to undergo group fission. Fissions may occur either when group size grows beyond what is optimal, or when severe external events like prolonged droughts cause low food abundance. Group fissions have been observed in a variety of mammalian species (Alvarado, Link, & Di Fiore, 2020; Furuya, 1969; Holekamp, Ogutu, Dublin, Frank, & Smale, 1993; Waterman, 2002). However, such events are rare and hence difficult to study in systematic ways. Here, we report three group fissions in vervet monkeys during a prolonged drought that occurred in 2016 in large parts of South Africa due to the El Niño phenomenon (Baudoin *et al.*, 2017). We addressed three different general questions. First, are there any behavioural changes that would allow predicting future group fissions? Second, can we predict who will stay with whom? Third, are there variables that predict which subgroup stays within the original home range and which subgroup shifts its home range?

Territory quality, size, ranging patterns, or inter-species or intra-species competition are crucial elements that govern life in groups (Campos et al., 2014; Gibson & Koenig, 2012; Harvey & Clutton-Brock, 1981; Lefebvre, Ménard, & Pierre, 2003; Seiler & Robbins, 2020). Individuals need to allocate their finite time budgets to different fundamental activities (Dunbar, 1992; Dunbar et al., 2009; Maher, 1997; Neuhaus & Ruckstuhl, 2002; Pollard & Blumstein, 2008) as any activity limits the fulfilling possible alternatives (Lehmann & Dunbar, 2009). Furthermore, beyond certain group sizes, compromises on resting or social time can arise (Dunbar, 1992; Lehmann, Korstjens, & Dunbar, 2007; Lehmann, Andrews, & Dunbar, 2010; Pollard & Blumstein, 2008). To overcome time limitations, individuals can make use of adapted flexible behavioural repertoires that may be useful under limation conditions (West-Eberhard, 1989; Dingemanse and Wolf, 2013; Lubbe *et al.*, 2014; McFarland *et al.*, 2014). Groups are, in a way, embedded networks of individuals whereby interactions mould group structures (Hinde, 1976; Maldonado-Chaparro et al., 2015; Rosenbaum, Maldonado-Chaparro, & Stoinski, 2016; van Schaik, 1989). In this view, one could assume that individuals can regulate social interactions in ways that preserve the group integrity (Focardi & Pecchioli, 2005; Kappeler & Schaik, 2002; Lehmann et al., 2007; Henzi & Barrett, 2007).

When changes in the biotic or abiotic environment occur (climatic phenomena, group population dynamics, competition within-group or between groups), individuals adjust through behavioural flexibility (Lack, 1970; Schlaepfer, Sherman and Runge, 2010). This is possible because adaptive skills like cue recognition (Neff and Sherman, 2002) permit gathering information that allows the evaluation of behavioural options (Williams, 2008; Shettleworth, 2009). Besides, the perception of environmental cues relies on pre-existing mental processes (Mayr, 1974; Cosmides and Tooby, 1987, 2013; Reeve, 1989) through evolutionarily acquired cognitive and sensory processing that permit information contextualisation (Mappes and Stevens, 2010; Stevens, 2010) and grants animals to behave flexibly (Ghalambor *et al.*, 2007). This chain of adaptations constitutes Darwinian Algorithms (DAs) (Cosmides and Tooby, 1987; Reeve, 1989; Neff and Sherman, 2002). Still, mental assessment of socio-ecological factors can also facilitate animals to break fitness-limiting constraints (Arnold, 1992; van Noordwijk & de Jong, 1986). Some examples of DAs or social flexibility are seen when animals display sub-grouping patterns in response to ecological variation, as seen in lions (Mbizah *et al.*, 2020), European shore crabs (Tanner and Jackson, 2012), killer whales (Foster *et al.*, 2012), northern pig-tailed macaques (Albert *et al.*, 2013), or zebra finches (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby, & Farine, 2018).

Overarching socio-ecological challenges represent situations that call for DAs and the adoption of reaction-norm responses that aim to promote or safeguard fitness through behavioural options (Cosmides, 1985; Cosmides and Tooby, 1987; Schlaepfer, Sherman and Runge, 2010; Seebacher and Krause, 2017). Severe drought conditions can seriously challenge fitness maintenance in pervading manners (Parmesan, Root and Willig, 2000; Loveridge *et al.*, 2006;

Walls, Barichivich and Brown, 2013; Yiran and Stringer, 2016; Prugh *et al.*, 2018), so they are suitable representatives of ecological tipping points (Jiang, Hastings, & Lai, 2019; Lenton, 2013). However, animals can make decisions in harsh times that are not necessarily optimal and therefore evolutionary transmitted. Any decision-making processes sit on cognitive skills that enable individuals or collectives to solve challenges that may arise in the ecological and social realm. Droughts can affect the cohesion and synchrony of groups, pushing individuals to make the most out of a bad situation and eventually menacing the continuity of groups' maintenance. A lack of reactivity to such extreme and life-threatening scenario would evidence a lack of behavioural flexibility and reveal animals as closed programs (Mayr, 1974).

Socio-ecological tipping points behavioural reactions (Cosmides, 1985) open behavioural avenues for individuals to invert deflationary cost to benefit ratio situations. As an example, animals can solve within-group competition by adopting fission-fusion strategies, helping groups to prevail while adopting flexible compositions (Aureli *et al.*, 2017) that permit higher foraging efficiency (Grove, 2012). This strategy is seen in bats, reindeer, fallow deer, roe deer, feral goats, elephants, spider monkeys or chimpanzees (Archie, Moss, & Alberts, 2006; Body, Weladji, Holand, & Nieminen, 2015; Busia, Schaffner, & Aureli, 2017; Focardi & Pecchioli, 2005; Kerth & König, 1999; Lardy, Fortin, & Pays, 2016; Lehmann, Korstjens, & Dunbar, 2007; Stanley & Dunbar, 2013). Similarly, individuals may recur to dispersion strategies when their fitness is compromised by unbridled food competition (Maag *et al.*, 2018). Thus, allowing positive payoffs can be obtained through dispersion (Green and Hatchwell, 2018) while helping entire groups to avoid extinction (Delibes, Gaona and Ferreras, 2001; Bowler and Benton, 2005). Fissions, like dispersal, seem to be dominated by kinship rules that configure groups' structure (Gardner and West, 2006; Larson *et al.*, 2018) and have bearing on cooperative behaviours (Green and Hatchwell, 2018).

Further, the social cohesion hypothesis (Bekoff, 1977) predicts that individual that is less integrated into the network make better candidates for abandoning the group, as found in yellow-bellied marmots (Blumstein, Wey, & Tang, 2009). How individuals make sub-grouping or assortment decisions may be the result of simple processes that foster non-random associations, i.e. acting as simultaneous feedbacks and characterise collective behaviour (Gersick and Rubenstein, 2017). Such feedbacks could also respond to physiological states

(Sapolsky, 2005), family ties (Gardner and West, 2006), association preferences (Sueur *et al.*, 2011; Firth and Sheldon, 2016; Palacios-Romo, Castellanos and Ramos-Fernandez, 2019) or social monitoring (Ågren, Davies and Foster, 2019).

Consequently, group fissions (fissions henceforth) are likely representatives of DAs and behavioural flexibility that could well portray animal social competence (Taborsky and Oliveira, 2012; Bshary and Oliveira, 2015) that enables individuals to solve challenging socio-ecological landscapes through the dilution of the original group into two (or more) daughter groups (Dittus, 1977). Fissions- differently from evictions- are not caused by an increase of aggressions from a subset of individuals towards another, i.e. banded mongooses (*Mungos mungo*; Cant, Otali, & Mwanguhya, 2001; Thompson, Marshall, Vitikainen, Young, & Cant, 2017); meerkats (Clutton-Brock et al., 1998; Stephens, Russell, Young, & Sutherland, 2005); rhesus macaques (*Macaca mulatta*; Larson et al., 2018), red-fronted lemurs *(Eulemur rufifrons*; Kappeler & Fichtel, 2012) or clown anemonefish (*Heteractis magnifica*; Buston, 2003). Fissions also lack the violence escalation component observed in chimpanzees or humans where a group eliminates or displaces another and drives it to extinction (Mitani, Watts, & Amsler, 2010; Wrangham, 1999). Fissions have been related to factors like the decline in reproductive success in chacma baboons (*Papio cynocephalus ursinus*; Ron, 1996) and dominance competition in chacma baboons (Ron, Henzi and Motro, 1994) and olive baboons (*Papio anubis*; Nash, 1976). Competition over resources and environmental stress surrounded fissions in black-tailed prairie dogs (*Cynomys ludovicianus;* Manno, Dobson, Hoogland, & Foltz, 2007*)*, toque macaques (*Macaca sinica*; Dittus, 1988) and black and white colobus (*Colobus guereza*; Dunbar & Dunbar, 1974). More, deterioration of group cohesiveness seem to have contributed to fissions in rhesus macaques (Missakian, 1973; Malik, Seth and Southwick, 1985), blue monkeys (*Cercopithecus mitis stuhlmanni*; Cords & Rowell, 1986), olive baboons (Henzi, Lycett and Piper, 1997), Cape ground squirrels (*Xerus inauris*; Waterman, 2002), northern muriquis (*Brachyteles hypoxanthus;* Tokuda et al., 2014*)*; hyenas (*Crocuta crocuta*; Holekamp & Smale, 1995), Tibetan macaques (*Macaca thibetana*; Li, Wang, & Han, 1996) and Schmidt's red-tailed monkeys (*Cercopithecus ascanius schmidti*; Windfelder & Lwanga, 1988). Besides, an elevation of aggressive interactions was observed in Nilgiri langurs (*Semnopithecus johnii*; Hohmann, 1990), rhesus macaques (*Macaca mulatta*; Larson, Ruiz-Lambides, Platt, & Brent, 2018) and chimpanzees *(Pan troglodytes schweinfurthii;* Feldblum, Manfredi, Gilby, & Pusey, 2018). Finally, some fissions were heralded by group clustering following relatedness; i.e in killer whales (*Orcinus orca*; Stredulinsky, Darimont, Barrett-Lennard, Ellis, & Ford, 2021) and humans (Yanomamo, *Homo sapiens*; Chagnon, 1975), or following social relationships in Indo-Pacific dolphins *(Tursiops aduncus*; Nishita, Shirakihara, & Amano, 2015*)*. And yet, despite the long list of potentially influencing factors (see Table 1 Appendix), little is known about how ecology shapes social connectivity and the stability of groups (Cantor and Farine, 2018; He, Maldonado-Chaparro and Farine, 2019) (see Table A.1. in Appendix showing different examples of fisison and eviction).

In situations like fissions, multiple individuals may be interacting with many others and playing dissimilar strategies, illustrating the importance of N-player games that take into account several players' payoff matrices (Nunn and Deaner, 2004). Thus, the decisions put in play by individuals in an N-player game (Archetti, 2009; Bach, Helvik, & Christiansen, 2006; Maynard Smith, 1979) during fissions merit a game-theory look if we understand such separation resulting from divergence of interests with possible Darwinian fitness connotations (Dugatkin & Reeve, 1998; Nowak, 2012; Smith, 1982). In fissions, behavioural options open as branches (Reichert and Hammerstein, 1983) for the adult females to decide whether to stay or to leave. While staying may be the safer option, those opting to leave may still find incentives. In that frame, strategies represent a sort of behavioural guide for individuals to adhere during a given game (Riechert, 1998) where multiple players simultaneously interact as originally registered by Pitcher et al. on shoaling fish anti-predator behaviour (Pitcher, Green and Magurran, 1986) and by Boyd and Richerson (Boyd and Richerson, 1988) approach to the evolution of reciprocity (McNamara and Leimar, 2010). As in any play, there are a set of strategies that individuals can take, concretely stay or leave with socio-ecological connotations. Under such premise, adult females experiencing a stark drought challenging their survival and that of their kin would strategize and follow decision rules to maximise their payoffs - or simply guarantees a prospect different than current (to self and close kin). However, ecological tipping points (Lenton, 2013; Pruitt *et al.*, 2018) may boost players to contemplate abandoning the maximum of "better devil known" and adopt the leaving strategy despite the costs of dispersion; i.e. predation, competition with other groups, gain and defence of a new territory (Waser, Creel and Lucas, 1994; Bowler and Benton, 2005; Clobert *et al.*, 2009; Maag *et al.*, 2019). After all, the re-occurring event of fissions is widely documented across many taxa, albeit not frequent, thus this phenomenon may constitute a relatively stable strategy (Hamilton, 1967; Smith & Parker, 1976) if interpreted at an evolutionary scale. Akin to foraging theories that describe strategies according to frequent-dependent traits (Sjerps and Haccou, 1994), vervet monkeys may be confronted with two drastic opposites. While staying may be safer, perceptions are likely to sway and condition risk assessment give way to risk-prone, risk-averse strategies (Caraco et al., 1990; Gaynor, Brown, Middleton, Power, & Brashares, 2019; Stephens, 1980) in response to deaths of kin members, energy shortfall prospects, or worsening of own's reproductive, health or stress states. The fission phenomenon offers a scenario of strategies and decision-making where risk perceptions may be involved.

Here, we studied three fissions in wild vervet monkey (*Chlorocebus pygerythrus*) that occurred at the Inkawu Vervet Project, in Kwazulu-Natal (IVP, South Africa) between the end of 2015 and early 2016 (van de Waal, van Schaik and Whiten, 2017). South Africa underwent severe drought conditions during 2015 and 2016 (Baudoin *et al.*, 2017; Monyela, 2017; Rosa *et al.*, 2017; Herring *et al.*, 2018; Archer, 2019; Karlie, 2020; Lottering, Mafongoya and Lottering, 2020; Odoulami, Wolski and New, 2021; Wolski *et al.*, 2021). Vervet monkeys live in female-bonded, female-philopatric groups and females spend their entire lifespans at their natal groups, thus constituting the core of the social group (Isbell, Cheney, & Seyfarth, 2002; Renevey, Bshary, & van de Waal, 2013; Wrangham, 1980). In the society of vervet monkeys, the females' hierarchy is rather linear and stable although nepotistic conflicts are commonplace (Cheney, 1992; Cheney & Seyfarth, 1990). Albeit the average group size rounding twenty-five individuals, sizes vary greatly between groups and across time (Isbell, Cheney, & Seyfarth, 1991; Isbell & Young, 1993). In female-bonded groups, females do not disperse unless their inclusive fitness is compromised due to food competition (Wrangham, 1980), from infanticidal males (van Schaik, 1989), or if their reproduction potential is compromised (Isbell and Young, 2002). In this light, the fissioning of three vervet monkey groups, where some adult females abandoned their territory opens pertinent questions about possible causal factors and underlying processes before the original groups' downfall. We set the focus on adult females (henceforward referred to as females) because females' sociality has a far-reaching influence on that of their groups' in female-bonded species (Brent, Ruiz-Lambides, & Platt, 2017; Ellis, Snyder-Mackler, Ruiz-Lambides, Hamede, Bashford, McCallum, & Jones, 2009; MacIntosh et al., 2012; Maldonado-Chaparro, Hubbard, et al., 2015).

Thus, we seek we address three blocks of questions (A, B, C) to elucidate if there are common behavioural patterns across two years before the three groups finally fissioned by setting time windows of three months (from one day before the fission to -24 months). By touching on several aspects, we hope to shed light on commonalities that the groups may have shared before splitting. First, we used a bottom-up approach (Cantor *et al.*, 2021) to investigate A) what causes may have precipitated the group fissions. For that, we describe the groups' demographics about juveniles and adult females' deaths (A.1.1), infant survival (A.1.2), and total group size (A.1.3). Concerning the likely causes, we expect the drought to affect survival, groups' demographics, and females' activity budgets. A survival deterioration of the groups' individuals could hint at fitness as reported in Cape ground squirrels (Sherman and Runge, 2002; Waterman, 2002). Likewise, group size increase may push towards the onset of a declining function of benefits to costs ratio of group living as hypothesised in killer whales (Stredulinsky, Darimont, Barrett-Lennard, Ellis, & Ford, 2021), savannah baboons (Van Horn *et al.*, 2007), and spider monkeys temporary fissions (Chapman, Wrangham and Chapman, 1995).

More, we studied if relevant activity budget changes accompanied the fissions, i.e. stresses to manage to feed, rest, move and socialising (grooming) (A.2). Resting facilitates digestion and thermoregulation (Korstjens, Lehmann and Dunbar, 2010) and socialising is key to keep social ties (Lehmann et al., 2007; Maldonado-Chaparro, Hubbard, et al., 2015), so changes at these levels could illustrate that females were under impending stresses. We evaluated if groups were more dispersed before the fission, as observed in rhesus macaques (Missakian, 1973; Malik, Seth and Southwick, 1985) (A.3), which could indicate low food availability shaping spatial cohesion. Since group sizes' variability is commonplace in group-living species (Peña and Nöldeke, 2016), some socio-ecology factors might add to groups' disintegration fate, such as prolonged and acute deleterious environmental conditions. More specifically, we expect drought-driven scramble competition (Sterck, Watts and van Schaik, 1997) conditions to affect females' activity budget limitations since they perform as members of a group (Isbell & Young, 1993). We expect moving to increase due to low resources' availability (Korstjens and Hillyer, 2016; Hunter *et al.*, 2020).

Secondly, we used grooming-based network parameters' variation to study if the females' connectivity – the overall connection between individuals - deteriorated before the fission at the individual and group-level (B). Social network analyses (SNA) permit the exploration of social interactions through the mesh of social interactions (Whitehead, 2008; Krause, Lusseau and James, 2009). Grooming data can be used to calculate individual-level and group-level parameters and shed light on social dynamics at different time scales (Brent et al., 2013; Koyama & Aureli, 2019; Larson et al., 2018; Matsuda, Fukaya, Pasquaretta, & Sueur, 2015), helping pinpoint changes across time. Further, SNAs can assist the identification of changes around seasonality (Brent et al., 2013; Cantor et al., 2012; Hamede et al., 2009; Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009; Silva, Diego, & Ranjeewa, 2011), resource variability (Henzi *et al.*, 2009), reproductive states (Brent et al., 2013; Patriquin, Leonard, Broders, & Garroway, 2010), or individuals' attractiveness (Oh and Badyaev, 2010). We evaluated females' connectivity in the network through individual parameters like degree as the sum of individuals that each female subject groomed or received grooming from (B.1.1) and strength, which measures how frequently or strongly an individual is connected to others (Blaszczyk, 2018; Crofoot, Rubenstein, Maiya, & Berger-Wolf, 2011; Farine & Whitehead, 2015; Jarrett, Bonnell, Young, Barrett, & Henzi, 2018) (B.1.2). Betweenness tells us about the number of shortest paths that go through an individual to connect others (James, Croft, & Krause, 2009; Wey, Blumstein, Shen, & Jordán, 2008; Whitehead, 2008).

Likewise, we evaluated adult females' grooming using grooming-derived group-level network parameters of density, transitivity and modularity (B.2). Density is informative of a network connectedness by considering the actual edges relative to the possible total (Dunbar, 2018; Leu, Farine, Wey, Sih, & Bull, 2016; Smith et al., 2010) (B.2.1). Transitivity shows the connectedness of triplets within a group, acting as a proxy of groups' connectivity (Gelardi, Fagot, Barrat, & Claidière, 2019; Wey, Jordán, & Blumstein, 2019) (B.2.2). And modularity is indicative of networks' cohesion (Marcoux and Lusseau, 2013), as observed in Gombe chimpanzees' variation around a fission event (Feldblum *et al.*, 2018) (B.2.3). Generally, being more connected would imply that individuals are integrated within a group structure and warrant the staying rather than leaving the group, as shown in yellow-bellied marmots (Blumstein, Wey, & Tang, 2009) in line with the Social Cohesion Hypothesis (Bekoff, 1977; Blumstein et al., 2009). In our case, we expect the penalising conditions of the drought to compromise females' connectivity; both at the individual and group-level, conditioning them to have lower grooming connectivity through degree, strength, and betweenness near the fission. Similarly, we speculate that density and transitivity decreased, and modularity increased due to progressive sub-grouping or clustering near the fission. In sum, females' deterioration of their connectivity through individual and group-level measures would reveal a "point of no return" that may have created the conditions for the strategy of leaving to gain ground.

One can view staying as risk-averse and leaving as risk-prone (Caraco *et al.*, 1990), so we evaluated variables that potentially affect decisions to stay or leave. Albeit not all decisions are fitness-relevant, and it is impossible to ascertain whether some decisions are optimal. We evaluated whether the females may integrate fitness-carrying information (payoffs) when strategizing overstaying or leaving (C1); i.e. through the number of dependent offspring they have (C1.1), their dominance rank position (C1.2) or by having experienced the death of close kin before the fission (C1.3). These factors may shape the adoption of risk-prone or risk-averse strategies (Riechert, 1998); if staying in the original territory represents the safe option compared to the risks and uncertainties around those that leave and must establish a new territory. As in the game of Producer-Scrounger (Giraldeau and Livoreil, 1998), some adult females may have considered the leaving strategy and be more risk-prone, and the prospects of staying are dreadful. Because the leaving and staying strategies can have colossal irreversible implications, we expect that females adopted risk-prone and risk-avoidance strategies along with the following reasoning: having more dependent offspring, having a higher rank position, and having recently suffered the death of close kin would be incentives to stay in the original territory. The contrary would tip the balance toward leaving strategies, whereby females put all their bets on what is, a priori, more uncertain ("better devil known"). Similarly, following the social cohesion hypothesis that was developed on yellow-bellied marmots' migration, we expect that less socially connected individuals are more likely to leave (Blumstein et al., 2009).

As another ramification of strategizing and decision-making, we evaluated fissions at the level of the resulting compositions of the daughter groups (whom to stay with?) as a form of individual assortment (Farine, 2014; Rose & Croft, 2020). We assessed if the daughter groups' compositions were influenced by higher affinity, which we studied through grooming networks (C2.1), proximity networks (C2.2), and relatedness (C2.3). We presume that females' assortment followed simple rules such as preferred partners (i.e. grooming, proximity, kinship) closer to the fission. Individual assortment shapes groups' composition (Dittus, 1988; Malik et al., 1985; Missakian, 1973; Nishita, Shirakihara, & Amano, 2015; Okamoto & Matsumura, 2001; Ron, 1996) and has implications on cooperation (Aoki, 1983). These aspects are used to evaluate social interactions (Allen et al., 2017; Hamilton, 1981) as they can inform about how relations are maintained, which has fitness implications (Cameron *et al.*, 2009; Carter, Schino and Farine, 2019) and affect cooperation-defection dynamics (Fletcher and Doebeli, 2009; Apicella *et al.*, 2012). Overall, we amassed ecological, demographical, social, and kinship information sources (Figure 1, sketch) to delve into possible causes, processes, strategies and underlying decision-making processes that may have influenced the unfolding three fission events of a wild primate. As irreversible as they are, group fissions may have evolved as heuristic adaptive responses that can assume high degrees of uncertainty, that allow groups to regulate their structure and adapt them to what the environment provides at a given time.

4.3. Methods

4.3.1. Study subjects

We study three fission events that occurred between 2015 and 2016 at the IVP in Mawana Game Reserve (28°00.327S, 031°12.348E, KwaZulu Natal, South Africa) in three groups (Ankhase= AK, Kubu = KB, Noha= NH) of vervet monkeys of different group sizes (AK=39; KB=20; NH=52). We selected females that were adults at the fission time in each group (NAK=8; NKB=7; NNH=12), and we discarded those that died during the two years.

4.3.2. Timing

The three groups that underwent fissions were regularly monitored at the IVP, where a mix of experimental studies and systematic data is combined. We considered that the different groups had fissioned upon the observation that the two daughter groups did not reunite again. Thus, we established in the calendar the last day in which each group was seen as one as the fission date, and we went back in time 2 years, structuring time within time windows of three months. We established eight-time windows that go from T0 (from the last day the group was observed together to three months back) to T7 therefore including two years of data for each group. The fissions coincided with an overall agonistic reactivity between the two newly-formed daughter groups when they encountered (pers. comm. with Erica van de Waal). The establishment of time windows allows investigating possible sociality changes across time (Bonnell & Vilette, 2021; Duboscq et al., 2016; Jacoby, Papastamatiou, & Freeman, 2016; Krause et al., 2013; Kurvers et al., 2013; Larson et al., 2018). We use this temporal approach to investigate if the activity budgets and group spread (A2, A3), grooming connectivity at the individual and group-level (B1, B2), and the decision making of whom to stay with (C1) were affected close to the time of fission - T0 (see Fig. 2 in Figures and Tables).

4.3.3. Possible causes that triggered the fission (A)

4.3.3.1. Rainfall data

We acquired rainfall data from Umfolozi (in Kwazulu-Natal, around 100 km away from IVP) to illustrate the ecological variation that the area underwent in the time surrounding the fission time of the three groups (A1) recurring to an online database service (**Fig. A.4. in Appendix**). A visual representation of the rainfall distribution from 2009 and 2021 provides an overall picture of the rain distribution. Moreover, we provide a visualisation of the PNPI (Percentage of Normal Precipitation Index) (Van Rooy, 1965) with permission from the authors (personal communication with Prof. Demlie; Fig. A.3. in Appendix) (Ndlovu and Demlie, 2020).

4.3.3.2. Groups' demographics (A1)

We use the 10-year-old life history of the IVP to gather information about the demography evolution of the three groups around the fission time. Most importantly, we present the two years we are interested in within a longer time scale that goes from 2013 to 2019 to have a better perspective. We show data on adult females and juveniles' mortality (A1.1, see Fig. 3.1.), as well as the number of births and percentage of infant survival (A1.2, see Fig. 3.2.).

4.3.3.3. Activity budgets (A2)

We used scan data (Altmann, 1974) that collected information on the focal individual activity, location within the group (centre, periphery, front, back), number of neighbours in 10 meters, close neighbours (in 5 meters, and at 1 meter, and group spatial dispersion) to investigate if the time windows prior the fission events registered significant changes in the main activity budgets. Scan data were systematically collected by research assistants, masters, PhD students and post-docs after successfully passing inter-observer reliability tests of individuals' identification and data collection in inter-observer reliability tests (this applies to all other data types). Scans were collected throughout the study period in all groups on an average of two to three days per week whereby scans took place for 10 minutes that were followed by 20 minutes of break that would be used to relocate and find other individuals before the new scan started. To study activity budgets, we calculated the proportion of time each subject dedicated to any of the following main behaviours: foraging, resting, moving and social (including sit in contact, mouth-to-mouth, play and grooming). The total data involves a total of over 2000 hours of scans in all groups during all time window (mean per group ± s.d = 669.61 ± 27.28 hours; mean per individual ± s.d = 74.4 ± 23.81 hours) from which percentages of individual allocation to each activity was calculated. To study the possible variation around the fissions, we evaluated each activity performance separately using linear mixed models (Bates *et al.*, 2014) (Zuur, Ieno, Walker, Saveliev, 2009) with the function *lmer* using in lme4 R-packages (Bates *et al.*, 2020) with R software (R Core Team, 2008). Each activity is represented as a percentage from the total occurrences of each female at the different time windows (T0-T7) and constitutes the response variable. Although the seasonality is a likely factor influencing activity budgets (Canteloup *et al.*, 2019), we did not integrate it in our analysis because the drought conditions made seasons to be ineffective, as summer should have come with rains (this logic is applied to all analysis). We used time windows as fixed factors in interaction with group identity, to assess how each activity varied in each time window compared to the one of most interest, that is, T0 (the one closer to the fission), and on each group separately by using the R function *emmeans* (Russell *et al.*, 2021) individual and group identity were set as random factors.

4.3.3.4. Group spread (A3)

Group spread information was systematically collected at the onset of each scan (Altmann, 1974). In the scans, we recorded group spatial information in five categories: ‘group spread less than 20 metres’, ‘between 20 and 50 metres’, ‘between 50 and 100 metres’, ‘more than 100 metres’ and ‘across the river that we aggregated in two biologically distinct ones*: i)* less than 100 metres and *ii)* more than 100 metres, and ditched across river data as it could encompass a great variety of distances. With the two categories of group spread, we had over 2200 hours of scans (average per group ± s.d = 752.94 ± 90.86 hours; average per individual ± s.d = 86.93 ± 31.77 hours). We conducted a general linear mixed model (GLMM) (Zuur, Ieno, Walker, Saveliev, 2009) using the function *glmer* available in *lme4* R-packages (Bates *et al.*, 2020; Russell *et al.*, 2021) in R (R Core Team, 2008) to examine if group spread varied close to the fission time. For that, we considered group spread as a response variable and an interaction of time windows and group identity as fixed factors after controlling for normality (Huang *et al.*, 2019). To avoid the possible pseudoreplication that group information may suffer through successive individual scanning, we considered date and time as random factors (Harrison, Morrogh-Bernard and Chivers, 2010; Clark *et al.*, 2012), that were converted as a factor and numeric predictors correspondingly. We investigate the differences of all time windows with T0.using the function *emmeans*.

4.3.4. Grooming data and network metrics at the individual (B1) and group-level (B2)

For the study of grooming-based network questions, we used ad-libitum data (Altmann, 1974; Gumert, 2007; Molesti and Majolo, 2017; Jiang *et al.*, 2019) as this is the best available grooming source that warrants covering the period of interest. Although different data collection methods can lead to different network properties (Marshall *et al.*, 2014; Davis, Crofoot and Farine, 2018), ad-libitum grooming data is highly correlated with focal grooming data at the IVP (Canteloup *et al.*, 2020). We incorporated over 1100 ad-libitum grooming events from the three groups during all time windows (average per group ± s.d =_373.33 ± 33.1 grooming interactions; average per individual ± s.d =_45.54 ± 7.46). Specifically, researchers systematically followed all individuals of the group attempting to follow them evenly to dispose of balanced ad libitum data sets as part of the IVP protocol.

We used weighted and directed grooming matrices to calculate individual and group-level metrics using the *igraph* package (Csárdi and Nepusz, 2006) in R (R Core Team, 2008). As individual-level metrics (B1), we calculated the number of females (edges) connected to the node (ego) through grooming given as a proxy of individuals' connectivity (Whitehead, 2008) (B1.1). We calculated strength (B1.2), which measures how frequently an individual is connected through grooming or being groomed by others (Blaszczyk, 2018; Crofoot et al., 2011; Farine & Whitehead, 2015). Moreover, we estimated betweenness, that is, the number of shortest paths that pass through a given individual (B1.3). Betweenness measures centrality based on topological distances so individuals with high values act as connectors to other individuals, potentially increasing groups' cohesiveness (Hanneman & Riddle, 2005; Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2011; Kasper & Voelkl, 2009; Lusseau, 2007). At the group-level (B2), we calculated network density (B2.1) that indicates how many edges or individuals are connected to and how the overall network is connected relative to the maximum possible (Dunbar, 2018; Larson et al., 2018; Leu, Farine, Wey, Sih, & Bull, 2016; Smith et al., 2010; Wey et al., 2008). Transitivity (B2.2) was estimated measures the connectedness of triplets in a group, therefore being a valid proxy of the group connectivity (Faust, 2010; Gelardi et al., 2019; Ilany, Barocas, Koren, Kam, & Geffen, 2013; Wey et al., 2008; Wey et al., 2019). Lastly, we evaluated if the global metric of modularity (B2.3) reveals any fragmentation or sub-grouping tendencies (Chen et al., 2015; Griffin & Nunn, 2012; Newman & Girvan, 2004; Pons & Latapy, 2006; Shizuka & Farine, 2016; Silk et al., 2017; Whitehead & James, 2015). Similarly to our aim to identify possible structural indicators of vervet monkeys' group fissioning, Feldblum et al. (Feldblum *et al.*, 2018) emphasized modularity as a valuable metric of group cohesion.

We used these metrics (B1, B2) to evaluate if there was relevant variation close to the fission time, using a GLMM for B1 for each metric as the response variable, and the windows are fixed factors in interaction with group identity (3 groups, N=27 individuals, thus having 216 data points) and the individual identities are random factors. For the analysis of the group-level (B2), we ran LMEs for each grooming network metric representing the response variable, time window the fixed factor, and group the random factor (3 groups * 8-time windows =24 data points). We use the *emmeans* in both analyses to see how different time windows compare to T0 (B1, B2), and each groups' variation (B1) and we compared all time windows with T0 to evaluate if there were significant changes in the time window that was closest to the fission time.

4.3.5. Strategies: Stay or leave (C1) and with whom (C2)

Here we consider three fitness-related factors with payoffs implications for the females to play strategy or another when deciding to stay or leave the original group (C1). First, we count the number of juveniles younger than 2 years old as individuals relatively dependent on their mothers (Amici *et al.*, 2019) (C1.1). Second, we calculate the rank position (C1.2) using explicit dyadic agonistic interactions with a clear aggressor (chase, hit, slap, bite, stand-up bipedal, take place) and a victim (retreat, jump aside, scream, flee) among any individual of the group using the *elo-rating* package (Neumann *et al.*, 2011; Sánchez-Tójar, Schroeder and Farine, 2018).

Thirdly, we counted the events where a close-kin – mother or offspring-member had died during the two years of study for each adult female (dead individuals only accounted for one adult female) and transformed it into a binary option (yes, no) (C1.3). We evaluated the possible association between these factors (number of dependent offspring, rank position, and death of close kin member) and the strategy stay-or-leave as a binary response using a Bayesian GLM with binomial error structure using the package *arm* (Gelman *et al.*, 2020). The Bayesian approach was necessary to deal with a perfect separation phenomenon (100% of cases with dead relatives adopted the stay strategy).

We evaluate if groups show a general tendency to form sub-groups of clusters closer to the fission time, that could reflect the final composition of the two resulting groups: the study group (i.e. the group that we continued to follow at IVP) and the daughter group (the split group that we did not follow). For this, we constructed for each group i) a binary matrix 'final composition of the group' encoded as 1 for the females who stayed in the study group after fission and as 0 for those who did not and formed the new daughter group; ii) 8 binary and symmetrical grooming matrices corresponding to each time window (T0 to T7) encoded as 1 for dyads who were involved in grooming at least once and 0 for those who never groomed each other; iii) 8 binary and symmetrical 'nearest neighbour' matrices corresponding to each time window (T0 to T7) encoded as 1 for individuals that were considered as nearest neighbours within

5m at least once and 0 for those who were never observed as nearest neighbour and iv) a binary kinship matrix encoded as 1 for dyads with relatedness scores higher than 0.375 and as 0 for those with such score lower than 0.375 (Van Horn, Altmann and Alberts, 2008; Thorington and Weigl, 2011).

For each group, we ran Mantel correlation tests between ‘final composition of the group’, ‘kinship’ matrices (except for KB where the relatedness was not available for all individuals), grooming matrices and ‘nearest neighbour’ matrices taken two by two. Because we collected social data on same-group individuals and that network data are not independent of each other, they did not satisfy the criterion of independence of data underlying most statistical tests. To deal with the non-independence of our data, we generated 2000 random networks by permuting the node labels and recalculating the Mantel correlation coefficients for each comparison. With these values, we then generated a null distribution of Mantel correlation coefficients values and calculated a significant value for the observed Mantel correlation coefficient value. We applied the sequential Bonferroni–Holm procedure (Holm, 1979; Rice, 1989) to our p values (*p′*) because we ran multiple comparisons using the same matrices.

4.3.6. Ethical note

All subjects were fully habituated to human observers. At the IVP, researchers collect data an average of 8 hours per day six days a week on six neighbouring groups living in wild conditions. Ezemvelo Wildlife Board (KwaZulu-Natal, South Africa), the University of Cape Town, and the van der Walt family that own Mawana Game Reserve where the IVP is located granted ethical permission for the collection of behavioural data, that adheres to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research (Buchanan *et al.*, 2012).

4.4. Results

4.4.1. Activity budgets (A2)

All three groups showed significant variation in their activity budgets. As the main effects, time window and group also showed a significant interaction (Table 1; Figure 4 below). Overall, AK rested less in the time windows belonging to the year when the fission took place (T0 to T3, or year 0), and rested more in T0 compared to T1, T2, T3, although only T0-T4 registered a significant difference. KB group seemed to have rested more in T0 compared to any other time windows apart from T3, and significant differences were not registered immediately close to T0, but in T5 and T6. NH resting in T0 was within the range of the entire study period, and only significantly different with T1 and T4, being near the fission higher. The moving activity registered less variation and compared to T0, significant changes are only observed in T6 in AK, no changes in KB, and NH experienced more variation in T0 with the other time windows, as it decreased in T0 compared to any time window and significantly in all but T1, T3, and T6. The groups of AK and NH increased their sociality in the time windows within the year when the fission took place (T0-T3, that is, year 0), and KB maintained very stable allocation levels. More specifically, despite AK having higher levels in the year 0, AK females decreased their social time in T0 significantly compared to T2, and T4 (same moment in the calendar a year before or in year 1). KB's dedication to social time was maintained stable throughout the two years of study and across time windows compared to T0, and T0 was slightly higher -although not significantly- before the fission where there is a soft increasing tendency. NH's allocation to social was not significantly different in T0 compared to any time window, although there is an increasing tendency from T4 to T0 compared to T7 to T3.

4.4.2. Group spread (A3)

Overall, the three groups differed in their group spread across time, and across years (year 0= T0 to T3; year 1= T4 to T7, see Table 2 and Figure 4 below). The group AK maintained a similar balance of spread of more and less than 100 metres in year 0, while in year 1 it followed a decreasing tendency of being above 100 metres from T7 to T4. We found that the KB group maintained more homogenous levels of group dispersion across time, presenting more frequently group dispersion of fewer than 100 metres, and that tendency increased in year 0. Differently, the NH group was more frequently spreads over 100 metres and did so throughout the entire two years of study. Interestingly, AK and KB seemed to be less spread during T0 than NH that was more frequently more spread during the same time window.

4.4.3. Grooming data and network metrics at the individual (B1) and group-level (B2)

The females' grooming metrics changed differently in the three groups as the time windows were approaching the fission time. Degree changed significantly with time windows (Chisq= 23.66, P-value= 0.001); group (Chisq= 11.76, P-value = 0.003); and the interaction between group and time window (Chisq= 41.60, P-value = <0.001). The group AK maintained very similar levels of a degree across time and we found that the females in KB had rather stable degree levels during the two years, that they increased in T0, thus having a significant difference between T0 and T1 (T0>T1). NH group shows a higher degree in the year 0, and in the comparisons of T3, T4, T6, and T7 with T0 show significance whereby T0's degree was higher in all of them (Figure 6.1. and 6.2. and Table 3 below). Females' strength varied with time following different patterns, while AK decreased it from T7 to T2, to increase shortly after; KB's females kept similar strength and increased it in T0, and in NH there was an increasing trajectory from T3 to t0. Overall, the general model revealed that the predictors of the time window and the interaction of time window and the group had a significant effect on strength (Chisq= 87.36, P-value< 0.001; Chisq= 113.08, P-value<0.001). In the AK group, T0 was significantly higher compared with T2, T4, and T5; in the KB group, in T1; and in NH, T0 was higher than all other possible time windows. Finally, the grooming metric of females' betweenness changed with time window (Chisq= 23.39, P-value <0.001), in fluctuating manners for the group of AK and KB, while in NH has a U shape that increases in both extremes of the two years of study. The comparisons of T0 with other time windows rendered no significant results in AK and KB, while in NH T0 was significantly higher than T2, T3, and T4.

The group-level metrics of density, transitivity and modularity shows that there is a variation of the measurements across time, although the model does not reveal any significant results in the response variables or the comparisons of any time window with T0. The trajectory of the density metric does not show a clear trend in any group although in KB there is a maximum peak attained in T0. Further, transitivity does not reveal clear tendencies, but rather, ups and downs all along. Lastly, modularity presents an increasing trend from T3 to T0, where it achieves a maximum (Figure 6.3. and Table 4 below).

4.4.4. Strategies: Stay or leave (C1) and whom with (C2)

The analysis of the Bayesian model exposed that the factor of females having experienced the death of a close kin member at any one time of the two years before the fission correlated perfectly (100% of cases) with the strategy of staying (death of kin= yes: Est= 4.66, P-value=0.011). The other two factors considered, the number of dependent offspring at the moment of the fission and the rank dominance of the females did not have a noteworthy effect on the strategy playing that the females practised (Est=0.54, P-value=0.43; Est=0.20, P-value=0.25) (Figure 5 below). Finally, we found, for the NH group only, that the "final composition of the group matrix" was correlated with the grooming matrix at T0 (Mantel correlation test= 0.43; P'=0.017) and with the "nearest neighbour matrix" at T0 (Mantel correlation test= 0.37; P'=0.032). All other correlations remained non-significant (P'>0.05; see Table 5, and Figures 7.1. and 7.2.).

4.5. Discussion

The blend of evidence we gathered suggest that fissions are yet poorly understood. Because group fissions may not happen frequently (time scale related to the individuals' lifespans), the paucity of studies covering different informational sources necessarily begs we acknowledge that we may only be touching on the surface, given the amalgam of factors that could drive groups to split or leave traces of future split. Given the existing literature evidencing the dramatic effect the drought had in South Africa during 2015-2016 (Lottering, Mafongoya and Lottering, 2020), and the approximate time overlap in which the fissions occurred, we can pin down as a likely factor the drought that deteriorated the life conditions and meeting of nutritional needs in the three groups. However, this argument may require more solid proof of environmental variables that assess the reaching of carrying capacity states due to ecological tipping points (Delibes, Gaona and Ferreras, 2001; Lenton, 2013). Strikingly, from all data sources we present, it seems that the occurrence of deaths on juveniles and adults near the fission and an infant survival of virtually zero at the climax of the drought may compose relevant information that individuals process and use to adapt behavioural responses (Reeve, 1989; Neff and Sherman, 2002). Even if we had a specific hypothesis about how female vervets would go about their activity budget management, our results suggest that there may be idiosyncratic differences in the behavioural response to times of adversity. Remarkably, we found a pattern contrary to our predictions, that is, individual grooming network parameters of the females did not weaken, but instead, increased in the time windows near the fission. Our analysis of the group-level network measurements indicates different fluctuation in the three groups while possibly facing analogous environmental difficulties. Furthermore, we discuss how strategizing and posterior decision-making in the frame of behavioural flexibility unfolds into decisions using a game theory approach, that reveal fission decisions as adaptive responses to catastrophic environmental conditions (Taborsky and Oliveira, 2012; Cosmides and Tooby, 2013; Webb *et al.*, 2014).

The rainfall data of the nearest area with the registry to the IVP (Figure A.4. Appendix), in the KwaZulu-Natal region, and the NDVI (Normalized Differentiated Vegetation Index) that serves as a proxy of diet for vervet monkeys (Arseneau-Robar *et al.*, 2017) assist us to understand the occurrence of deaths in juveniles and adults, as well as the ensuing low infant survival (in two groups out of three) (Figure A.5. for South Africa and Figure A.6. for the study site). Interestingly, another severe drought whipped South Africa and the KwaZulu-Natal region in 2019 (Hulsman, Savenije and Hrachowitz, 2021) not prompting fission responses in any of the six vervet monkey groups that are monitored at the IVP. This raises several questions: are group fissions something cyclical, that occur around tipping points, but that also help groups to self-regulate their demographics and adapt them to their relatively stable home ranges? Do extreme hazardous environmental conditions feed cognitive systems and set off a chain of reactions within a narrowed and constrained behavioural suite of options due to the intensification of scramble competition (van Schaik and van Noordwijk, 1988; Sterck, Watts and van Schaik, 1997; Koenig, 2002; Teichroeb and Sicotte, 2018) where fissioning becomes a “good way out” and the maximum of “better devil known” loses grip? As it turns out, the BD group did not split during the period studied here, although it did so twice in the previous years (van de Waal, van Schaik and Whiten, 2017).

Even if traditional paradigms help the general understanding of how groups develop (Dunbar, 1987), our study on three different-sized groups challenges the view that size alone suffices to precipitate a chain of deleterious effects that threaten groups’ survival as the variability of territory quality and factors like growing pressure from neighbours possibly add on the obvious within-group competition (Grove, 2012). As a result, the need to ponder about how groups resolve social dilemmas that involve n-players seems appropriate, as groups may need to find optimums or near-optimums that adapt to what their habitats can offer (Archetti, 2009; Archetti and Scheuring, 2010) like food, safety from predators, between-group competition, within group-competition urging evaluation of payoffs and an assessment of post-fission cooperation dynamics. Different South African studies uncovered the overall importance of the drought on the land ecosystems across the different regions and how the desertization conditions were severe in unprecedented ways (Monyela, 2017; Abraham, Hempson and Staver, 2019; Lottering, Mafongoya and Lottering, 2020; Wolski *et al.*, 2021) (see Figures A.3., A.4., A.5., A.6. of Appendix).

The study of activity budgets can inform about how animal societies function within climatic, socio-ecological and mating landscapes (Isbell & Young, 1993; Maher, 1997; Nakagawa, 2000; Rasmussen, 1985; van Doorn, O'Riain, & Swedell, 2010; van Schaik, van Noordwijk, de Boer, & den Tonkelaar, 1983) and how these shape group cohesion (Neuhaus and Ruckstuhl, 2002). Albeit this, our results on the activity budget variation of the three groups tell us that, if anything, activity budgets seem to be more complex than anticipated (Figure 4, Table 1). This is perhaps due to the mingled underpinnings that acute ecological stressors may impinge on group-living animals. Our main predictions were not met, as we expected animals to increase their foraging time, which we may not see if due to the sheer lack of resources and the extreme dispersion of fallback foods, vervets may have adopted energy-saving strategies that emphasized resting time (as seen in KB and NH in the year 0) which could confirm the relevance of this behaviour (Korstjens and Dunbar, 2007). This contrasts with the AK group that seem to have opted to give up some resting time but interestingly increased social time in the time windows of the year 0. Intriguingly, the foraging behaviour does not render confirmatory results to our predictions, and only the group NH increased in the time windows close to the fission time. What is more, we could not foresee that females in the three groups would increase their dedication to social time in the time windows of the year 0 compared to the year 1 (the year before the fission).

This result forces us to reconceptualise how vervet monkeys assign importance to the different activity options at stake, and the crucial role that being social has, even at the doorstep of the group disintegration. Overall, we conclude that groups' different time budget management could only be fully understood if combined with other information sources: food abundance, territory competition with other groups, or physiological states. Notwithstanding, we need to clarify that foraging behaviour included also "searching for food" so maybe even if groups were foraging this did not translate into increased feeding rations. Additionally, if foraging was less efficient during the drought, one could expect to decrease with time. This is interesting since groups did not homogenously upregulate foraging time which may indicate that the situation could have achieved a dire dimension where investing more units of foraging time would render negative payoffs (more metabolically costly than beneficial).

Our analysis of group spread (Figure 5, Table 2) reveals that contrary to our conjecture that groups under critical ecological contexts increase their dispersion (Missakian, 1973; Waterman, 2002; Baden, Webster and Kamilar, 2016). Only NH group increased higher group spread in the year 0, and in the time windows close to the fission (T3-T0), while AK and KB group maintained rather stable higher group spread dynamics. Groups spreading beyond certain thresholds, especially in open habitats could have very damaging consequences as predation risks would augment, mainly through increased predation (Beauchamp, 2014; Hirsch, 2007; Janson & Goldsmith, 1995). Despite that, this finding could corroborate that vervet monkeys may prefer other behavioural responses before systematically adopting group dispersions that are likely to increase predation risks (Thaker *et al.*, 2010). Although not studied here, it could be of interest to delve into groups' ranging patterns across time, as we did for the variables we studied. Our knowledge of the study site and the populations within let us affirm that out of the three fissions evaluated here, only one of the daughter groups that played the strategy of leaving ended having small territories that were amid some of their previous neighbouring groups (AK). The other two sub-groups that formed left their original territory to adventure into more unknown areas. KB split group left and established across the opposite side of the river, in an area only hardly ever visited before the fission, and NH stands out even more, as they settled in an area far from the original territory that was unknown to them.

As it stands, it appears clear that the three groups did not behave consistently in T0, implying that the causes that lead to the fission events remain unclear. We expanded the social behaviour of the females by assessing different selected social network parameters using grooming data at the individual and group level (considering adult females only). As Feldblum et al. (Feldblum *et al.*, 2018), we acknowledge the data constraints that we had, although our groups were systematically followed by IVP researchers which granted us a huge dataset comparable in quality with focals (Canteloup et al., 2020). Importantly, we found that females were more connected among themselves (grooming degree) in the time windows close to the fission (Figure 6.1. and 6.2., Table 3). This contrasts highly with studies on female baboons that found narrowing of social networks when the environmental conditions became harsher (Henzi *et al.*, 2009) and rhesus macaques around fission, where spatial fragmentation induced acute social fragmentation studied through grooming (Missakian, 1973). Altogether, the analysis suggests that different groups appear to have reacted to the impending drought conditions differently. Although one could predict that fissions result from progressive deterioration of connectivity between key members of a given society (females in the case of vervet monkeys), it deserves mentioning that females in all groups appear to increase their group-level metrics closer to the fission. This could be understood as a “last resort” strategy to salvage the unity among females and reveal females importance attribution to keep the core of the society connected and seeing that the three groups ended fissioning beg for further investigation. Differently, individual-based metrics vary greatly among all groups and time windows in ways that hint at variation in itself as a probable indicator that deserves more attention, perhaps extending the time frame of study which would enable to conclude more strongly on whether higher variations may represent, per se, indicators of network disorder or entropy. (Boucherie *et al.*, 2016).

At the group-level, we predicted the metrics of density and transitivity to decrease, and modularity to increase closer to the fission, under the assumption that fissions in female-bonded groups occur after a stark process of female-female connectivity deterioration. Instead, we found density to vary across time windows in AK and KB, and increase timidly in NH close to the fission (Figure 6.3., Table 4). We interpret these results suggesting that density variations that tell us about how many connections (between females) happen from the total possible (Wey et al., 2019) may be illustrative in itself, as could be hinting at network entropy (Gomes, Boogert and Cardoso, 2021). In addition, KB seems to be decreasing in most of the time windows close to the fission, only arising at the very end, which opens the question of whether this represents a sort of "last resort" attempt to maintain the female connectivity. Interestingly, transitivity also fluctuates notably in AK and KB, possibly signalling instability (Beisner et al., 2011). Our prediction on the trajectory of modularity assumed a progressive clusterisation or subgrouping in the time windows close to the fission time, as previous studies reported (Dittus, 1988; Malik et al., 1985; Missakian, 1973; Windfelder & Lwanga, 1988). We found this prediction met only in KB, while the remaining groups did not show clear trends. Thus, although the analysis of social networks commonly aids the gain of knowledge of relationships' variation, maintenance and disintegration (Feldblum et al., 2018; Godfrey, Sih, & Bull, 2013; Larson et al., 2018; Murphy, Wittemyer, Henley, & Mumby, 2021; De Silva, Ranjeewa, & Kryazhimskiy, 2011), we cannot wind up our findings here in ways that could evoke pre-fission groups to follow certain converging behavioural rules. Instead, this builds on the activity budgets' findings, and further supports that different groups with different group sizes, group compositions and territory qualities may respond flexibly to unfavourable conditions in diverse – even opposite – manners.

Because our analysis of grooming-derived social networks does not support the social cohesion hypothesis (Bekoff, 1977; Blumstein, Wey, & Tang, 2009), we hypothesise that our study groups may have experienced different pressures (or pressure intensities), giving leeway to idiosyncratic motivations to fission. In that light, our approach to fissions using the framework of game theory, strategies (Dugatkin & Reeve, 1998; Reichert & Hammerstein, 1983; Maynard Smith, 1979), and decision-making (Sanfey, 2007; McNally, Brown and Jackson, 2012; Rosati, 2016; Guayasamin, Couzin and Miller, 2017) provides interesting insights. Fissions exemplify contexts where one individual alone cannot be influential enough to tip the balance for a group -and the females- to split into female-bonded groups. Alternatively, fissions are interesting because they can be studied from the perspective of certain individuals, and a subset of individuals that compose a collective, as we concentrated on the adult females. If groups split in two one can associate this phenomenon to an n-player game (Archetti, 2009). In such a scenario, individuals are confronted with the valuing of their circumstances and the symmetry they hold with the aggregate of individuals' perceptions that compose a group. These may be based, to some extent, on the quality of relationships that likely sculpt assortment (Farine, Strandburg-Peshkin, Couzin, Berger-Wolf, & Crofoot, 2017; Farine, 2014; McDonald, Farine, Foster, & Biernaskie, 2017; Walker & Hill, 2014) and the composition of the two daughter groups (Larson et al., 2018; Nishita et al., 2015; Stredulinsky, Darimont, Barrett-Lennard, Ellis, & Ford, 2021). And yet, the results presented here cannot support our initial hypothesis, which again may necessitate alternative looks on how individuals interacted before the fission.

Because strategies are likely to be shaped by personal circumstances, in an n-player game like group fissions, fitness-related characteristics can be pivotal. We chose the number of dependent offspring, the dominance rank, and having experienced (or not) the death of close kin members as factors that could modulate risk perceptions (Giraldeau and Livoreil, 1998; Heilbronner *et al.*, 2008). Our predictions established that risk-prone attitudes would be represented by the females that abandon their natal group and play the leaving strategy given the high costs of dispersal (Bonte *et al.*, 2012). On the contrary, risk-averse perceptions would be more akin to females that are worse-off due to additional costs of having dependent offspring or having experienced the death of a close kin individual. This strategy may be further benefited if vervet monkeys were able to adapt risk-taking behaviours to the personal standing (associated to dominance rank) that they have in the group and how this may impact their potential benefitting of a niche (Caraco *et al.*, 1990; Meunier, 2017). We found that the death of a close member influenced individuals to play the strategy of staying (Figures 7.1. and 7.2.). Nonetheless, we need to put this finding in perspective while assuming certain limitations due to the number of adult females involved in the three fissions that we studied (only 27 individuals).

Our correlation analysis showed that what we found is that the "grooming matrix" at T0 was correlated to the "final group composition matrix" and the same applies to the "nearest neighbour matrix" only in the NH group. Moreover, in the NH group, this correlation was significant only at T0 which further supports that adult female assortment was related to grooming and proximity (Table 5, Figure 7.2.). Still, how females were assorted in AK and KB group would need additional analysis that considers alternative behaviour measurements that could allow assortment estimations. We found no other significant correlations between group assortment matrix and grooming, kinship or nearest neighbour matrices (grooming and nearest neighbour being illustrative of bond, (Reddy & Sandel, 2020; Silk, Cheney, & Seyfarth, 2013). Still, these results deserve caution for two reasons: first, because multiple pairwise comparisons on the same matrix (kinship, same group or different) inevitably lower the statistical significance (Rice, 1989), and second, kinship is positive on a small subset of individuals considered per group, which may thwart the pinpointing of possible linkages. We can see this in Figure 7 where green nodes (females that played stay) and red nodes (females that played leave) seem more connected among themselves. Interestingly, NH was the group that had a higher number of females which may have been a key factor either for the behaviour dynamics discussed above or perhaps smaller groups' data like AK and KB may have provided comparably lower power of analysis.

Further, Figure 7.2. shows that all the female dyads that were kin stayed together. More studies delving into this and similar alternatives that have fitness implications like the lack of group synchrony or differential foraging efficiencies as part of volunteers' dilemma may shed light on how individuals perceive risk and the strategies of stay or leave manifest. If being part of a group pays off to certain lower-ranking individuals, even if they cannot have priority of access to food sources, it may well be that payoffs radically change under heavy ecological constraints and continuous scramble competition. Under such circumstances, the strategy of leaving (by lower-ranking individuals and some middle-ranking ones. Fig. 7.1.) may become more interesting if some players are worse off, even when ecological conditions are equally harmful to all because they need to adhere to others' decisions that touch on group movement. Moreover, we can exclude power ambition as a motivating factor (Figure A.1. and A.2. in Appendix) since rank dominance of the females stayed above 0.8 (scale 0-1) and there were no rank overtakes among the females. Not sticking to the group automatically raises the danger of being predated, and fissioning may partly resolve that issue by creating a sub-group that is under the same pressures but can navigate their landscapes playing a bigger role in the constant decision-making of a day or compromising less to keep a certain degree of synchrony and group cohesion. Fissions and consequent sub-grouping yield the setting of new scenarios for another potential ingredient causing volunteers' dilemmas: vigilance for predators (McNamara and Houston, 1992; Archetti, 2009) where n-players can renegotiate their involvement and assess potential payoffs which would open new avenues for strategies and cooperation to blossom (Hamilton, 1981; Raihani & Bshary, 2011). Strikingly, most of the dead individuals were higher-ranking, making the rank status and deaths factors be confounded, and eliciting questions about which causes may have precipitated such correlation.

Altogether, our study undresses the yet-poorly-understood phenomenon of group fissions in female-bonded groups. More investigations are needed to understand which behaviours indicate group disintegration or progressive group cohesion deterioration. With the evidence we put forward, it seems that fissions that occur under extreme pernicious ecological conditions may have acted as stimuli to the activation of a somewhat dormant behavioural option (de Witt, Sih and Wilson, 1998; Lotem and Halpern, 2012; Sachser, Kaiser and Hennessy, 2013), in our case, of group disintegration. However, we need to highlight that most of the predictions we made could not be verified and that previous studies that found group size a constraint to groups' maintenance (Holekamp et al., 1993; Malik et al., 1985; Ménard & Vallet, 1993; Widdig et al., 2006; Windfelder & Lwanga, 1988) which may be worth considering in combination with habitat quality aspects so to estimate the carrying capacity situation that individuals may be facing, independently of how many individuals live in the group. The fissions we report here provide evidence of flexible responses that confirm social competence to adverse conditions (Cosmides and Tooby, 2013; Bshary and Oliveira, 2015), but we cannot provide additional information about how adaptive these decisions were for the players of the different strategies.

Why individuals make such crucial -and uncertain- decisions, with the prospect of leaving bonds, losing the security of territory with known foraging and sleeping sites, where one knows how big a deal out-group-related menaces are is therefore still a puzzle. Empirical research and mathematical models that incorporate ecological, territorial, social networks and fitness measurements could help unveil how group-living animals can decide for different strategies with inherent risk nuances. Continuous monitoring of the populations before and after the fissions that touch on physiological evidence on stress levels, health states, sociality and cooperation behaviours could aid to have precise data on fitness correlates and assess how adaptive the stay and leave strategies result for the players of the fission game. Ultimately, this may assist to incorporate the complexity of a changing climate (Mason *et al.*, 2014; Eggeman *et al.*, 2016; Beever *et al.*, 2017; Estrada *et al.*, 2017) into the management and conservation of similar wild populations living in natural and comparable habitats if the causes of fissions could be detected.

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4.6. References

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4.7. Figures and tables

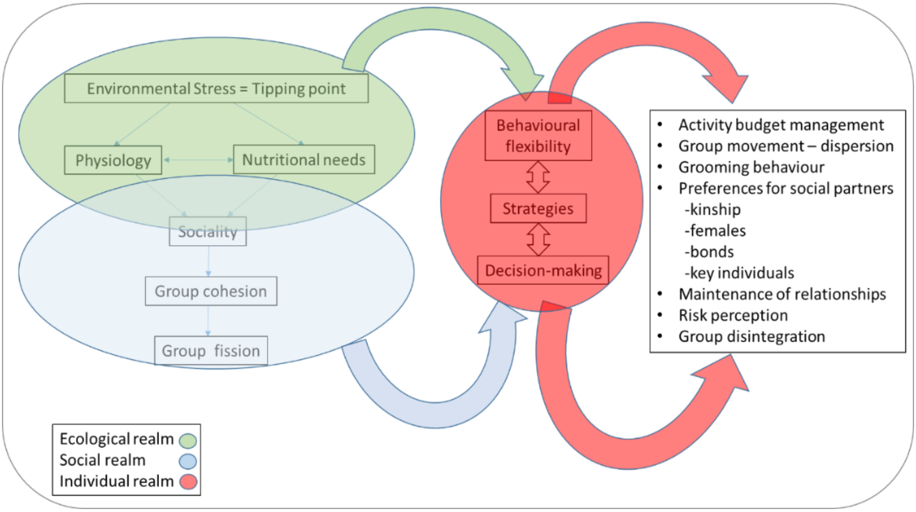

Figure 1. Scheme representing the embeddedness scope of the different dimensions that affect life in a group. Different areas or realms are: the ecological realm, societal realm, and cognitive realm. Socio-ecological aspects have been key drivers for evolution to provide adaptive responses in the form of behavioural flexibility, strategies, and decision-making. Finally, decision-making can cover the individual and collective spectrum that may not always be in synchrony, as it may happen when groups fission.

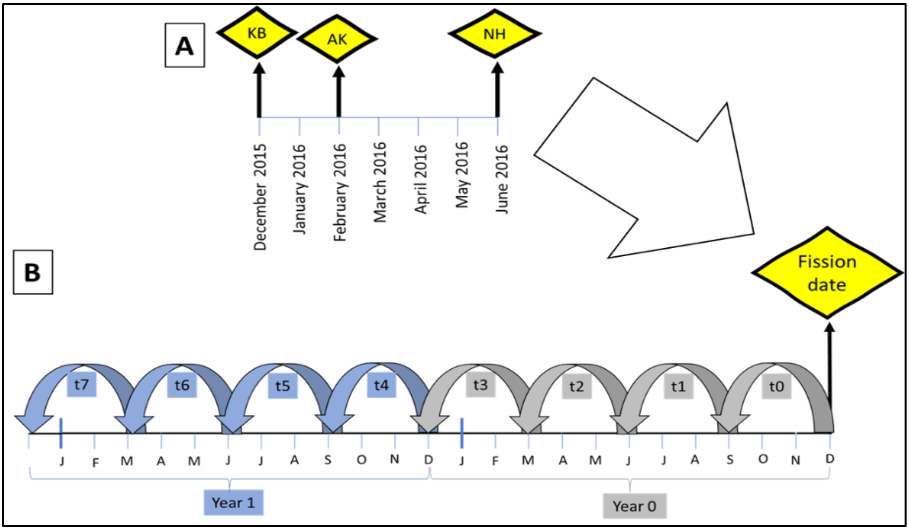

Figure 2. Sketch A illustrates the fission dates of each group (AK, 29 February 2016; KB, 15 December 2015; and NH, 19 April 2016). Sketch B shows the breaking of the two years into time windows according to the fission date using the example of KB (December). A day was subtracted from the first day the original group was split into two sub-groups and the time window zero (T0) goes from that day to three months back having a total of eight-time window (year 0= year of the fission, year 1= year before fission)

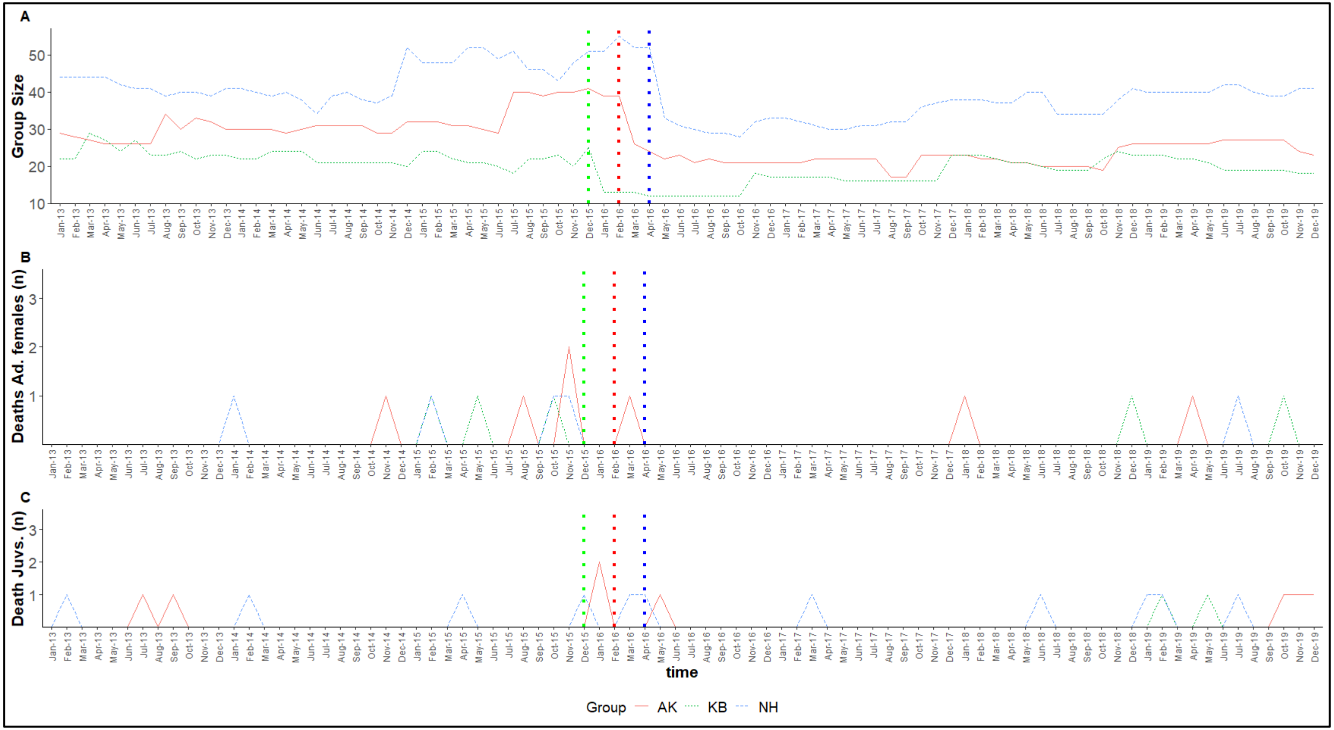

Figure 3.1. Demography evolution of the three groups (AK in red, KB in green, NH in blue) from January 2013 to December 2019. Vertical lines indicate the last day of the original group existence before the fission with colour assigned relative to each group identity. Figure A shows the evolution of the total group size; B represents the death of adult females, and figure C the death of juveniles.

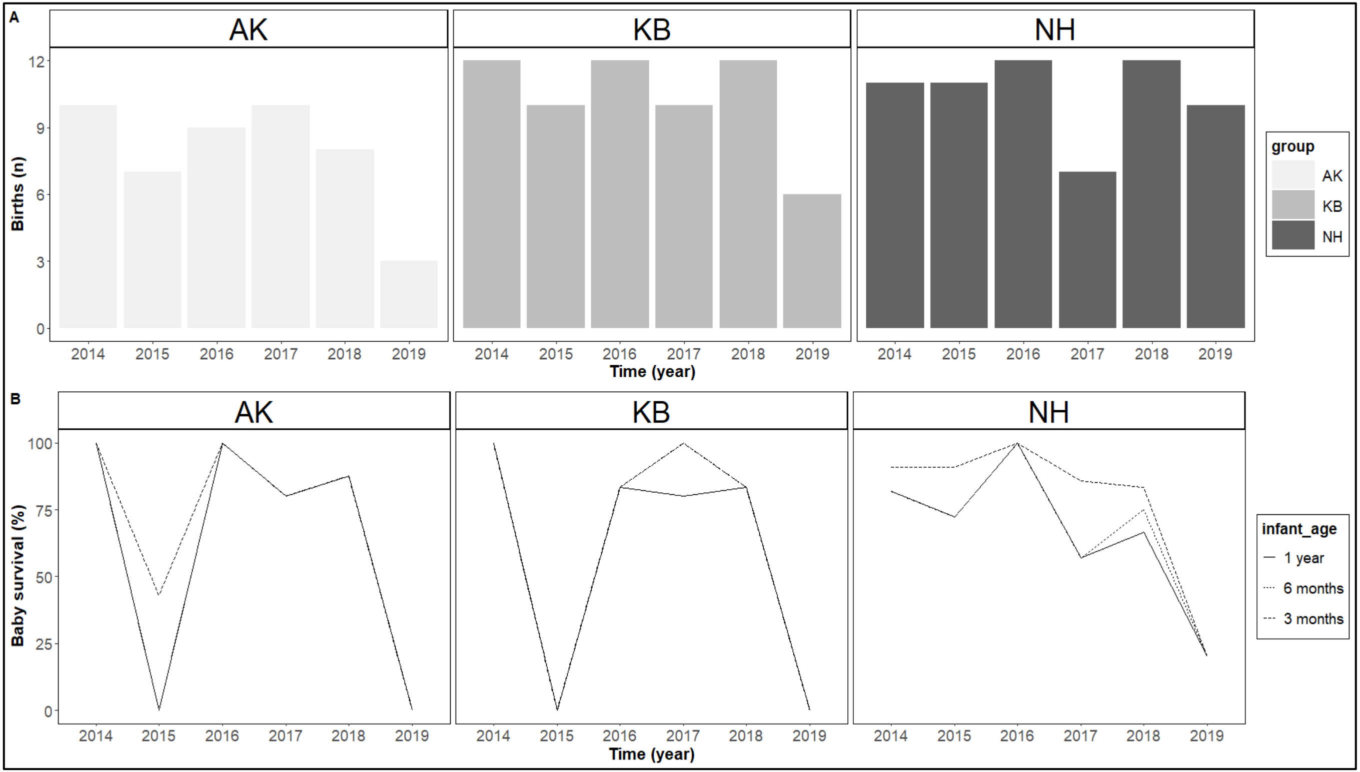

Figure 3.2. Fig. A- Total number of births across time, from 2014 to 2019 in the three groups of interest. Shown from left to right are the different groups: AK, KB, and NH. Fig. B show the percentage of birth survival at three different ages (full first year, 6 months, and 3 months) shown in lines of different thickness, across the same time frame for the same groups.

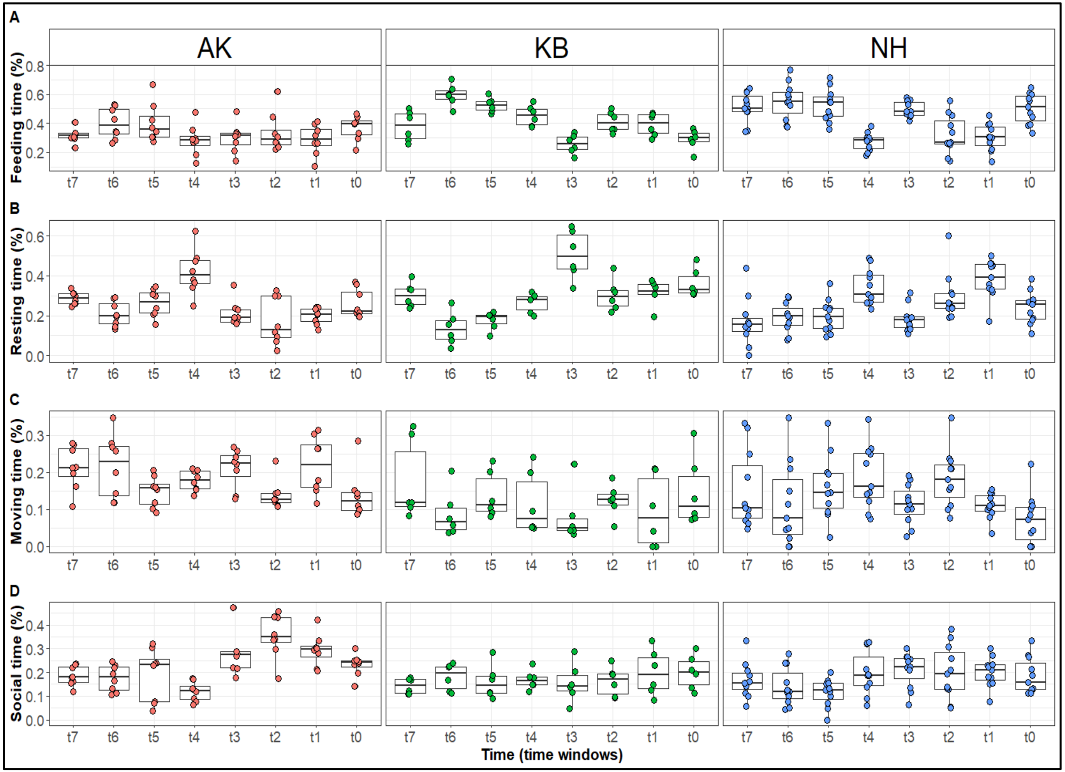

Figure 4. Activity budgets for the different groups and time windows studied. Activity budgets of foraging (labelled as feeding-A), resting (B), moving (C) and social (D) as a proportion of the total appear along the y-axis for the three groups (AK in red, KB in green, and NH in blue). Time windows are displayed along the x-axis so T7 (leftmost) represents up to 2 years before the fission, and T0 (rightmost), the moment right before the fission.

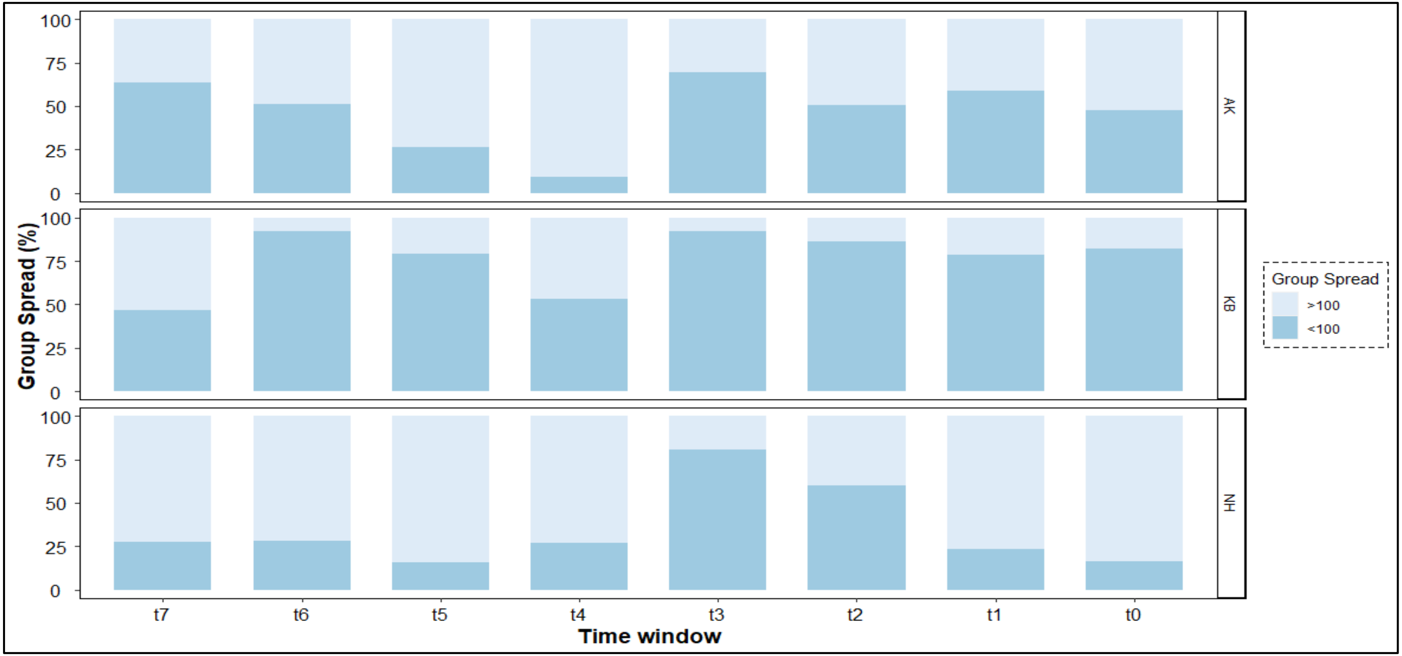

Figure 5. The proportion of times each group (AK, KB, NH) was more dispersed than 100 metres (light blue colour) and less than 100 metres (darker blue). The 2 years of study is presented along the x-axis, from more time away to less time away to fission going from left to right.

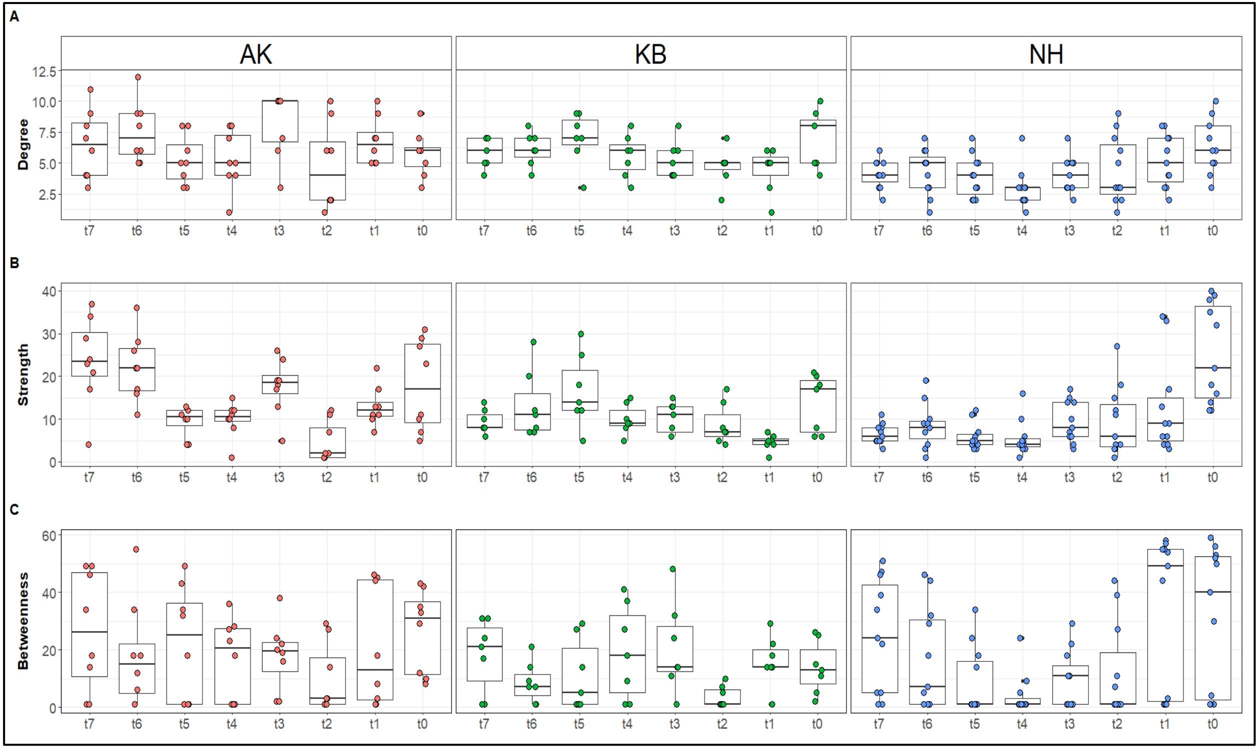

Figure 6.1. Bar plots of individual-level grooming metrics. Shown the different metrics from top to bottom row are shown the different measures of degree (first row; A), strength (second row; B), and betweenness (bottom row; C). Each female individual is represented as a point. Time appears on the x-axis so older time windows appear to the rightmost, and the closest time windows to the fission to the leftmost.

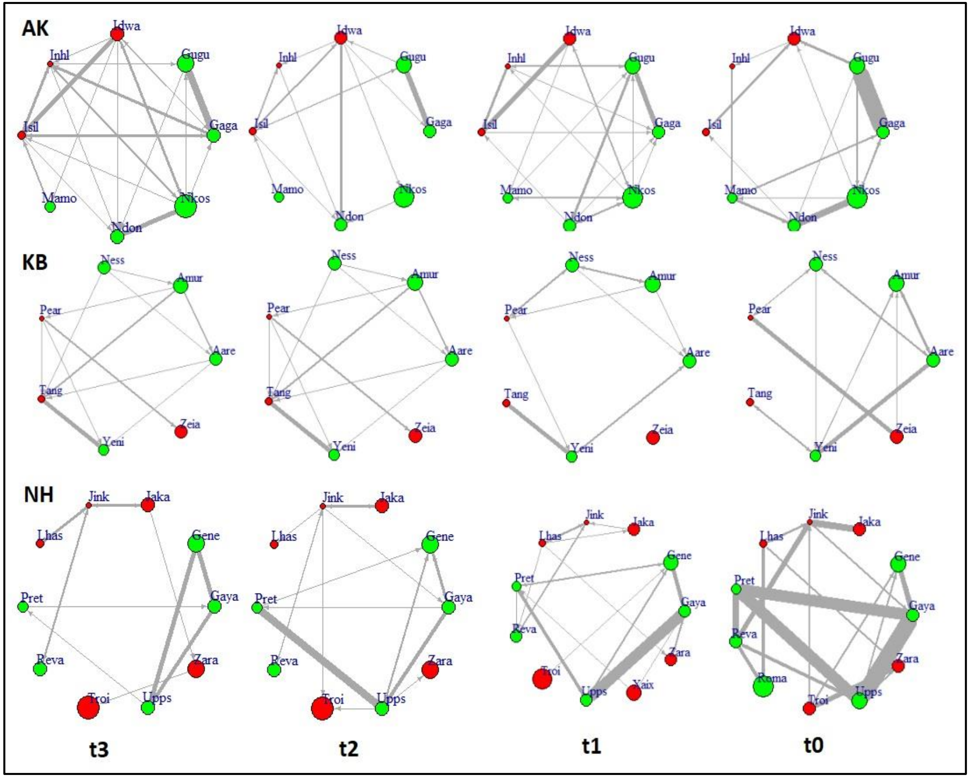

Figure 6.2. Grooming network evolution in the time windows along the x-axis from left to right from further away to closer to the fission. The thickness of the nodes represents the individual metric of degree, and the width of the connections or edges, by the individual metric of strength. Red nodes symbolize the females that played the strategy of leaving while green nodes symbolize the females that played the strategy of staying in the original group.

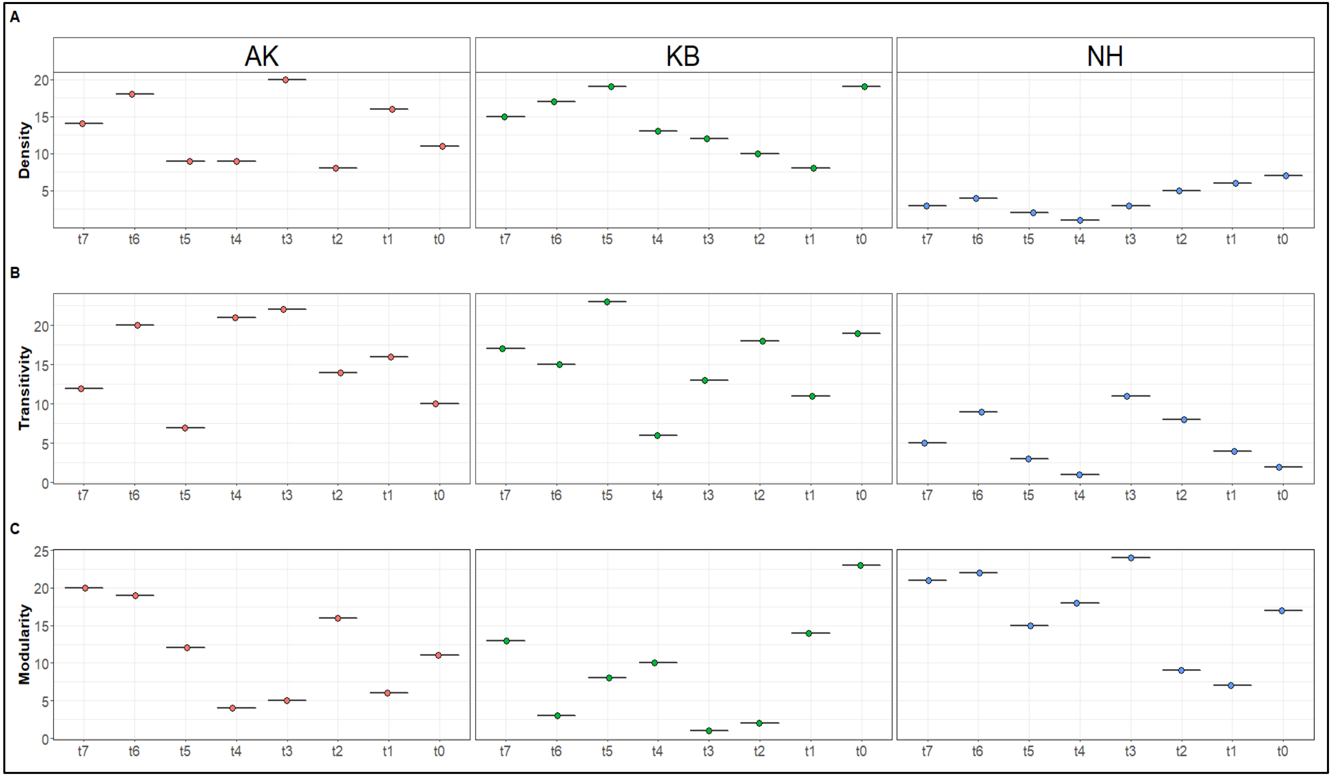

Figure 6.3 Bar plots of group-level grooming metrics. Shown from top row to bottom row are the measures of density (first row; A), transitivity (second row; B), and modularity (bottom row; C). Each metric consists of a single group measurement that reflects the interactions between all females. The timeline is shown in the x-axis, going from left to right as time windows further away from the fission approach the fission moment

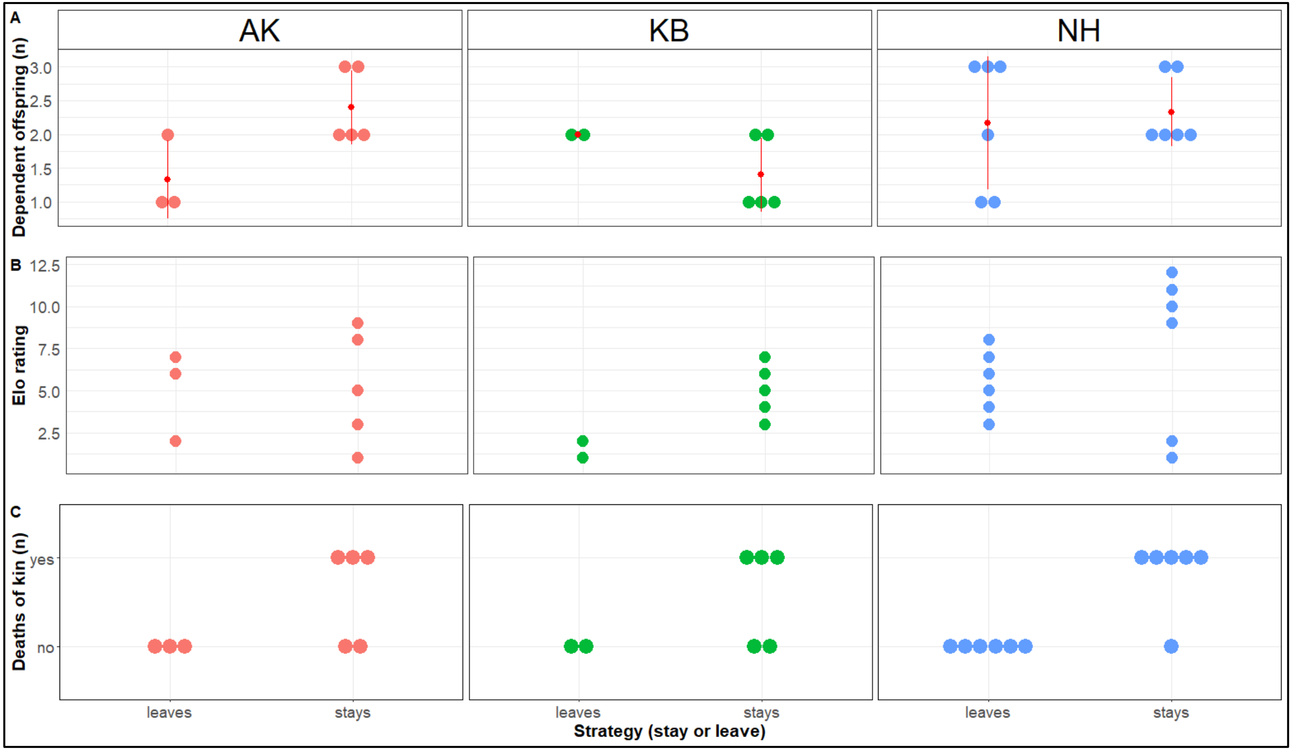

Figure 7.1. Graphs showing the three factors considered in the shaping of decision-making around the two possible strategies of staying or leaving that the females manifested during the fission. On the top row, Fig. A shows the number of dependent offspring (younger than 2 years) of each female. Fig. B shows the rank dominance through Elo-rating scores before the fission time in each group. Finally, Fig. C summarizes if the females experienced the death of any close kin (above 0.375 relatedness values) during the two years of study.

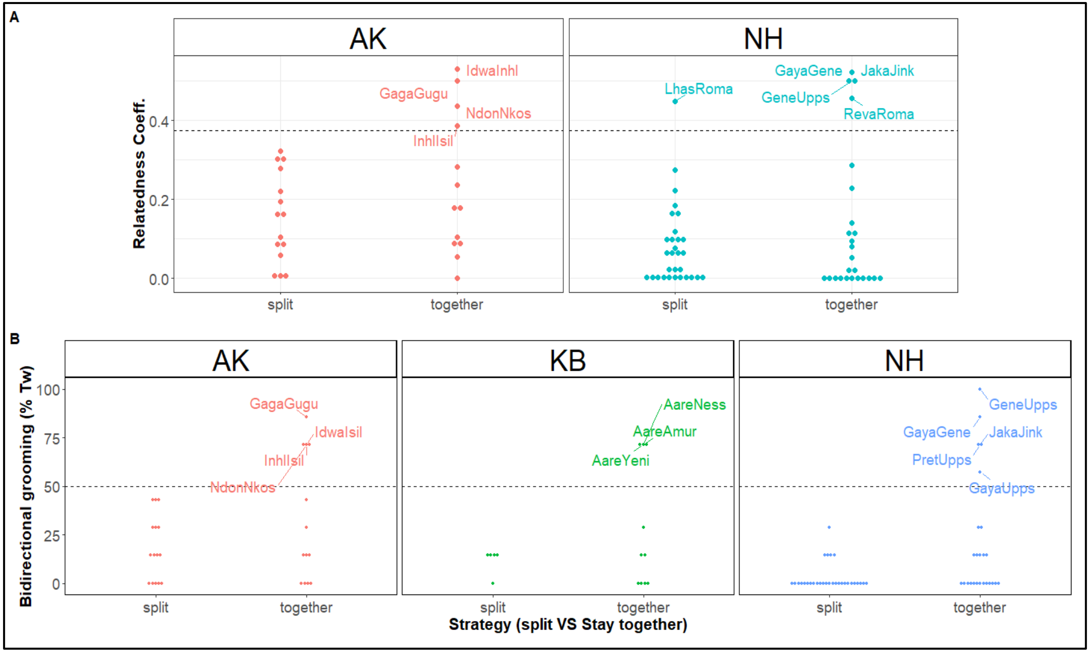

Figure 7.2. Strategies of stay and leave that the adult females finally played with regards to with whom to stay. The two options appear in the x-axis as a split which involves that the two females no longer belong to the same group; and as together when they end up belonging to the same group, independently of whether they do so in the original territory or have to find a new one. Each dot represents a female dyad. Figure A shows the relatedness coefficient with a dotted line representing the threshold we considered to determine kinship (relatedness data not available for the KB group). Figure B depicts bidirectional grooming as a measure of grooming reciprocity between each female dyad. Y-axis represents the percentage of time windows in which the grooming between the dyads was bi-directional, and the dotted line marks the more or less than 50% chance.

Response variable	Predictor	Chisq	Df	P-value	AK Group			KB Group			NH Group		
					T0 - Tw	Estimate	P-value	T0-Tw	Estimate	P-value	T0-Tw	Estimate	P-value
Foraging	Tw	146.45	7	*<0.001*	T1	0.082	0.200	T1	-0.101	0.144	T1	0.197	*<0.001*
	Group	12.28	2	*0.002*	T2	0.034	0.874	T2	-0.120	0.055	T2	0.179	*<0.001*
	Tw: Group	117.58	14	*<0.001*	T3	0.069	0.359	T3	0.032	0.932	T3	0.008	0.997
					T4	0.085	0.172	T4	-0.161	*0.003*	T4	0.230	*<0.001*
					T5	-0.032	0.896	T5	-0.236	*<0.001*	T5	-0.024	0.929
					T6	-0.031	0.900	T6	-0.305	*<0.001*	T6	-0.051	0.491
					T7	0.053	0.601	T7	-0.090	0.238	T7	-0.009	0.995
Resting	Tw	85.56	7	*<0.001*	T1	0.061	0.402	T1	0.048	0.730	T1	-0.144	*<0.001*
	Group	4.11	2	0.128	T2	0.088	0.096	T2	0.059	0.571	T2	-0.054	0.368
	Tw: Group	165.52	14	*<0.001*	T3	0.048	0.633	T3	-0.143	*0.006*	T3	0.057	0.321
					T4	-0.160	*<0.001*	T4	0.098	0.120	T4	-0.101	*0.010*
					T5	-0.001	1	T5	0.186	*<0.001*	T5	0.041	0.628
					T6	0.052	0.553	T6	0.227	*<0.001*	T6	0.047	0.510
					T7	-0.260	0.928	T7	0.060	0.560	T7	0.0714	0.130
Moving	Tw	20.91	7	*0.003*	T1	-0.081	*0.036*	T1	0.051	0.475	T1	-0.038	0.493
	Group	6.19	2	0.045	T2	-0.001	1	T2	0.023	0.967	T2	-0.111	*<0.001*
	Tw: Group	51.06	14	*<0.001*	T3	-0.074	0.075	T3	0.067	0.230	T3	-0.042	0.391
					T4	-0.040	0.582	T4	0.032	0.834	T4	-0.116	*<0.001*
					T5	-0.010	0.991	T5	0.008	0.997	T5	-0.088	*0.004*
					T6	-0.078	*0.047*	T6	0.059	0.350	T6	-0.042	0.399

					T7	-0.075	0.062	T7	-0.028	0.882	T7	-0.080	*0.010*
Social	Tw	50.73	7	*<0.001*	T1	-0.062	0.274	T1	0.001	1	T1	-0.016	0.967
	Group	8.28	2	*0.016*	T2	-0.122	*0.002*	T2	0.038	0.797	T2	-0.014	0.975
	Tw: Group	50.15	14	*<0.001*	T3	-0.044	0.607	T3	0.044	0.704	T3	-0.023	0.884
					T4	0.113	*0.004*	T4	0.032	0.876	T4	-0.013	0.980
					T5	0.043	0.609	T5	0.041	0.760	T5	0.071	0.068
					T6	0.057	0.349	T6	0.020	0.971	T6	0.046	0.410
					T7	0.048	0.524	T7	0.060	0.467	T7	0.018	0.943

Table 1. Activity budgets GLMM analysis for the different groups. Tw represents time windows. Time window comparisons are shown concerning T0, so the proportion registered at any other time window is substracted to T0 (Estimates), and the P-value of each group is calculated using *emmeans* to evaluate the difference with T0. Results are shown in italics when P-values are smaller than 0.05.

Response variable	Predictor	Chisq.	Df	P-value	Group AK			Group KB			Group NH		
					T0-Tw	Estimate	P-value	T0-Tw	Estimate	P-value	T0-Tw	Estimate	P-value
Group spread (>100 metres)	Tw	204.36	7	*<0.001*	T1	1.152	*0.041*	T1	-2.754	*<0.001*	T1	-1.62	*<0.001*
	Group	278.54	2	*<0.001*	T2	-0.647	0.540	T2	-1.875	*<0.001*	T2	1.185	0.095
	Tw : Group	222.88	14	*<0.001*	T3	1.654	*0.002*	T3	2.153	*0.010*	T3	1.919	*<0.001*
					T4	-2.805	*<0.001*	T4	-2.80	*<0.001*	T4	0.422	0.883
					T5	-0.122	0.997	T5	-1.892	*0.002*	T5	-1.745	*0.060*
					T6	0.593	0.677	T6	-0.073	0.999	T6	0.953	0.303
					T7	0.064	0.999	T7	-3.898	*<0.001*	T7	1.811	*0.008*

Table 2. Summary of analysis of group spread variation with time window (Tw) and the group as fixed factors and its interaction. Main results are provided for the predictors, and specific changes in each time window compared to the time window before the fission, that is, T0, is shown for each group separately. Estimates are calculated for the proportion of group spread above 100 metres, so when estimates are positive in the difference of T0 minus some other time window it reflects that in T0 the proportion of times the group was spread more than 100 metres was higher. Results are shown in italics when P-values are smaller than 0.05.

Grooming networks	**Response variable**	**Predictor**	**Chisq.**	**Df**	**P-value**	**Group AK**			**Group KB**			**Group NH**		
						T0-Tw	**Est.**	**P-value**	**T0-Tw**	**Est.**	**P-value**	**T0-Tw**	**Est.**	**P-value**
Individual level	Degree	Tw	23.66	7	*0.001*	T1	-1	0.738	T1	2.57	*0.045*	T1	1.273	0.391
		Group	11.76	2	*0.003*	T2	1	0.738	T2	2.28	0.095	T2	2	0.053
		Tw :Group	41.60	14	*<0.001*	T3	-2.5	0.033	T3	1.71	0.321	T3	2.36	*0.014*
						T4	0.5	0.963	T4	1.43	0.500	T4	3.46	*<0.001*
						T5	0.5	0.963	T5	0	1	T5	2.55	*0.006*
						T6	-1.75	0.240	T6	0.86	0.854	T6	2.18	*0.028*
						T7	-0.75	0.878	T7	1.14	0.691	T7	2.36	*0.014*
	Strength	Tw	87.36	7	*<0.001*	T1	4.87	0.357	T1	9.14	*0.017*	T1	12.73	*<0.001*
		Group	5.78	2	0.055	T2	13.25	*<0.001*	T2	4.86	0.426	T2	15.82	*<0.001*
		Tw :Group	113.08	14	*<0.001*	T3	0.25	0.999	T3	3.43	0.727	T3	15.82	*<0.001*
						T4	8.0	*0.030*	T4	3.71	0.669	T4	19.73	*<0.001*
						T5	8.37	*0.020*	T5	-2.86	0.830	T5	19.46	*<0.001*
						T6	-4.37	0.464	T6	0.43	0.999	T6	16.82	*<0.001*
						T7	-5.75	0.205	T7	4.29	0.547	T7	18.73	*<0.001*
	Betweenness	Tw	29.39	7	*<0.001*	T1	5.75	0.919	T1	-2.14	0.997	T1	-2.82	0.985
		Group	3.16	2	0.206	T2	16.62	0.181	T2	10.14	0.689	T2	19.36	*0.027*
		Tw :Group	22.81	14	0.06	T3	8.62	0.754	T3	-6.71	0.896	T3	21.82	*0.009*
						T4	9.62	0.679	T4	-5.29	0.949	T4	27.36	*<0.001*
						T5	4.12	0.970	T5	2.71	0.994	T5	22.73	0.006
						T6	8.38	0.77	T6	5.29	0.949	T6	14.73	0.153
						T7	0	1	T7	-4.14	0.976	T7	6.55	0.819

Table 3. Summary results of the model that evaluates the change of individual grooming network parameters concerning the predictors time window, group, and interaction of the two. Comparisons for each group address the variation between any time window and T0, that were obtained using the *emmeans* function. P-values are indicated in italics when a value smaller than 0.05.

Grooming networks	Response variable	Predictor	Chisq.	Df	P-value	T0-Tw	Estimate	P-value
Group-level	Density	Tw	5.53	7	0.596	T1	2.33	0.914
						T2	4.67	0.536
						T3	0.67	0.998
						T4	4.67	0.536
						T5	2.33	0.914
						T6	-0.66	0.998
						T7	1.67	0.968
	Transitivity	Tw	3.67	7	0.817	T1	0	1
						T2	-3	0.928
						T3	-5	0.723
						T4	1	0.998
						T5	-0.67	0.999
						T6	-4.33	0.804
						T7	-1	0.998
	Modularity	Tw	5.79	7	0.565	T1	8	0.564
						T2	8	0.564
						T3	7	0.669
						T4	6.33	0.736
						T5	5.33	0.828
						T6	2.33	0.985
						T7	-1	0.999

Table 4. Results of GLMM model evaluating the change of the different group-level grooming parameters at the individual level (density, transitivity, modularity) with the predictors of the group, time window, and its interaction. From left to right: Chi-square, Degrees of freedom (Df), and P-value correspond to the output of the general model. T0-Tw, Estimates, and P-value correspond to the output of T0 compared to each time window, from the perspective of T0, following the logic that if estimates are positive, T0 was higher.

Group	**Stay in same group & Grooming**				**Stay in the same group & Proximity**			
	Tw	**Obs. corr.**	**P-value**	**P’**	**Tw**	**Obs. corr.**	**P-value**	**P’**
AK	T0	0.433	0.056	0.896	T0	0.322	0.15	2.25
	T1	0.215	0.208	2.912	T1	0.06	0.549	4.392
	T2	0.124	0.375	3.75	T2	0.258	0.267	3.471
	T3	-0.072	0.812	4.06	T3	0.258	0.275	3.300
	T4	0.131	0.354	3.894	T4	-0.029	0.776	4.656
	T5	-0.113	0.876	3.504	T5	-0.045	0.734	5.138
	T6	-0.215	0.945	2.835	T6	-0.207	1	1
	T7	0.131	0.4	3.600	T7	-0.207	1	2
KB	T0	0.472	0.10	1.53	T0	0.33	0.19	1.88
	T1	0.462	0.13	1.862	T1	0.145	0.52	2.605
	T2	0.389	0.29	2.058	T2	0.248	0.23	2.106
	T3	0.389	0.14	1.755	T3	0.34	0.24	1.904
	T4	0.392	0.15	1.617	T4	NA	NA	NA
	T5	0.462	0.15	1.740	T5	-0.213	1	1
	T6	-0.135	0.85	1.708	T6	0.015	0.70	2.812
	T7	-0.135	0.82	2.448	T7	0.139	0.46	2.76
NH	T0	0.428	0.001	*0.017*	T0	0.364	*0.002*	*0.032*
	T1	0.208	0.086	0.688	T1	0.379	*0.012*	0.168
	T2	0.169	0.126	0.882	T2	0.267	*0.04*	0.4
	T3	0.314	0.033	0.363	T3	0.031	0.595	1.785
	T4	0.151	0.263	1.315	T4	-0.084	0.856	0.856
	T5	-0.008	0.646	1.292	T5	0.059	0.455	1.82
	T6	0.347	0.013	0.169	T6	0.249	0.032	0.384
	T7	0.407	0.004	0.06	T7	0.161	0.129	0.774

Table 5. Mantel correlation analysis comparing the binary strategy of stay and leave with grooming and proximity matrices (binary values) during all the period of study (T0-T7). P-values follow the significance of ranks (Rice, 1989) to obtain corrected P-values (P’). Significant P values are in italic.

4.8. Appendix

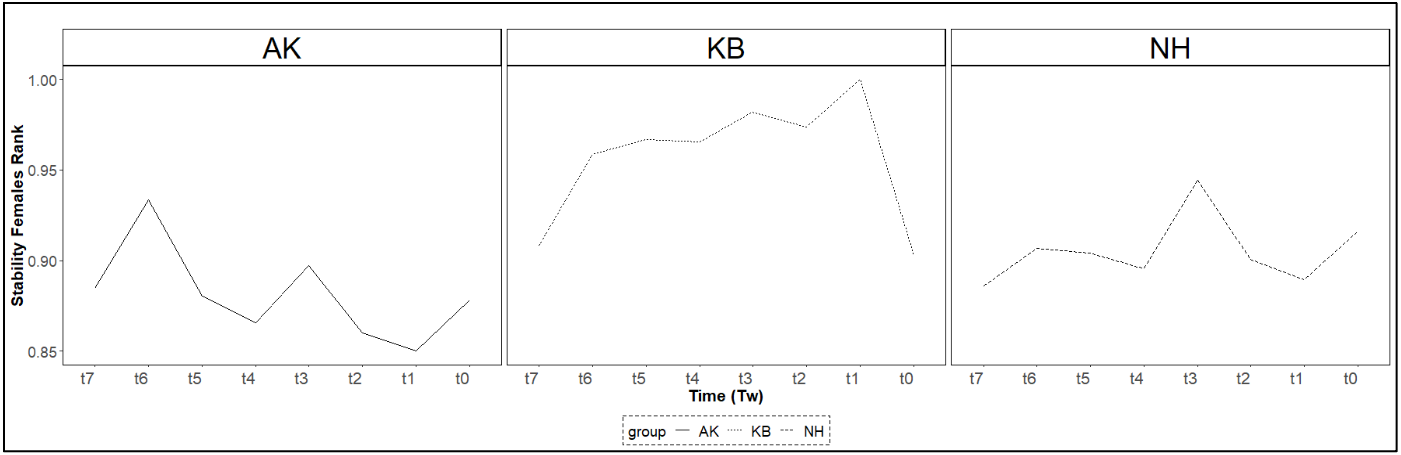

Figure A.1. Stability of rank dominance of all females in each one of the groups. For each time window. Ranks were calculated using Elo-rating and the function *stab elo* was used to calculate how much a given subset of individuals experience variation in their scores.

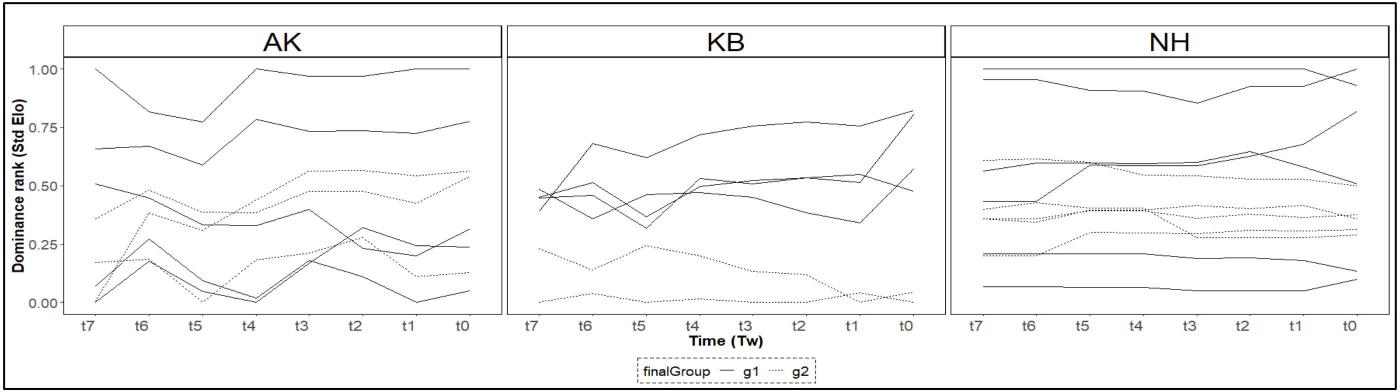

Figure A.2. Evolution of rank dominance through Elo-rating scores of each female in the three groups. Higher dominance associated with higher values, which are the result of standardization, so scores range between zero and one. Continuous lines represent females that played the strategy of staying (here symbolised as *g1*), and dotted lines represent the females that played the strategy of leaving (here symbolised as *g2*).

Phenomena described	Species	Social structure	Preceding causal/conditioning factors	Possible benefits from phenomena	Referece
Eviction, dispersal	Banded mongoose (*Mungos mungo*)	Cooperative breeders	Aggression intensification	Dominants in better control of groups’ reproductive output (and of subordinates’ one)	Cant et al. 2001
Eviction	Banded mongoose (*Mungos mungo*)	Cooperative breeders	Reproductive competition	Litter size in evictors increased (but decreased in evictees)	Thompson et al. 2016
Eviction	Meerkats (*Suricata suricatta*)	Matrilineal groups where males and females seldom disperse	Not specified	Group size regulation by the dominant, and dominant maximization of inclusive fitness	Stephens et al. 2005
Eviction	Rhesus macaque (*Macaca mulatta*)	Female philopatric, multi-male multi-female	Changes in social partners for grooming in evicted females received also more aggression	Cohesion maintenance after better balancing time budget restrictions and grooming relations	Larson et al. 2018
			Increase in group size, progressive cohesion loss and sub-grouping	Smaller new groups that formed having high birth rates the first year and low infant mortality after fission	Malik et al. 1985
			Spatial fragmentation and cessation of grooming in two subgroups	Formed groups maintain social ties	Missakian 1973
			The average degree of relatedness decreased. Loss of connector females increases the likelihood of genealogy divide	Higher average relatedness in newly formed groups	Chepko-Sade and Olivier 1979; Chepko-Sade

					and Sade 1979
			Rapid population growth (provisioned by humans)	Maternal lines preserved in new groups, accelerate population differentiation	Melnick and Kidd 1982
			Not specified	Genetic differentiation between newly formed groups	Cheverud et al. 1978
			Group cohesiveness deteriorated affecting dispersion. Partial increase in matrilineal size	Maternal half-siblings stayed together	Widdig et al. 2006
			Subgrouping patterns in grooming interactions and more aggressive reception by evicted females.	Evicted females were kin, inclusive fitness	Larson et al. 2018
Fission	Cape ground squirrel (*Xenus inauris*)	Female philopatric	Saturated habitat, lower juvenile survival before fission	Better coping with predators, perhaps inactivation of reproductive suppression of females in a smaller group	Waterman 2001
Fission	Black-tailed praire dogs (*Cynomys ludovicianus*)	Colonial breeders	Intragroup competition	Genetically distinct new coteries (family groups)	(Manno *et al.*, 2007)
Fission	Spotted hyena (*Crocuta crocuta*)	Multi-male, multi-female clans	Clan size increase, low ranking females pregnant in the periphery of the group, within-group competition. High male juvenile sex ratio bias	Maintenance of kin lines, better feeding opportunities in the smaller new group. More balanced juvenile sex ratios	Holekamp and Smale 1995
		Multi-male, multi-female, female philopatric	Intraspecific food competition, unusual high density, rank competition, availability of vacant neighbouring habitat	New subordinate clan better coping with high-density and low food availability. Kin maintenance, Some individuals	Holekamp et al. 1993

				tried to re-join the original group (got injured and lost rank as a result)	
Fission	Blue monkeys (*Cercophitecus mitis*)	Female philopatric, one male, multiple females	Females that groomed and stayed in proximity stayed together	Males gain control over receptive females	Cords and Rowell 1986
Fission	Red-tailed monkeys (*Cercophitecus Ascanius*)	Female philopatric, one male, multiple females	Subgroup spatial separation, an increase of group size	Rapid turnover of males in one daughter group, increase in the number of males in another daughter group	Windfelder and Lwanga 1988
Fission	Formosan macaques (*Macaca cyclopis*)	Female philopatric, multi-male, multi-female	Lower-ranking females experience increasing costs due to ecological pressure or population growth	Increased reproductive benefits for males	Hsu et al. 2017
Fission	Tibetan macaque (*Macaca thibetana*)	Female philopatric, multi-male, multi-female	Troop oversize, difficulties to keep group cohesion, intra-troop competition for food	Social relations more in tune in resulting groups	Li et al. 1996
Fission	Moor macaques (*Macaca maurus*)	One male/multi-male, multi-female groups	Not specified	Mothers and offspring stayed together. New establishment of home ranges	Okamoto and Matsumura 2001
Troop division	Barbary macaques (*Macaca sylvanus*)	Female philopatric, multi-male, multi-female	Group size increase, decrease in acorn production, instability of inter-individual associations (male-female, female-female)	Maternally related individuals stayed together. Improved female cohesion and males impeding stranger males to join the group	Ménard and Vallet 1993

Fission	Barbary macaques (*Macaca sylvanus*)	Female philopatric, multi-male, multi-female	Peripheralisation of subgroups, mainly young adult males	Female kin, even large matrilines stayed in the same groups (support during conflicts). More variable sex-ratio	Kuester and Paul 1997
Fission	Japanese macaques (*Macaca fuscata yakui*)	Female philopatric, multi-male, multi-female	Possible rank reversals preceding fission increased antagonism among females	Separation of groups obeying kinship and dominance, rearrangement of social relationships over a population, also involving males' relationships	Oi 1988
Fission	Wild toque macaque (*Macaca sinica*)	Multi-male multi-female	Sub-grouping before fission, group size increase and high intragroup competition for resources. Change in dominance relations in individuals that fissioned. Harsh ecological conditions after cyclone	Maintenance of kinship lines, low ranking females more able to cope with intragroup competition for resources. Maturation of young females in new groups imposing less risk upon older females in more reduced resulting groups.	Dittus 1988
Eviction	Redfronted lemurs (*Eulemur rufifrons*)	Multi-male, multi-female (all from the same matriline) with male transfer and female eviction	Group size constraining reproductive success of females	Possibly an adaptation to deal with chronic stress and securing individual reproduction and survival in small groups (theoretically)	Kappeler and Fichtel 2012
Fission	Ring-tailed lemur (*Lemur catta*)	Female-philopatric, multi-male,	Within troop competition, escalated aggression	More cohesive groups than previous one, less agonistic and more affiliative	Hood and Jolly 1995

		multi-female groups			
Fission	Tana river mangabey (*Cercocebus galeritus*)	Multi-male, multi-female, both sexes' migration (?)	Not specified	The resulting groups maintained the original home range but did not overlap the majority of the time, reducing direct feeding competition	Wieczkowski 2013
Fission	Ursine colobus (*Colobus vellerosus*)	Uni-male/multi-male multi-female groups	Not specified	Increased average pairwise relatedness and dispersion of new groups	Goodfellow et al. 2019
Fission	Chacma baboon (*Papio cynocephalus ursinus*)	Multi-male, multi-female	Not specified	Rank promotion in the new group, females maintain male associates	Ron et al. 1994
		Multi-male, multi-female	High cost of male sexual competition, increased tendency for sub-grouping before final fission	Increased male reproductive success	Ron 1996
Fission	Olive baboon (*Papio anubis*)	Female philopatric, few males, multiple females	Male rank instability, social bonds and kinship distinctive prior fission	Unspecified	Nash 1976
Fission	Yellow baboon (*Papio cynocephalus*)	Female philopatric, multi-male, multi-female	Inefficiency in keeping social relationships with group size increases	Alleviation of difficulties to maintain social relations	Henzi et al. 1997
Fission	Savannah baboons (*Papio*	Female philopatric,	Underlying feeding competition and presence of a subgroup of individuals with mutually shared interests	Opportunity for females to disperse and improve their benefit to cost ratio of living in	Van Horn et al. 2007

	cynocephalus)	multi-male, multi-female		a group while staying with their kin. Smaller group size enhances female reproduction	
Fission	Nilgiri langurs (*Presbytis johnii*)	One-male group/multi-male, multi-female groups	Loud call vocalisations by males preceded fission. Aggression increased around fission time	New groups acquired the formation of one-male groups. Resulting groups having several mature males and females (VS founder group having one male only)	Hohmann 1990
Fission	Norther muriquis (*Brachyteles hypoxanthus*)	Male-philopatric, multi-male, multi-female, female migration	Progressive sub-grouping, spatial segregation of original group, possibly motivated by food competition	Not specified	Tokuda et al. 2014
Fission	Wild mountain gorillas (*Gorilla beringei beringei*)	One male (sometimes a few subordinates queuing) and multiple females system	Not specified	Two resulting groups more homogenously distributed with regards to paternal relationships	Nsubuga et al. 2007
Fission	Chimpanzee (*Pan troglodytes schweinfurthii*)	Male-philopatric, multi-male, multi-female	Subgrouping in grooming and association networks, male dominance instability, reproductive competition as a possible catalyst	Formation of two independent, distinctive and cohesive groups	Feldbum et al. 2018
Fission	Humans (several ethnicities)	Analyses of different group	Internal political conflict	Kin bias in a residential assortment	Walker and Hill 2014

	(*Homo sapiens*)	structures, multi-male,-multi-female			
Fission	Humans (*Homo sapiens*), Yanomamo	Multi male,-multi-female	Increase in group size	Greater genetic divergence between daughter villages, reduction of village sizes, rate of human radiation within (and possibly among) tribal population is accelerated	Chagnon 1975
Split	Killer whale (*Orcinus orca*)	Matrilineal groups	Population growth and its influence on group structure	Formation of more optimal groups (female dispersal) maintaining familiar social relationships	Stredulinsky et al. 2021
Split	Indo-pacific dolphin (*Tursiops aduncus*)	Multi-male multi-female and fission-fusion	Male sub-grouping association patterns before fission	Resulting groups more cohesive possibly benefiting cooperation to obtain access to reproductive females	Nishita et al. 2015

Table A1. **Example of studies reporting the phenomena of eviction, group fission and splitting in different animal taxa. For** the sake of brevity, only examples of wild and unprovisioned mammals are included. The terms split and fission are interchangeable, and scientific names appear as referred to in the publications.

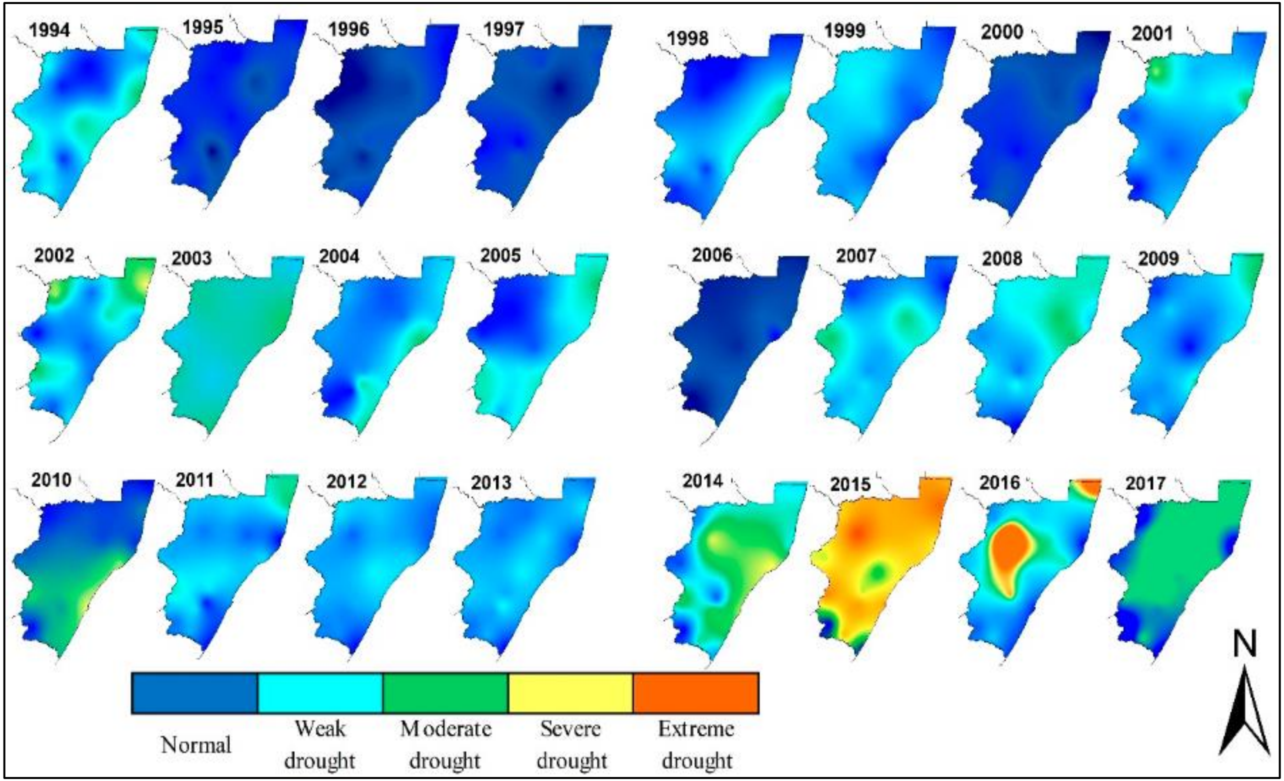

Figure A.3. Spatiotemporal distribution of PNPI index across the Kwazulu-Natal province in South Africa. Extracted from the 1970-2017study of Prof. Demlie Molla (image use authorised by the author).

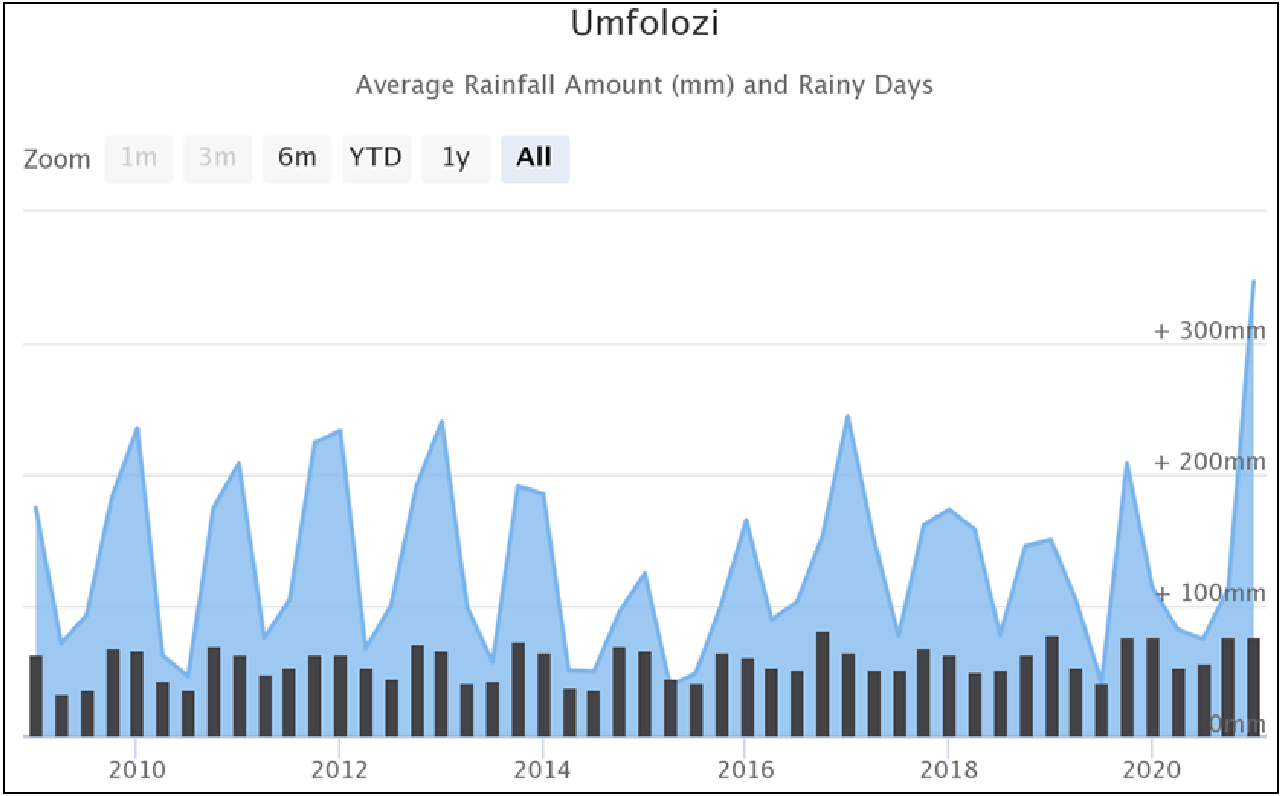

Figure A.4. Rain distribution for the period 2010-2020 in Umfolozi area. Umfolozi is located in Kwazulu-Natal region, approximately 100 km away from Mawana Game Reserve where the Inkawu Vervet Project is located. Extracted from: https://www.worldweatheronline.com/umfolozi-weather-averages/kwazulu-natal/za.aspx.

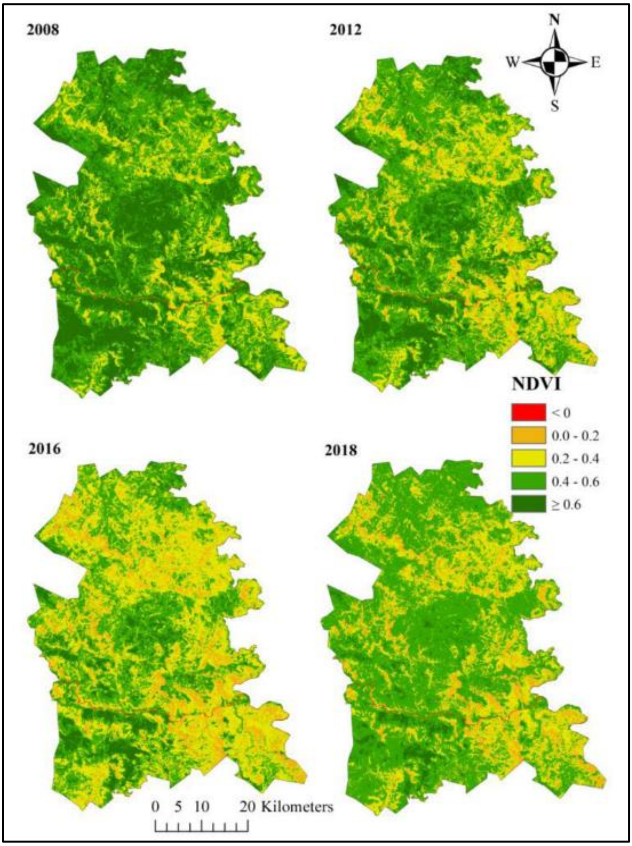

Figure A.5. NDVI representation of the uMsinga region. Extracted with the permission of Dr Lottering (Lottering, Mafongoya and Lottering, 2020) representing the NDVI maps (Normalised Difference Vegetation Index) in the uMsinga region, in Kwazulu-Natal province (200 kilometres away from IVP approximately), with yellow colours indicating lower values of NDVI.

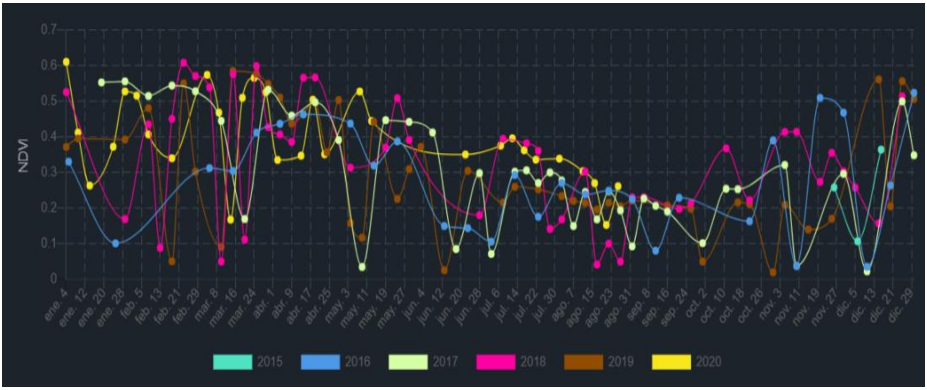

Figure A.6. NDVI values for the different groups that the Inkawu Vervet Project surveys regularly. The period of 2015 to 2020 is represented, showing an acute decline during the summer-rainy moment of the season in 2015. This coincides with the rainfall data of Ndlovu et al (Ndlovu and Demlie, 2020) and the NDVI mapping of Lottering et al. (Lottering, Mafongoya and Lottering, 2020). We can appreciate that the NDVI values achieve bottom levels that would correspond to 0.2-0.1, which would be representing more severe drought states than Ndlovu et al. Moreover, it can be appreciated that NDVI values plummet in 2019 during the summer-wet moment of the year, which further equates to a moment when the survival of babies plunged and there some juveniles and adult females were reported to die (Courtesy of Dr Miguel de Guinea).

CHAPTER 5. Laboratory protocols for analysis of hormones using vervet monkey urinary samples

Appendix A. Steroid analysis protocol for vervet monkey urine samples

Miguel Gareta García, Philippe Vullioud, Redouan Bshary, Gaétan Glauser

Sample preparation
-Prepare a mix of internal standard (IS) solution (80 ng/ml cortisol-D4, 40 ng/ml testosterone-D3, and 400 ng/ml for DHEA-D5) and Na phosphate buffer (0.2M) in a ratio of 1/40.
-Add 400 of the IS/buffer mix into an Eppendorf
-Add 25 ul of urine sample
-Add 2.5 ul of β-Glucuronidase from *E.coli*
-Vortex the sample
-Incubate the Eppendorf tubes for 1 hour at 50 degrees at 500 rpm
-Centrifuge briefly the Eppendorf tubes.

Extraction
1) Use C18 SPE cartridges (e.g. Waters Sep-Pak C18, 100 mg, 1cc or Biotage Isolute C18 EC, 100 mg, 1 cc).
-Condition the cartridge with 1ml MeOH 100%.
-Equilibrate the cartridge with 1 ml MeOH 5%.
-Load samples
-Wash with 1ml MeOH 5%.
-Wash with 1 ml of hexane.
-place a new Eppendorf tube below the cartridge
- Elute with 1ml ethyl acetate

2) Evaporate at 35°C in a Speedvac (CentriVap LABCONCO).

3) Reconstitution

-Re-suspend in 100 ul MeOH 50 %
-Vortex 20 seconds.
-Ultrasonic bath 1 minute (30 seconds, then stop, then 30 seconds again).
-Vortex for 20 seconds.
-Centrifuge for 3 min at 13’000 RPM.
-Collect 80-90 ul and transfer to HPLC vials fitted with conical inserts.

Specific gravity (measured using ATAGO pen-refractometer) to be calculated for all hormone samples even the C/T ones. This has to be done when the sample is perfectly thawed. Also, vortex the sample before taking specific gravity measures. The measurements should be taken thrice and average the results to keep on the record.

-Ready to measure using HPLC machine

Appendix B. Oxytocin protocol: solid-phase extraction and Elisa

Miguel Gareta García, Zegni Triki, Redouan Bshary, Gaétan Glauser

Prepare the solutions (Part I)

-Phosporic acid solution: for 30 ml = 0.48 gr in 30 mL H2= 100%.
(1N phosphoric acid = 0.33 M, to prepare 0.5 N solution = 16.35 gr of 1 N PA in 1 litre of H2O)
-NH4 (25%) 5% solution: 5 ml NH4 (25%) + 95 ml H2O = 100 ml of the solution.
-Assay buffer: 10 ml assay buffer + 90 ml H2O 100% (fresh one for each use, discard the rest).
-Wash buffer: 20 ml + 380 ml H2O 100% (to be kept at room temperature).

Solid-phase extraction (Part II)- Urine samples

-To each sample (100 ul) add 200 ul of HQ water.
-vortex for 3 minutes.
-Ultrasonicate 30 seconds.
-Centrifuge the tubes at 8000-10000 rpm for 5 minutes.
-Use (mixed mode) non-polar/strong cation exchange cartridges e.g. Biotage Evolute Express CX 25mg 1ml or Waters Oasis MCX 30 mg, 1cc.

1. Condition with 1 ml methanol
2. Equilibrate with 1 ml H2O
3. Load sample
4. Wash with 1 mL of 2% formic acid in H2O
5. Wash with 1 mL of 100% methanol
6. Elute with 1 mL of ammonia 5% (of a 25% solution) in methanol
7. Evaporate in a Speedvac at 40°C for 1-2 hours until dryness
8. Store at - 80 °C for further analyses

Kit preparation (Part III)- ELISA: Enzyme-Linked Immunoabsorbent Assay

Adaptation to the general Enzo's guidelines (**http://www.enzolifesciences.com/fileadmin/redacteur/pdf/adi/ADI-901-153.pdf)**
*Note: Allow all reagents to warm at room temperature before use in the room with no outside light.

Prepare solutions (II)

*Important: Everything should be labelled with the exact date
1-The standards:
ST1: 900 ul Assay buffer, ST2 to ST7: 500 ul Assay buffer.
Alternatively: It can be also 5 ml AB and 45 of water as it would still be the same concentration and some material can be saved for future plates.

*Before step 2), vortex 10 seconds OT standard
2- Add 100 ul OCT standard (Oxytocin standard) in ST1, vortex for approximately 1 min, then take 500 ul from ST1 (ST stands for the standards) to ST2, etc. repeating the same until ST7 (which will be 1 ml volume after the dilutions).
-Take out of the fridge the equipment, Vortex OCT as it will be used later.
-Do washing as we empty the content of STs.
-Vortex 1 min ST1, fill up and empty 3 full times before passing to ST2.
*Important: Change pipette every time any ST is moved to the next, repeat the process until ST7. Do so ensuring the walls or the bottom of the Eppendorf tubes are not touched by the pipette tips. Keeping the elbows on the table adds more stability to the pipetting.

3- Reconstitute the extract (urine sample that was extracted using solid-phase extraction) with 250 ul of assay buffer, vortex well: approximately for 1 min.
-Can shake AB and WB fill standards

Buffer preparation

Assay Buffer: 1:10 keep concentration independent of the volume needed.
It's a transparent liquid, just move up and down two times, there is no need to shake as the liquid is rather viscous and shaking it would form bubbles that would only disappear after a long time. We can use different volumes but keep the concentrations always.

Standards to prepare

They need to be used within one hour, if possible, with the minimum difference between the first standards and the lasts.

Assay procedure

General advice:

-Vortex before each pipetting.

-While pipetting try to put it vertically without touching the well.

*Note: Do so without touch walls or the bottom, can only touch the surface of the liquid, especially when we see there is still small droplets in the pipette tip and we want to put it into the well.

-Ensure the pipetting is done properly, train before running “real material” and you can pull out the liquid and pull in to avoid any possible resistance to the flow of a first to have a stable amount of the solution.

-Keep track of the last pipetting is a must as an error in the different serial pipetting would unavoidably induce undesired errors that would compromise the validity of the work and complicate tracking back concentrations. Make sure when pipetting the impact of moving liquids do not cause drops to come out of the wells since we would be losing volume without being able to bring volume from one well to the next.

-When removing the columns, maximum care is a must. Carefulness does not require force as otherwise, they break. Instead, shaking them progressively from one side to another helps as they will get loose eventually coming out easily.

Steps:

1) Vortex the tube before each pipetting then Pipet 100 µL of Assay Buffer into the NSB and the Bo wells.

2) Vortex the tube before each pipetting thenPipet 100 µL of Standards #1 through #7 into the appropriate wells.

3) Vortex the tube before each pipetting then Pipet 100 µL of the Samples into the appropriate wells.

4) Vortex the tube before each pipetting then Pipet 50 µL of Assay Buffer into the NSB wells.

5) Pipet 50 µL of the blue Conjugate into each well, except the Blank wells.
-Fill rack with blue conjugate, do washing as we pipette, multi pipette later in vertical always.
-Put back the content of the conjugate that is leftover, as it is a very expensive and precious material.

6) Pipet 50 µL of the yellow Antibody into each well, except the Blank and NSB wells.
Do the same as done with conjugate (fill a rack, and bring back leftover material).
*Note: Every well used should be Green in colour except the NSB wells which should be Blue. The Blank wells are empty at this point and have no colour.

7) Shake the plate gently for 15 min in dark (put it back in the sealing bag and a note with the exact date and hour when the plate is inserted).
*If needed put some tape to make sure it is not falling outside of the dish that is flat and open, and never use a high-velocity mode for the shaking as the volume in the wells can exit easily and a mix of volumes could happen. Instead, use a smooth velocity.

8) Seal the plate and incubate at 4°C for 18-24 hours
-Put it inside a grey package that comes with the plate in the kit and store it at a laboratory refrigerator, make sure the position is stable and opening/closing the refrigerator will not affect the plate stability.

9) 24 Hours max incubation.

10) Empty the contents of the wells and wash 400 µL X 3 times.
-Test first the washing on a pilot plate and clean the holes if necessary to ensure everything is working well. Washing with incorrect solutions will surely affect the final readings which would make all the work inefficient and inaccurate and the equipment would have been wasted.
-Make sure the readers are available with other researchers in the building that may make use of it unannounced. For that write your name down next to the machines and specify your name, lab group, and desired hour and day of intended use.

11) Add 5 µL of the blue Conjugate to the TA wells.

12) Add 200 µL of the pNpp (Phosphate) Substrate solution to every well.

13) Incubate at room temperature for 1 hour without shaking

Following steps need to be conducted in the room where there is a reader (in room 011 at the Faculty of Biology, Unine):

14) Add 50 µL of Stop Solution to every well. This stops the reaction and the plate should be read immediately.

15) Read the optical density at 405 nm, preferably with a correction between 570 and 590 nm. If the plate reader is not able to be blanked against the blank wells, manually subtract the mean optical density of the blank wells from all readings.

16) Use the software for the analyses: use 4 parameters curve for values calculation.

17) Correct the values by the dilution: for exp: if you elute 1 ml of saliva and you reconstitute by 250 ul assay buffer: divide the OCT values by 4.
*Note: The liquids are no longer usable and therefore should be disposed of in the correct containers.

GENERAL DISCUSSION

D.1. Summary of the four chapters

In Chapter I, I studied the adult females as subjects of study and amplified the time-lapse from the average fifteen minutes of Borgeaud and Bshary (Borgeaud & Bshary, 2015) to more than three hours to test the occurrence of tolerance or aggression at the boxes set up following a grooming interaction to test how reciprocity exchanges would unfold. Contrary to previous studies that could not support the exchange of grooming for tolerance in Barbary Macaques (*Macaca Sylvanus*) (Molesti and Majolo, 2015), I could find experimental evidence of reciprocity in a three-hour benchmark. This builds on the previous knowledge that female vervets exchange grooming for tolerance and establishes a suitable methodology for conducting similar investigations in other species. Several studies conducted in chimpanzee reciprocity exchanges suggest that grooming is reciprocated for itself, for support in agonistic conflicts, and meat for sex over months-long or even year-long periods (Gomes and Boesch, 2009, 2011; Gomes, Mundry and Boesch, 2009). Differently from these studies, my investigation covered the time-space of a few hours, but the systematic following for such period constitutes an asset as I provided information about additional grooming partners and certified that the females of the dyad did not engage in any additional interactions (affiliative or agonistic) in the time that spanned from the grooming to the experimental setup. This approach, therefore, brings the rigour of data collection in a wild set up to a maximum and could be extended easily to other wild group-living species. In the end, it is fundamental to acknowledge that with wider time frames (weeks, months) one cannot avoid missing out on observations where some behaviours may be inter-changed and agonistic interactions may also induce “masking effects” as socio-positive or socio-negative interactions may accumulate. Parallelly, studies on rats showed direct reciprocity in action unfolding over periods of days (Schweinfurth *et al.*, 2019). Finally, inspired by previous work by Jaeggi et al. (Jaeggi, De Groot, Jeroen M G Stevens, *et al.*, 2013) that listed factors like the relationship quality, social distance, or behavioural mediation as possibly relevant to reciprocity dynamics, I considered the study of bonds (a measure of relationship quality) among other descriptors of the grooming interaction. All in all, my study provided a neat approach to study contingency of behaviours evidencing reciprocity based on i) total duration of the grooming interaction, and ii) the decay function of tolerance that was predicted to last about six hours, where iii) the exact time of grooming given, iv) the surplus grooming received, and v) the relationship quality of the dyad did not affect the reciprocity process. What is more, the reference distance used here and based on Borgeaud and Bshary (Borgeaud & Bshary, 2015) might provide an interesting idea for similar methodological conceptions that have the potential to assist us in conducting original experiments where the effect of relationship quality can be brought to common baseline levels.

In Chapter II, exposed some selected female individuals in four groups (one dominant and one subordinate per group). The analysis of activity budgets (i.e. GLMM) revealed that the fed subjects changed their feeding, resting and social behaviours significantly while they were fed compared to the non-fed individuals. I used a null-model hypothesis (Farine, 2017) approach to compare some selected network parameters of the fed subjects with non-fed ones during the treatment. I suggest this method as a valid one to evaluate changes in different time scales because social network parameters (and social network analysis) help identify how social structures respond to the social interaction patterns of the individuals that compose a social group. This approach is widely used in observational-descriptive studies as done by Brent et al.'s rhesus macaques changes of sociality with seasonality (Brent *et al.*, 2013). This approach has been recently integrated into experimental studies, one brilliant example is the test conducted by Ripperger et al. (Ripperger *et al.*, 2019) comparing the same vampire vat individuals in captive and wild conditions. Even though individuals were found to be rather consistent in their network position from one year to the next in a previous study conducted at the IVP (Canteloup and Waal, 2021), I found supporting empirical evidence that i) fed females preferentially target members of their family, ii) bonded, and iii) female partners when seeking grooming interactions as reported earlier by Borgeaud et al. using observational data (Borgeaud *et al.*, 2016). They also (fed females) iv) showed remarkable flexibility in their grooming strength variability when the two control phases were compared to the treatment period (control-before VS treatment measured as strength; treatment VS control-after measured as carryover). The fed females also v) increased their grooming given compared to the grooming they received (grooming reciprocity index), which illustrates a benevolent predisposition towards establishing grooming interactions beyond the grooming they received suggesting that score-keeping was not at work and alternative benefits could be obtained by the females' dedication to grooming. These findings show that the fed subjects strategically changed their grooming while fed, which can be interpreted as a manifestation of social behaviour flexibility that hints at possible strategic exploitation of their social environment and thus social complexity and intelligence (Jolly, 1966; Humphrey, 1976). Taken together, these results indicate that strategic plastic changes in grooming might help females improve their social standing when their feeding needs are covered which further raises important questions about how sociality could have promoted more strategic individuals in societies where foods are not a restricted resource.

In Chapter III, I evaluated whether vervet monkeys incorporated territory and ecology knowledge in the shaping of strategic group decision-making during intergroup encounters. Using a novel approach, I estimated the ecological value at different time scales of i) here and now, ii) average of the year, iii) maximum in the year to assess whether vervets integrated such information when deciding to defend a location against a neighbour group. The results suggest that encounters were more frequent in high-quality areas (using NDVI-Willems, Barton, & Hill, 2009; Willems & Hill, 2009) and core areas when the time scale used was here and now and the annual average. This finding highlights the importance that groups attribute importance to areas not only valuing them at a time snapshot (here and now), but also relied on a perspective that averaged quality to make strategic decisions about fighting a rival group. Further, I calculated relative values for the focal group (ecological, territorial) in a way that computed the encounter group to assess whether this impacted the winning likelihood which would allow making inferences about value perception. The field of game theory has been traditionally used in behavioural ecology contexts. However, game theory often evaluates two-player games (Maynard-Smith, 1974; Maynard-Smith & Price, 1973; Maynard-Smith, 1979) while encounters adjust better to N-player games' logic (Noë, 1990; Bach, Helvik and Christiansen, 2006; Nunn and Lewis, 2010; Barrett, Howley and Duggan, 2011). The lack of significance shown by the different relative ecological and territorial measures suggests that vervets did not follow a Bourgeois strategy (Maynard-Smith, 1982) to outfight rival groups. Strikingly, contrary to the classical argument that group size represents a key tenet determining the fighting ability or resource holding potential of a group during intergroup encounters (Kitchen, Cheney, & Seyfarth, 2004), my results showed that smaller groups won systematically bigger groups. This finding can only be compared to Lewis et al.'s in Verreaux's Sifaka (*Proithecus verreauxi*) (Lewis *et al.*, 2020) requires a collective action problem (CAP) (Olson, 1965) interpretation. What is unprecedented, and it seems rather pertinent, is a combined look at social dilemmas like the one that intergroup encounters represent that amalgamates the theory of CAP in the frame of volunteer's dilemma (Archetti, 2009). It could be argued that groups face coordination problems at the onset and during intergroup encounters (Brosnan, Beran, Parrish, Price, & Wilson, 2013; Gintis, 2009; King & Cowlishaw, 2009; Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2003; Van Vugt, Hogan, & Kaiser, 2008) as it has been hypothesised in human warfare where CAPs can be highly influenced by leaders (Lopez, 2020). Albeit, even if I cannot fully resolve this, it seems that the recruitment of "warriors" to enter the battlefield before the battle is key, and not guaranteeing a sizeable collective may not be easily offset if your enemies' recruitment is bigger.

In the fourth Chapter, I studied whether three vervet monkey groups showed signs of behavioural variation indicative of strategic decision-making in the two years that preceded fission events. Specifically, I tested changes in adult females' i) activity budgets, finding that even if the fissions occurred amid an ongoing drought (Lottering, Mafongoya, & Lottering, 2020) that surely intensified the scarcity of food resources and prompted acute scramble competition conditions (van Schaik & van Noordwijk, 1988), activity budgets did not uniformly increase their allocation to travelling nor decreased their resting and social time (Dunbar, 1992). The study of ii) groups' spread revealed that it did not change according to the assumed under increased food dispersion situation (Reyna-Hurtado *et al.*, 2018). This suggests that for non-fission-fusion animals, keeping group cohesion might be pivotal. If this holds, attempting to ensure such group cohesion may have helped reduce predation though imposed a heavy toll on foraging efficiency which may have driven vervets to a sort of social tipping point where strategic drastic decisions are needed. Unexpectedly, iii) females increased their social network metrics (degree, strength, betweenness) closer to the fission time, although the same was not observed for the collective ones (density, transitivity, modularity), except for modularity that increased suggesting progressive sub-grouping closer to the fission as found in Gombe's chimpanzees (Feldblum *et al.*, 2018).

To this date, there is no study reporting on several almost-simultaneous fission events in wild animals, and if anything, these blend of results suggest that decision-making options may follow strategic rules that integrate not only external influences (food availability), but also internal ones (group structures, group "styles", group leaderships). In that case, and until more in-depth studies follow providing interesting evidence of physiology states (i.e. urine c-peptides, Surbeck, Deschner, Behringer, & Hohmann, 2015), I understand these results assuming that decision-making in crucial moments like the ones under investigation here may have a strong idiosyncratic component. In the last two aspects of the study, I studied how the adult females would make decisions using a game-theoretic approach (Dugatkin & Reeve, 1998; Maynard-Smith, 1984; Maynard-Smith, 1979). On the v) whom to stay with, I assessed whether they ended up in a daughter group where they had a higher affinity closer to the fission (grooming, proximity, kinship) similar phenomenology of preferential assortment before fission which had been previously reported in dolphins (Nishita, Shirakihara and Amano, 2015), rhesus macaques (Missakian, 1973) or blue monkeys (Cords and Rowell, 1986). However, this supposition only adapted to one group (NH) of three. Lastly, the study of the vi) "staying" versus "leaving" strategy assuming that the first represented a "risk-averse" strategy, and the second a "risk-averse" one. To date, there is no precedent extending the idea of risk to strategic decision-making in the context of fissions although previous studies have shown more risk-prone hunting was found in chimpanzees in periods of high diet quality (Gilby and Wrangham, 2007) although the risk-aversion strategy around food benefits from wide support when habitats are highly changeable as seen in lemurs (MacLean, Mandalaywala and Brannon, 2012) and bisons' fission-fusion decisions (Merkle, Sigaud and Fortin, 2015). If risk-averse behaviours help economise variation in foraging time on patchy habitats (Caraco, 1981) and reduce predation risks (Merkle, Sigaud and Fortin, 2015), it is plausible that female vervets only choose to fission when risk-averse alternatives are no longer an option that would align well with the females' increase in individual network metrics.

D.2. The big picture

D.2.1. Social networks and the potential to study dynamic changes of social behaviour

Results from this thesis have broad implications for the understanding of how grooming interactions shape relationships and have an effect on the structure of animal social networks. Previous studies using social networks permitted the identification of individual roles within a group (Sueur *et al.*, 2011; Balasubramaniam *et al.*, 2018), and how individuals' positioning in the structure is something dynamic (Borgeaud, Sosa, Sueur, & Bshary, 2017; Kurvers, Krause, Croft, Wilson, & Wolf, 2014). While some studies advanced relevant information about the linkage of factors like seasonality on network structures (Adams, Arseneau-Robar, Bonnell, Stead, & Teichroeb, 2021; Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009) and even extreme events (Larson *et al.*, 2018; Testard *et al.*, 2021), no study to date had addressed the phenomenon of group fissions in several groups. Here I brought some combined evidence about different behavioural measures that included aspects like activity budgets, group spread, and individual and group-level grooming network metrics over two years until groups split in two. What is more, it is known that social networks can aid the study of cooperation dynamics (Brask et al., 2019; Carter et al., 2018; Rand, Arbesman, & Christakis, 2011; Rezaei & Kirley, 2012), so in this context, a logical extension to the use of social networks would be to evaluate whether more central individuals (i.e. eigenvector centrality) or individuals that are connected to more individuals (i.e. degree) could shed light on participation in cooperative participation in collective action problems like intergroup encounters. Accordingly, it would be very interesting to apply a social network approach to the specific context of intergroup encounters where individuals can present cooperative behaviours by participating in the group defence. Hence, studying how the strategies that individuals adopt, can be either participate (cooperate) or defect link with social network metrics.

Albeit the broad collection of participation levels during intergroup encounters is highly challenging in wild populations because of the vibrancy of such contexts (unless using collars that measure activity), a similar approach could be undertaken using assemblies of individuals through categories. Suitable categories could be the rank position (high, medium, low) or the sex category (adult female VS adult male), or within males the length of tenure (less than 6 months, 6 months – 1year, >1 year). Even more, different categories could be assessed using multiplex networks (Snijders, 2017; Liu *et al.*, 2018; Smith-Aguilar *et al.*, 2019; Beisner *et al.*, 2020). What is more, a combination that includes game theory looks with social networks remains widely unexplored, and it would seem convenient to assess collective action problem contexts like intergroup encounters would certainly fit into this panorama. More specifically, game theory conceptions whereby individuals can play cooperative or defective strategies could assist us to better understand whether joining in collective action to defend ones' group could have a social network (i.e. individual-level: centrality; group-level: density or modularity). As alleged in previous sections of this thesis, it may well be that vervets need to resolve a coordination problem in the particular collective action problem scenario of intergroup encounters which may mingle with the need to build up a minimum collective as the volunteer's dilemma posits (Archetti, 2009).

A component that I mentioned in the study of group fissions but that I did not directly address around is that of the coordination to forage. Again, this aspect could well be studied using collars dispositive that offer geospatial positioning information with which one can extract collective movement as seen already in capuchin monkeys (Crofoot *et al.*, 2007). Beyond, coordination also implies group movement (King and Sueur, 2011), what would be of maximum interest would be to directly address questions about the relevance that being centric in the network has for individuals to have credit enough to their partners so their movement decisions are followed. Moreover, interesting aspects could be tested empirically through exposing selected individuals with playback sounds to evaluate the agreeability of the listeners to take the direction of the playback (playback using a movement call of a specific individual, ideally having multiple samples that represent varying ranks). Similarly to the possible relationship between cooperation dynamics and social networks, another avenue that I did not explore was the possible ramifications of the social network position with reciprocity exchanges of grooming for tolerance. As evidenced before, the boxes experiment tests conducted at the IVP have helped elucidate that female vervet monkeys engage in direct reciprocity interactions, but not generalised reciprocity (Borgeaud & Bshary, 2015) and that audience effect exert an influence on the tendency of the dominant individual to show tolerance or aggression (Borgeaud & Bshary, 2018; Borgeaud, Schnider, Krützen, & Bshary, 2017).

Taking on this, an interesting extension would be to evaluate whether the dominant individual of the dyad would display different attitudinal reciprocity rules in that exchange (as shown in Chapter II) according to their centrality. Connecting to my second Chapter, where I found that the fed subjects became more social when they had more time to do other things than feeding. Beyond this apparent finding, I interpreted the grooming "targeting" of specific individuals as an example of social network positioning improvement which can be understood as a form of social competence (Bshary & Oliveira, 2015; Taborsky & Oliveira, 2012). Now, even if the Machiavellian Intelligence Hypothesis (MIH) appears to be a distinct topic, I interpreted my results in the light of this theory because self-promotion driven actions fit well the list of possible behavioural manifestations that Machiavellian abilities can represent, that include innovation, social learning, flexibility, self-awareness, social problem solving, social knowledge and theory of mind. Besides, an extension of this hypothesis emphasizes the importance of strategic capacities oriented towards improving one's fitness (i.e. through coalition formation or tactical deception) (de Waal, 1982). Such interpretation may be worth further investigating, as different studies authenticate the fitness implications of being well connected in a network (i.e. centrality, degree), as shown in species as disparate as Barbary macaques (Lehmann, Majolo and McFarland, 2016), and killer whales (Ellis *et al.*, 2017). Making strategic decisions that enhance one's social standing in the group through voluntarily offering grooming services thus represents a form of social strategising that fit the key tenets of the MIH (Byrne and Whitten, 1997). Moreover, rewiring one's social networks is a mechanism of regulating interactions in the highly dynamic and changing conditions of wild populations (Farine, 2019). As it stands out, female vervets proved to rewire, if only temporarily documented, their networks, therefore, supporting these ideas and giving insights about the flexibility of the underlying decisions that were caused in my experiment by altering significantly their nutritional states.

D.2.2. Grooming behaviours to study strategic behaviour and cooperation

Grooming has been a centrepiece form of social behaviour in primatology studies since the beginning (Bolwig, 1959; Imanishi, 1960; Stammbach and Kummer, 1982). Grooming interactions (including bird allopreening) have aided the understanding of rank systems (Seyfarth, 1977; Tiddi et al., 2012; Foster, Gilby, Murray, Johnson, & Wroblewski), social relationships and bond formation (Schoof and Jack, 2014; Morales Picard *et al.*, 2020; Reddy and Sandel, 2020), social styles (Balasubramaniam et al., 2018; Berman & Thierry, 2010, 2008; Gilby & Pusey, 2009; Sonnweber et al., 2015), and social behaviour ontogeny (Glick *et al.*, 1986; Barale, Rubenstein and Beehner, 2015; Kulik *et al.*, 2015; Lonsdorf, 2017; Amici *et al.*, 2019). Because grooming is the most conspicuous form of social behaviour (Dunbar, 2010), it has been widely used to address questions comprising exchanges in the context of cooperation and reciprocity by linking a given interaction to subsequent ones (grooming or different). Moreover, grooming has been interpreted in the light of Biological Market Theory to explain exchanges of goods and services (Hammerstein, Noë, & Noë, 2016; Noë, 2016; Noë & Hammerstein, 1994) through concepts like commodities, partner choice or outbidding competition.

Consequently, grooming is a key element to study cooperation dynamics in the form of grooming reciprocity and its correlation with sex-ratios (Hemelrijk and Luteijn, 1998), the evaluation of different group styles (more egalitarian, more despotic; Kaburu & Newton-Fisher, 2015), or the effect of rank on individuals' matching of grooming given and received (Li et al., 2013). Also, reciprocity processes that involve grooming can include alternative behavioural services like food tolerance (Borgeaud & Bshary, 2015; Tiddi, Aureli, Polizzi Di Sorrentino, Janson, & Schino, 2011; Ventura et al., 2006), coalition formation (Borgeaud, Schnider, Krützen, & Bshary, 2017; Hemelrijk & Ek, 1991; Ventura et al., 2006) and support during conflicts (Carne et al., 2011; Koyama et al., 2006; Ventura et al., 2006) or access to sexual partners (Gumert, 2007b). Moreover, grooming has been related to behaviours like peace-making, consolation and reconciliation (Aureli, Cords, & van Schaik, 2002; Aureli & Schaik, 1991; de Waal & van Roosmalen, 1979; Kutsukake & Castles, 2001; McFarland & Majolo, 2011; Palagi, Paoli, & Tarli, 2004; Peter Henzi & Barrett, 2007). All in all, these processes of interchange, beyond the specific terminology that surrounds its descriptions, allowed researchers to wonder about empathy and emotions as parts of cognitive machinery that moulds social behaviour (Clay, Palagi, & de Waal, 2018; Fehr & Mcelreath, 2003; Parr, 2001; Rosati & Hare, 2013; Schino & Aureli, 2009; Schino, Geminiani, Rosati, & Aureli, 2004) and offered a platform to study distinctive brain areas roles (Dolan, 2002; Bechara, 2004; Bernhardt and Singer, 2012).

Grooming is the common conduit that helped me connect direct reciprocity exchanges (Chapter I), behavioural flexibility when gaining a surplus time and strategizing over who to direct grooming efforts (Chapter II), and individual and group-level social network metrics across time before groups fissioned and assortment into the newly-formed daughter groups (Chapter IV). As advanced in the previous section (D.2.1.), and hinting at the only chapter where I did not use grooming-based information new approaches could be thought of that evaluate if social networks based on grooming interactions could be compared to social networks based on participation in intergroup encounters. Specifically, there are no studies to date reporting on the relationship between social dilemma solving and the required collective coordination with overall connectivity of group networks (groups as a whole, or subsets of the group like the female one in the case of vervet monkeys).

Both Chapters I and II centred the focus of attention on grooming interactions. Yet, our knowledge of how animals may engage in attitudinal reciprocity-like interactions over long periods would be of remarkable interest. More explicitly, we know that attitudinal reciprocity is a plausible mechanism that enables cooperative interactions to unfold over relatively short periods (de Waal, 2000; Suchak & de Waal, 2012), however, empirical tests that extend time frames could broaden our understanding of the time dimension underpinnings of such mechanistic route. In particular, it would be very interesting if the strategical grooming usage that the adult females did while fed (Chapter II) could hint at attitudinal reciprocity at work. Differently from how I collected the data for that project (all adult females, fed and non fed), the exclusive following of a single individual during the treatment period would allow me to investigate it. However, an important shortcoming would be the "tiredness" tax the protracted focal follow would inevitably cause in the sujects (personal observation, as I followed adult females for six, seven and even thirteen hours straight observing baby handling-stealing behaviours). This limitation could be compensated by selecting the individuals that are more comfortable with the researchers' presence. Beyond, given vervet monkeys' extensive social knowledge (i.e. kin recognition, third-party and third-party rank relationship knowledge; Borgeaud, Alvino, van Leeuwen, Townsend, & Bshary, 2015; Borgeaud et al., 2017), and similar species' capacity to integrate information of others' kinship and bond ties to form strategic coalitions (Crockford *et al.*, 2007; Wittig *et al.*, 2007; Cheney *et al.*, 2010) an interesting pondering is whether attitudinal reciprocity could explain some behaviour dynamics between specific dyads. As an example, one could look at different prosocial markers like coalitions, proximity, tolerance in proximity while feeding, grooming, or sleeping (night, day naps) in body contact. (positive behaviours that could indicate benevolence of the recipient of grooming efforts toward the donor or fed individual, assuming it would increase significantly its grooming efforts). Additionally, given the ample knowledge of matrilines available at the IVP, it would be interesting to evaluate possible whether the fed individual grooming efforts (donor) could translate into possible benefits reaped by her offspring in what could represent a form of "generalised kin-biased reciprocity" akin, but of positive sign, to kin-oriented redirection of aggression (Aureli, Cozzolino, Cordischi, & Scucchi, 1992; Schino & Marini, 2014), although this has not been studied yet.

My prolonged fieldwork dedication provided me with observations where I was able to observe interesting grooming behaviours during intergroup encounters. As reported by Arseneau et al. (Arseneau-Robar et al., 2016), female vervet monkeys can use grooming to stimulate participation in intergroup encounters, especially to recruit hesitant males that may naturally be more undecisive no being the philopatric sex. However, I sometimes found striking examples of such "ritualistic" use of grooming sessions. In a way, it seems as if the two contending groups that may have been already fighting heavily consented in a form of "break" to restitute forces to keep going. Shockingly, these times could stretch up to ten minutes, sometimes half an hour, and as suggested by Arseneau et al., (Arseneau-Robar et al., 2016) it appeared to me that females were "working things out". And yet, I was sometimes struck by what looked as odd grooming dyadic combinations where the initiative was eminently female-dominated. Studies in the future could deepen into this particular grooming context with regards to what was observed before the "break" in terms of individuals that had participated or not and the future participation later on, and link it with specific details of the grooming interaction (initiator, time grooming given, time grooming received, body parts, sex of the individuals, male tenure, etc.). Beyond the resource defence-driven motivation of females to outfight rivals during intergroup encounters (Arseneau-Robar et al., 2016), grooming sessions during “consented breaks” could represent an instance of strategic behaviour in two ways: i) both groups tactically agree on having a break, ii) females’ targeting of particular grooming partners, potentially reluctant ones to participate or willing ones to reinforce the agreement, and iii) females’ initiative and commitment to grooming other partners may permit to raise the stakes (Roberts and Sherratt, 1998) so to jointly collaborate in group defence after the break is over. Alternatively, a different possibility could explain such instances if females grooming behaviour constituted a form of “testing the ground” as if checking the ammunition they have to fight the war. If that was the case, it could well be that females operate as army commanders that evaluate their fellow army partners’ strength and availability for battle. Again, this option would need to be contrasted with dedicated observations, but a priori, it seems feasible given that “grooming breaks” are sometimes not followed by intergroup encounter start overs.

D.2.3. Strategic decision-making at the group level around social dilemmas

Strategic behaviours could be understood as actions that provide benefits that “outweigh costs (at least in the long run) and integrate a complex set of information” that can include one’s relationships and those of potential social partners (Cords, 1997). Participation in coalitions represents an example of strategic behaviour where the payoffs that an individual can receive by participating are dependent on the partners’ status or relationships concerning the self. In this context, a potential observer of a conflict could evaluate the situation in real-time and a decision to support one individual or another must be taken rapidly when opportunities arise and are not necessarily straightforward dichotomous ones (Harcourt, 1988). Examples of strategic coalitions are therefore instances when potential risks are minimized by supporting kin or when the target is of inferior rank to the supporter (Gouzoules, Gouzoules and Marler, 1986; Harcourt, 1988). An original study on chimpanzees found that chimpanzee victims of aggression were integrating the identity of the individuals in their vicinity and exaggerated their screams whenever the audience was of a similar or higher rank than the aggressor

(Slocombe and Zuberbuhler, 2007). In a similar vein, cleaner fish are more cooperative in the presence of an audience (Pinto *et al.*, 2011).

During my field seasons, I managed to observe interesting behaviours that I would qualify as strategic, although I cannot present data to support my impressions. As a first example, I observed how a relatively high-ranking female from BD (Hippie) got severely injured as you could see the bone at the ankle joint, probably as a result of a failed eagle predator attack. Her condition deteriorated over a few weeks because as she could not climb trees to access food. During that time, I witnessed how not only her physical condition worsened, but also lower-ranking females aggressed her when "she was on the way" of food. Unfortunately, these observations were noted during urine collection work, so I could not concentrate on this particular individual, but it would be very interesting to observe the rigid status quo of adult females' hierarchy systems can be challenged in the presence of different audiences. As a second example, I attempted to carry an experiment based on experimental observations where a low-ranking adult female had identified high-quality food sources (termite mount with a massive abundance of termites exiting) and emitted a call to announce the food source to others when there was no visible audience in more than fifty metres. Along these lines, I also observed a low-ranking male sneakily foraging on another rare, ephemeral and abundant food source (the mushroom patches usually appear after heavy rains at the study site. Differently from the female example around the termites, this male had neighbours in his proximity (more than ten individuals in less than twenty-five metres, and he not only remained silent, but also foraged in what seemed an accelerated and nervous pace, but also stood up to check if others had spotted the patch (vegetation was thick therefore granting certain invisibility). This ignited the interest to mimick similar conditions using apple pieces that would be shown to an individual having i) no audience, and ii) not having an audience nearby. These two conditions would be ideally tested in both adult males and adult females of different ranks perhaps using monopolisable and non-monopolisable food items. Unfortunately, the pilot study did not work as the monkeys learnt early on to identify our intention and given that we conducted a few pilots during the dry season, they reacted in an agitated, exited-like fashion that elicited the attention of others before we could present the food. Albeit this, similar approaches must be possible and could help combine cooperation-cheating behaviours in the light of retrieving information from others (do monkeys know how to keep secrets?) with vocal production (innate or volitional; Nieder & Mooney, 2020). These situations happen more or less regularly in the wild (finding high-quality food items like cicadas, scorpions, bird eggs, mushroom patches, abundant sap secretions, etc.), although are hard to document in full detail due to the unpredictability and sheer rapidity.

Because of that, experimental approaches that capture these situations of potential conflict of interest (announce VS not announce the food) allow for interesting game theory interpretations. It is possible that simple heuristics come into play here and responses simplify the complexity of the audience into dichotomic situations (audience yes VS audience no), but it is possible that as Harcourt advanced, strategic decision-making is not necessarily straightforward (Harcourt, 1988) if one considers the rank, the "goodness" or richness of the food, and the risk of "being caught". Therefore, as explained above for the female that announced the termite mount secret, perhaps she opted to play a stag-hunt like a strategy (Pacheco, Santos, Souza, & Skyrms, 2009; Skyrms, 2004). Even if such strategy could have meant calling and making the food source available to others hoping to share it, she was repelled from the zone rapidly as soon as the dominant matriline arrived (she was aggressed by the dominant female and her daughter). I was not able to document what followed so it remains a puzzle whether her sharing of valuable information (cooperative act) could have ensued which may open the way for attitudinal-like scenarios. Contrarily, the male that opted to remain silent assumed the risk of others detecting the source of food and perhaps assumed that possibility by checking insistently to trigger a rapid scape response and avoid receiving aggression (the male was most bottom in rank and also smallest in size, with a handicapped hand). I interpret his behaviour as a form of Machiavellian intelligence, although I cannot fully evaluate the risks that being detected could have represented as he managed to deplete the food patch and if the speculation of leaving the zone unscathed could stand. Besides, I believe that a game theory interpretation of this needs to integrate a certain degree of conjecture, that is, some prior assumptions, i) that their calling was volitional and ii) by doing so they did not expect to be pushed out of the food source (as otherwise, it would be smarter to leave right after producing the call). This automatically opens two scenarios: 1) food calls are (at least) sometimes innate, or 2) if individuals make inferences about their chances to exploit the food source after announcing, this can lead to unexpected outcomes. Following the second option, one could posit that the male made the strategic decision of cheating in a simplification of a two-player game (given that all other individuals were considered as one, as being the lowest-ranking male in an unusually rich food source would imply not exploiting it again). If that male played cheating in a classic iterated prisoner dilemma (PD) situation where each (only one player here) can either cooperate (share information) or defect (not do so) (Luce and Raiffa, 1957). However, this game could be slightly different if one thinks that the strategy cooperating has little prospects of offering a sharing scenario where both parties benefit. I, therefore, emphasise the importance of natural observations that are representative of potential behaviours and suggest the development of a database that explicitly gathers such observations in as much full detail as possible and in as much a methodological sable approach as possible. With this one could bridge together the observations that the simplified contexts that experiments help us test with more dynamic, complex and perhaps day-to-day natural observations. In the end, the merging of the two can be of tremendous help to better understand the species of interest and key behaviours.

The boxes experiment study (Chapter I) adds information about how dominant females make reciprocity decisions towards previous grooming partners (Borgeaud & Bshary, 2015b). My results can be put in the perspective of strategic decision making if we consider that the dominant female of the dyad could have "let go" the reciprocity towards the subordinate counterpart and given priority to steal her food or aggress her partner, although this could have instilled the subordinate's fear ins subsequent experiments. Notwithstanding, dominant females reciprocated their previous grooming partner independent of the relationship quality that united them deserves some attention as this may indirectly indicate a decision rule that prioritises reciprocation through tolerance. One way to interpret this could be that if females restricted being contingent co-operators (Cheney *et al.*, 2010; Schonmann and Boyd, 2016) merely to previous grooming partners based on the goodness of one's relationships, this could perhaps coerce the emergence of more large-scale cooperation required to solve social dilemmas like collective action problems (Willems, Hellriegel and van Schaik, 2013; Willems and van Schaik, 2015) or would maim the decision of some individuals to step up as volunteers to solve collective goods (Archetti, 2009; Archetti & Scheuring, 2010; Diekmann, 1985), probably making less viable cohesive group-living. As it is often the case, the necessary mechanisms at play can only be speculated, so I hypothesise that the fact that precise counting of grooming given and received (measured through surplus) did not impact the observed reciprocity dynamics, and the fact that total grooming received by the dominant did influence them, may suggest that perhaps complex cognitive underpinnings like score-keeping did not intervene, and instead, attitudinal reciprocity was the proximate mechanism (Brosnan & de Waal, 2002). Precise counting or score-keeping relies on mental (memory) abilities that incorporate the different behavioural insights to decide whether or not to reciprocate a social partner (Brosnan & de Waal, 2002). An argument supporting attitudinal reciprocity in similar contexts like the one I registered, is the reciprocity of capuchins (*Cebus apella*) during an experiment involving food between two individuals instead of score-keeping is that this mechanism would enable match predisposition states without demanding precise counting that which would imply much higher memory requirements (de Waal, 2000). More generally, score-keeping reciprocity is though rare due to the limiting conditions it is thought it would have imposed on many animal taxa, which contrasts with the memory abilities that would be required (Stevens, Cushman and Hauser, 2005; Stevens, Hallinan and Hauser, 2005; Hauser, McAuliffe and Blake, 2009) which automatically gives relevance to more parsimonious explanations (Connor, 2010). Moreover, alternative psychological mechanisms like relationship quality could regulate reciprocity relationships over longer periods without the burden of the memory demands of calculated score-keeping (Jaeggi, De Groot, Stevens, & van Schaik, 2013).

Data provided in the first Chapter evidenced that females engage in direct reciprocity exchanges that can last up to several hours, and that the most notable factor regulating such exchanges was the time dimension (declining function) and the total duration of the grooming service. The second Chapter outlined some aspects of the females' decision rules. To grasp a fuller sense of strategic grooming behaviours (grooming reciprocity balance, widening the social network, altering reciprocity balance, showing a preference for bonded, kin and same-sex individuals). An interesting follow up of both studies would be to evaluate whether adult males show similar or dissimilar strategic responses to a feeding treatment, perhaps attempting to launch the feeding experiment in groups with a varying number of adult males and of different ages. It is possible that when they are in a group with many other males, when they are young (in their first migration), and are low-ranking may not exhibit prominent displays of strategic behaviour (personal observation). This conjecture can accommodate the possibility that young males (recently acquired sexual maturity and thus adult age) are either experiencing a somehow “social learning phase” or/and are still building enough muscle power (personal observation) since male individuals at the age of four when they first migrate are not comparable in strength with older males. Such a test would help understand whether and to what extent age and rank may shape strategic Machiavellian decisions (i.e. tactical deception, flexible behaviour, social knowledge, problem-solving). A similar approach could be brought to the boxes experiment to study whether adult vervet monkeys engage in grooming for tolerance reciprocity exchanges in ways akin to adult females (Borgeaud & Bshary, 2015b). As mentioned in section D.2.1 (social networks), the combination of these two experimental ideas could well combine social network details of the male individuals. Further, one could evaluate the concept of inequity aversion (Brosnan, 2011) at the boxes set up after a control situation (no previous grooming) or following a recent grooming interaction. This idea could be more easily applied to females since they groom more often, and help testing how tolerance to aversion if the subjects were trained with equal/unequal food rewards as payoffs and they could perceive it while approaching the box (through a different colour-code or size of box).

Altogether, we need game theory approaches that permit switches between games (grooming interaction, tolerance, joint attack) at different timescales (i.e. short-term attitudinal reciprocity, longer-term friendship or increase in social network centrality). In the third and fourth Chapters, I explored group social behaviour in the context of intergroup encounters and group fission. Although the data I collected in the different analysis of the later chapters was not conclusive, some of the background game theories acquire relevance when interpreted in combination with the results encountered. N-player games apply to conditions that involve collectives of individuals (or groups) that face similar competing interests to two-player games and can be mostly represented by the tensions derived from the options individuals are faced with to play defection or cooperation in a group setup (Archetti et al., 2011; Bach et al., 2006; Barrett et al., 2011; Noë, 1990; Nunn & Lewis, 2010; Peña et al., 2015; Rezaei & Kirley, 2012; Robert & Frey, 2010; Van Veelen & Nowak, 2012). Different N-player games have been conceptualised and incorporated into the study of animal behaviour like i) the N-stag hunt game (Skyrms, 2004; Pacheco *et al.*, 2009) where individuals need to collaborate with others to gain the highest payoff, while not collaborating and playing a selfish strategy would render a smaller (still positive) payoff (hunt a stag VS hunt a hare). Secondly, i) the N-snowdrift game requires one player to cooperate for others to benefit just the same as the one that cooperated but not incurring any cost derived from the cooperative action (Souza, Pacheco and Santos, 2009; Van Veelen and Nowak, 2012). Thirdly, iii) the volunteers' dilemma as a game that requires coordination of several individuals for the benefit to be produced (Archetti, 2011; Archetti & Scheuring, 2010; Archetti et al., 2011; Diekmann, 1985; Franzen, 1995). The fourth could be iv) the collective action problem (Olson, 1965) as a form of social dilemma where higher participation ensures higher payoffs but is challenged by cheating individuals with conflicting interests complicate and compromise the effectiveness of the joint effort (i.e. defection during intergroup encounters) (Willems, Arseneau-Robar, Schleuning, & van Schaik, 2015; Willems & van Schaik, 2015).

First, the framework of the snowdrift game (Van Veelen and Nowak, 2012) translated to the encounter context suggests that a single individual shovelling the snow to remove the roadblock would not suffice, as a concerted effort is required to win encounters. The second game (stag hunt) applied to intergroup encounters could represent that losing against a rival cannot be paralleled to winning the hare unless individuals that fail to cooperate and therefore incur cheating behaviour obtain other benefits. Although here playing hare may be possible through cheating by hiding or moving out of the area where the two groups are fighting, or by foraging in a tree far away if the tree itself represents the good at stake. This second option seems logical as value perception may have deviated from the collective one, and yet, because groups have evolved communicative repertoires to announce encounters and synchronise behaviours, the individual would be self-driven opting to eat/defend its food source. Still, the distribution of payoffs in the n-player stag hunt game seems not to address the specific issue that the VD does effectively, that is, the number of co-operators needed to produce a public good (Archetti & Scheuring, 2010). In its extreme form, the volunteer's dilemma (VD) posits that a fixed number of co-operators is necessary to produce a given public good (in this case territory defence and territory use as an extension of winning) with a step function (Archetti & Scheuring, 2010b). However, the volunteer's dilemma could also be resolved with non-linear sigmoid functions that would stipulate that more contributors may help increase the value of the public good (Archetti and Scheuring, 2010a; Archetti, 2011). The key point about a VD situation is that there is negative frequency dependency: if many contribute my best option is not to, if few contribute my best option is to join. Hence, how many contributors represent the optimal strategy depends upon the investment-benefit function. The pertinent question is therefore whether the particular context of intergroup encounters could be better understood by integrating the logic of two games, the collective action problem on the one hand and the volunteer's dilemma on the other.

The concept of coordination can be linked to the synchrony of strategies played in any one game, or as a game itself during collective moment – which could be useful for the evaluation of intergroup encounters and group fissions. Different studies on collective behaviour argue about how animal groups make decisions and suggest different approaches can serve the purpose of staying together and interesting facets like leadership and followership, voting system, or consensus come in handy to evaluate social dilemmas that individuals face during collective action problems (Archetti, 2009; Archetti & Scheuring, 2010b; Arseneau-Robar et al., 2016; Willems et al., 2013). Hence, the coordination idea may suit well the finding shown in Chapter III, whereby smaller groups systematically winning bigger groups. This puzzling finding merits more investigation, perhaps using a modelling approach that integrates relevant group data like group size, number of adult females (that are in principle more interested in winning and safeguarding a good territory), number of males and perhaps accumulated tenure years (as males that have been longer in the group may have a higher incentive to contribute to the public good).

Additionally, coordination theory may also be informative in this context, although there is no published study to date successfully unwrapping the extent to which intergroup encounters are the result of a leader guiding the behavioural reaction that the rest of the group progressively adopt, or which methods a leader would use, and whether leaders may integrate vocal/gestural communication. Are leaders subtle and merely based on the predisposition that an important figure behaves in a particular way suffices for others to incorporate this information following a rule of thumb and to join?

Here individuals would be confronted with playing the “follow” or “not follow” strategy to the leader individual that initiated a defensive response against the rival group. How big the role of policing and punishment can be to make groups’ concerted action effective to win a rival – or at any rate, “fight a decent battle”? In any case, smaller groups may have the ability to evaluate their rival groups steadily enough to activate what could constitute a form of soft-tactical deception. More precisely, smaller groups could enact what is known as bluffing by successfully coordinating in a more agile and uniform fashion than their bigger rival group. Bluffing or bluffs constitute an alternative to honest signalling that may permit avoiding costly and direct confrontation but that has the risk of being highly costly if the opponent does not “take the bait” (Gardner and Morris, 1967; Riechert, 1998). Therefore, bluffing are displays of bravado and mantis shrimps (*Gonodactylus bredini*) elegantly exemplify this behavioural strategy when they are at their weakest due to moulting and therefore unable to fight but still deterring stronger intruders that would easily invade the cavities where they live (Mesterton-Gibbons and Adams, 1998). This idea and the concept of collective action necessitating coordination and the resolution of the volunteer’s dilemma are not necessarily mutually exclusive. Bluffing behaviours are considered evolutionary stable strategies because the benefits that they offer are higher when the individuals are at their weakest point and they would have no alternative means to fight off competitors, making the net gain of bluffing higher for weaker than stronger individuals (Mesterton-Gibbons & Adams, 1998; Gardner & Morris, 1967). Rewards through grooming and punishment through aggression have been described as female strategies to engage reluctant males (Arseneau-Robar et al., 2016). However, it is difficult to conceive a large number of males being compelled to battle merely through punishment as this would logically increase the need to exert punishment by several individuals thus compromising the actual public good of fighting the rival group. However, it would be interesting to clarify how policing and punishment come together around encounters, especially how it helps to recruit a minimum number of volunteers to outcompete the rival and resolve the collective action problem effectively. In the end, one can even contemplate the possibility that the individual perception of the public good may be dependent on factors like rank, age, tenure (males), number of dependent offspring, territory quality and moment in the year (dry season, wet season).

An ideal modelling approach should also include the group spread information that groups present at the onset of the encounter may condition winning chances. If individuals are far enough from the area where the intergroup encounter is taking place, perhaps individuals' perception of the collective good is shifted when they are calmly feeding on a tree, especially if the individual is a low-ranking one and is benefited from others' being away, which would act as an incentive not to take into consideration the vocal displays that announce encounters (and usually help to recruit). Could it be that the public good of an individual in that situation is the actual tree? More, could it be that being separated geographically from where the action is taking place allows individuals not to be penalised by females thanks to not being in a visual range as if an antithesis of a dilution effect were being far from the group opens the possibility of positive payoffs? Here individual characteristics like rank (or age and tenure in the case of males) and group characteristics like group size may condition defection rates. If group encounters have a commonality with general group movement in the fact that the figure of leaders may be of relevance for those that are followers, it is possible that cooperatively participating in the intergroup encounter does not render positive payoffs. This could happen if those that follow will have limited access to the food sources at stake on the generalised assumption that groups fights have a pronounced motivation to defend food sources (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017). Such a scenario could be tested (see D.2.5. future directions) using playbacks that simulate the presence of a rival group. As a result, it could be that cheaters "measure" the potential gain of going to the frontline to participate when making decisions over whether to move or not which may be linked to the likelihood they will have to exploit the resources (where they to be won) due to their rank position or sheer food abundance. Such conceptions could benefit greatly from modelling approaches.

In any case, the role of leaders, volunteers and cooperators is just as interesting as the role of defectors and studying them more in-depth could help elucidate the complex game scenario animals are in when there are obvious conflicts of interest. At last, could it be possible that bigger groups adopt a sort of "laid back" strategy when confronted with smaller groups if they are capable of recognising that a smaller group does not challenge their "sovereignty"? In the end, and as mentioned earlier, encounter defeats in vervet monkeys do not usually translate into injuries and even if defeated groups abandon the area, they can return to it even the same day and even sleep in it near the rival group (personal observation). Under such premise, the concept of nagging behaviour may be worth some consideration (Stamps and Krishnan, 2001) as monkeys may adopt a sort of boxing *rope-a-dope* technique whereby taking on non-vital hits from the opponent may eventually exhaust it, as done by Muhammad Ali against George Foreman in 1974 epic fight (https://en.wikipedia.org/wiki/Rope-a-dope#cite_note-1). Also, it is possible that in the specific case of vervet monkeys, years are needed to "wear off" an opponent and withdraw real victories that translate into progressive territorial appropriation that involves the rival's displacement.

On a similar note, the study of group fissions offers some interesting game theory extensions. Recent studies inform that knowledgeable (older) adult females are the leaders when it comes to movement decision making in vervet monkeys (Lee and Teichroeb, 2016), although group movement is also known to change in response to food resources availability (Reyna-Hurtado *et al.*, 2018). One of the main and accentuated conflicting interests that the different group members may have undergone during the drought may be represented in the cost that followers probably had to undertake when adhering to the leaders' movement decisions (Bullinger, Wyman, Melis, & Tomasello, 2011; King & Sueur, 2011; Petit et al., 2009; Petit & Bon, 2010; Sueur & Petit, 2008). If the drought conditions made more punitive the adoption of follower roles to the point that it was either unbearable –or close to it, perhaps this acted as a tipping point (Jiang, Hastings and Lai, 2019). This type of scenario could have therefore acted as a trigger that motivated some individuals to contemplate the leaving strategy. If so, assortment could have followed, establishing progressively a divide on the founder group that leads to the creation of daughter groups although I could only detect assortment according to grooming, proximity and kinship in the NH group. Still, an interesting alternative to study female assortment before fissioning could be to evaluate the relevance of grooming reciprocity relationships between the different dyads.

A good source of information to corroborate this hypothesis could come in the form of urinary C-peptides that measure energy balances (Grueter *et al.*, 2014). If a subset of followers cannot forage efficiently enough because the extreme scramble competition conditions force them to revisit zones that have been foraged upon before by others, one could hypothesise that the volunteer's dilemma could explain the emergence of an individual that suggests a change of bearing. This does not necessarily imply that groups cannot escape fission, but instead, that milder forms reflect a lack of group consensus and "day splitting" could offer release from the costs of following as often seen at the IVP, although there is something eminently different with fissions as future encounters are aggressive from the splinter date onwards (personal observation). And if such conditions become stagnant, perhaps the strategy of leaving becomes an alternative to the status quo that is represented by the strategy of staying. Thus, the question here would be, how does the figure of a volunteer emerge acting as a leader for others to join (most likely a female)? As it appears, this has resemblances to the type of leadership that could in the initial phase of intergroup encounters. Beyond, similarly to alleged above for the intergroup encounters, if the figure of a volunteer – or several – emerges in the case of fissions, one wonders how what could be an initial individual decision transcends into a subset of the collective. The social dilemma represented by the alternative strategies of "stay" and "leave" could also be approached through the concept of "war of attrition" (Hammerstein and Parker, 1982) that expect the players to adopt a similar strategy to that of the opponent. Here, adult females would be waiting for (not evicting) others to do the next move, and hoping the others decide to make the next move and play the "leave" strategy. However, the concept of war of attrition seems more used in open conflicts like fights between neighbouring groups (Ydenberg, Giraldeau and Falls, 1988; Sun *et al.*, 2019). Some interesting facets that could illuminate how fissions build up in time could be obtained through an exploration of group ranging data before the fission happens as when food availability is low groups may have enlarged their ranging habits beyond the usual (Hemingway & Bynum, 2009; Li, Ma, Zhou, & Huang, 2020; Reyna-Hurtado et al., 2018), or how sleeping sites may have also been located at rare sights.

D.2.4. Wrap-up and future directions

My first Chapter adds on to previous work conducted by Borgeaud (Borgeaud & Bshary, 2015b, 2018; Borgeaud et al., 2017) that delved into how adult females engage in cooperative interactions with other females. Thanks to this work we know more about how individuals perceive others while integrating shared –or not (Borgeaud & Bshary, 2015b, 2018) past affiliative interactions. My second Chapter evidenced that adult female vervet monkeys can flexibly adapt to important changes in their grooming behaviours concerning their investment in grooming and their phenotypic assortment to who they target. This study, therefore, added on the pre-existing information that vervet monkeys' social networks are dynamic structures (Borgeaud et al., 2017), and the notion that ecological conditions are important drivers of sociality (Henzi et al., 2009). Here, as alleged above, it would be interesting to assess how some of the relationships that were developed during feeding treatment could stabilise and how these could solidify in stable interdependencies. If this could be evaluated, interesting facets such as how this would impact local networks (perhaps triadic relationships, transitivity), and whether the rigidity of the rank system characteristic of females could experience promotions in the event a subordinate is benefiting from the bond she shares with a higher-ranking "godmother-like" figure. One could argue that the first two Chapters would be greatly benefited if more work was to follow, this time setting the focus on the adult males. It would be of great interest to uncover the puzzle of contingent cooperation using the same boxes setup on males. Although we know the female system relatively well, approaching the male system with an experiment design already known to work efficiently would permit testing adult males with adult males. Likewise, the same could be attempted on male-female dyads, even more, incorporating female audience or not, as we know that males can be scolded and aggressed by females when they join in coalition in different primate species (Henzi & Barrett, 2007; Tokuyama & Furuichi, 2016; Ventura et al., 2006).

Generally, it would be interesting to conduct similar studies to the one I present in Chapter I to further deepen the understanding of males' strategic behaviours when launching the experiments on different groups with a varying number of males (personal observation: in groups where there are many males- more than 5 approximately, some seem to put their power ambition on hold, and instead learn to develop alliances, friendships and effective ways to deal with conflict, and to prevent conflict) and on males in different positions of the hierarchy (low, medium, high)? How much grooming investment would males dedicate to females, i.e. how much interest would they show having in increasing their degree specifically with females? Additionally, it seems pertinent to evaluate how males provide services to the group concerning their tenure and genetic ties with the infants and juveniles of the group. What is more, an interesting extension of the second Chapter could be to evaluate how dominant and non-dominant fed males could make strategic decisions about how to invest their surplus time grooming others. For example, male Arabian babblers (*Turdoides squamiceps*) increased sentinel behaviour while exposed to a feeding treatment (Wright, Maklakov, & Khazin, 2001), and a similar study conducted in the same species found no difference in overall sentinel behaviour between males and females (Wright, Berg, De Kort, Khazin, & Maklakov, 2001), which coincides with the comparable response that meerkats displayed while receiving food supplements (Clutton-Brock *et al.*, 1999). One could assume that similar decision rules would be at play as inferred from the study on adult females, and whether males could use a possible improvement of relationship quality with females to outcompete other males (directly through aggression, indirectly through daring more to be closer or grooming more other females). Would males be similarly driven to flexibly adopt a keen interest in grooming others? If yes, which underlying decision rules would shape their predilection (if any) towards certain partners due to their intrinsic characteristics (as we know, males are also capable of third-rank relationship knowledge; Borgeaud et al., 2015). Even more, it would be very interesting to study the strategic nature of males' preference for certain females for the implications that this may have (i.e. good relationship quality with direct male competitors for rank, central females, already bonded female partners).

The topic of intergroup encounters that I investigated in the third Chapter has experienced very significant progress in the last years in many animal taxa. In the specific case of vervet monkeys' encounters, the work conducted by Arseneau-Robar and colleagues helped advance the knowledge that males can de-escalate conflicts (Arseneau-Robar et al., 2018), females can alternate "carrot" and "stick" methods to engage males into participating (Arseneau-Robar et al., 2016), females are more prone to participate in encounters when not having infants or when being supported by males (Arseneau-Robar et al., 2017), and that males motivation to defend food in the territory may be a form of by-product cooperation as they may find more incentives to do so to increase their status (Arseneau-Robar et al., 2016). Despite the innovative approach that bringing ecological and territorial features to the study and having relativized each terms taking on the perspective of the focal group concerning that of the encounter group, it seems pertinent that the intriguing detection of smaller groups defeating almost systematically bigger groups begs more attention. Regarding this, different ideas could be pondered, i.e whether the concept of public good could vary depending on the exact geographical position of the individual. Could individuals being further away (i.e. more than 100 meters) from the epicentre of the encounter have a different perception of which public good worths being defended while foraging in a good tree? This, again, could be tested in wild conditions relatively easily using playbacks of group encounter vocalisations of different individuals (high-ranking or low-ranking females, bonded or non-bonded, female or male) to subjects that are in the periphery or the centre of the group. Nevertheless, the already available group spread data may also serve to test the adequacy of the volunteer's dilemma in the frame of group size, sex ratios, number of adult females, and number of adult males. Perhaps, as hinted by Archetti (Archetti, 2009), the fact that volunteers may benefit less in bigger groups than in smaller groups, suggesting a declining function of volunteer predisposition to volunteer. If that were the case, one could speculate that defection, when a certain threshold has been surpassed, can be more contagious than cooperation? Notwithstanding, the chimaera of how cooperation and defection strategies unfold at the individual level relative to whether the rival group is bigger or smaller should also be integrated with a possible modelling approach.

Finally, in the fourth Chapter IV, I studied the phenomenon of group splinters in ample detail. Here I first must acknowledge that although the nature of the data analysed coerces the development of potent conclusions, some of the results provide a broad brush into how fissions may materialize from the perspective of the most influential of sexes in the group. Although I cannot provide any analysis providing further information on whether a coordination problem potentially eroded groups' movement synchrony, which would represent a social dilemma where the hypothetical modelling approach mentioned above could potentially offer some insights that would give more ground to the fission topic. Furthermore, the way I approached the fissions (rewind in time from the fission moment) could be complemented by a forward-look that evaluates how the "freshly-born" network of the daughter group that was followed re-structured by using time windows that could help observe the development of progressive cohesiveness in the group (density, transitivity) and the emergence of bonds. Along these lines, recent research on rhesus macaques revealed a notorious capacity of individuals to increase their social network after the occurrence of a hurricane event (Testard *et al.*, 2021), similarly to some of my second Chapter's findings suggest. If that were studied, would all individuals be equally motivated to establish bonds (high-ranking or lower-ranking females)? It could be argued that higher-ranking females were used to benefiting from their prominent status, while lower-ranking ones may perceive the new situation (the foundation of the daughter group) as an opportunity to "work harder" to gain certain status. In a way, these considerations fit the attempt made in the second chapter to compare the dominant and subordinate fed subjects, and even if the sample size was very low, subordinates invested more in grooming than the dominant subjects.

During my PhD, I dedicated eighteen months to vervet monkey's urine samples to study what were considered to become two integral chapters of this thesis related to underlying oxytocin levels, firstly the topic of grooming behaviour and underlying oxytocin levels, and secondly, the participation in intergroup encounters. Beyond the fieldwork, I worked for almost a full year on the development of an oxytocin protocol after realising that already existing protocols (Crockford *et al.*, 2013; Benítez *et al.*, 2018; Rincon *et al.*, 2019; Schaebs *et al.*, 2019) rendered odd results (i.e. concentrations of one sample varied too greatly when measured in one Elisa plate to the measurement obtained when measured in a different plate). Although I managed to solve most of the issues observed at first (solid-phase extraction, parallelism conducting serial dilutions, extraction efficiency comparing spiked and non-spiked samples, assay accuracy using different spiked concentrations), repeatability only stayed within the accepted variance (about 15%) when a given sample was measured in the same plate. Due to technical impediments that far surpassed my capacity and due to the compromising situation that continuing the work on perfecting a method would have caused me, I temporarily interrupted my dedication to solving this issue. At the moment, work is in progress thanks to the different collaborators and I hope the samples collected for the abovementioned projects can be someday analysed. Albeit this, I present the protocols I developed with some colleagues in Chapter V (Appendix A: cortisol-testosterone, and Appendix B: oxytocin.

The grooming project aimed to replicate the study conducted by Crockford et al. (Crockford *et al.*, 2013) and consists of more than 300 samples of adult females and males mainly from one group (BD). These samples reflect the riches of the conditions aimed to be tested, that is, grooming direction (grooming received, given, or reciprocal), grooming duration, relationship quality (through a bond index using a script developed in collaboration with Dr Wubs), sex combination (female-female, female-male, male-male), age combination (female-juvenile, male-juvenile), kinship (kin, non-kin), and the number of grooming partners (we established a maximum of two partners to avoid masking, overlapping effects). Additionally, some interesting facets of how oxytocin oscillates could be studied, as it is assumed that oxytocin needs approximately fifteen minutes from the observed social behaviour to show in the urine and the window of collection stays valid until 60 minutes have passed (Crockford *et al.*, 2013). The study of a different primate species could shed light on oxytocin expression and clearance times through urine (Seltzer and Ziegler, 2007; Benítez *et al.*, 2018; Ziegler, 2018). On the other hand, the potential to study a form of group cooperation like intergroup encounters stays a priority in my research agenda if we manage to resolve the technical issues that are still impeding the analysis. This project has around 75 samples on adult individuals that were collected under very challenging conditions and could help unveil the connexion of neuro-hormones with the participation levels (measured through focal following of individuals, which opens the opportunity to discuss the role of defection too), which could potentially interact with factors like tenure (males' samples), and rank. I propose below three potential projects that could be conducted with the existing set of samples and integrate grooming interactions, connectivity in the social network of the group, and male migration.

First, a straightforward study could benefit from the samples that are already available by evaluating the effect of grooming, and by extension, the partner involved, the direction of the grooming, duration of the grooming, the sex-age combination, and the number of grooming partners. Even if the grooming (preening, allopreening) is approached from multiple perspectives, only a handful of studies empirically test their physiological stress underpinnings. For example, ravens (*Corvus corax*) with higher corticosterone concentrations showed higher proximity indices and allopreening behaviour toward partners (Stöwe *et al.*, 2008). A study on the cichlid fish (*Neolamprologus pulcher*) exposed that the subjects exposed to a cortisol treatment reduced their affiliative behaviours and did not affect submissive behaviours (paper Culbert).

Differently, social interactions seemed not to affect glucocorticoid levels in wild Verreaux's sifakas (*Propithecus verreauxi*) (Rudolph *et al.*, 2020). Two important studies have targeted directly the concept of grooming and glucocorticoids, the first one shows that Barbary macaques (*Macaca Sylvanus*) present lower stress levels when they give grooming rather than receiving (measured using faecal samples which may not be the most suitable method to address such short-lived events) (Shutt *et al.*, 2007). A second study showed rank-specific cortisol levels varied depending on whether the grooming was focused on specific partners or distributed evenly (Sonnweber et al., 2015) in Barbary macaques (*Macaca mulatta*). Even if a note of caution is mandatory when interpreting glucocorticoid concentration variation due to their intrinsic plasticity (Creel *et al.*, 2013; Sonnweber *et al.*, 2018; Guindre-Parker, 2020; Sapolsky, 2021), the large sample size I collected over the last few years might help control for such eventualities.

Secondly, my samples could be used to move from the classic idea that rank is related to stress levels, i.e. dominant individuals in savannah baboons, *Papio cynocephalus*, presenting higher stress levels (Gesquiere *et al.*, 2011), subordinate individuals present higher stress levels (Abbott *et al.*, 2003), no rank-related glucocorticoid expression in baseline levels (Anestis, Bribiescas and Hasselschwert, 2006) and compare hormone levels to the individuals' position in the network. Ample research has shed light on our current understanding that across the animal taxa, individuals standing in the network can have implications for fitness (Oh and Badyaev, 2010; Hougen *et al.*, 2012; Royle *et al.*, 2012; Stanton and Mann, 2012; Lehmann, Majolo and McFarland, 2016; Ellis *et al.*, 2017; Ostner and Schülke, 2018; Rose and Croft, 2020). Under such premise, a look into how stress levels connect with the connectivity of an individual (i.e. through degree, and more specifically degree with females and degree with males, or centrality) would complement greatly the concept of social standing in a group. A pioneering study conducted in the cichlid fish (*Astatotilapia burtoni*) showed that changes between dominant and subordinates were higher in less stable networks (higher levels in dominant individuals) (Maguire *et al.*, 2017). Another interesting study revealed that manipulated avian stress hormone corticosterone in nesting zebra finches (*Taeniopygia guttata*) had weaker associations after reaching independence (Boogert, Farine and Spencer, 2014). In the same token, a comparison of wild house finches (*Haemorhous mexicanus*) with wild ones found that the wild phenotype- also more explorative, had a higher social network degree (Moyers *et al.*, 2018). Moreover, a study in rhesus macaques (*Macaca mulatta*) indicated that high ranking females had higher glucocorticoid levels when their proximity networks were smaller and more focused (Brent, Semple, Dubuc, Heistermann, & Maclarnon, 2011). Another study on crows (*Corvus macrorhynchos*) showed that females and males show a sex-reversed relationship of glucocorticoid corticosterone (males at higher rank higher levels, females at higher rank lower levels) (Ode *et al.*, 2015). Altogether, an investigation of the vervet monkeys' glucocorticoid concentrations may add to the comprehension of how individuals cope with daily challenges, and how being socially well connected may assist.

Lastly, the subset of the samples I collected on adult males could help evaluate how males' characteristic strategy of moving from group to group after abandoning their natal group could be connected to a physiological baseline measured through cortisol. Males face important challenges with migration (accentuated exposure to predation risks by separating from the group, insecurity in acceptance, the possibility of being a satellite individual during some time, being aggressed by the individuals of the new group, suboptimal foraging, etc.) hen(Alberts & Altmann, 1995; Bonte et al., 2012; Greenwood, 1980; Travis et al., 2012; Waser, Creel, & Lucas, 1994)was, so it one could expect males to face such event at their optimal (higher cortisol and testosterone levels). Male migration encompasses and demands involving behavioural aspects that go beyond reproduction, as freshly arrived males need to integrate (at least to some extent) into the new group, develop social relationships, test themselves with other males and possibly assess their mating potential concerning male-male competition. There is evidence that stress levels (cortisol) are higher after migration in crested macaques (*Macaca nigra*) (faecal samples) and decrease after arrival (Marty *et al.*, 2017). Similarly, recently migrated female chimpanzees (*Pan troglodytes)* had higher cortisol levels than non-migrated females (Kahlenberg *et al.*, 2008). A lack of significant cortisol or testosterone variation was observed in male yellow and olive baboons (*Papio cynocephalus, P. Anubis*) following immigration (Akinyi *et al.*, 2017) (faecal samples). Differently, cortisol levels of migrated hyena males were higher than those of group-born individuals (Holekamp and Smale, 1998) (blood). Equally, male chacma baboons (*Papio hamadryas ursinus*) had higher cortisol levels in the month after immigration (Bergman 2005, Beehner 2006) (faecal). The most in-depth study revealed no difference in faecal cortisol levels in the 60 days before emigration relative to baseline levels (more extended period), nor when the baseline was compared to the 60 days after immigration in vervet monkeys (*Chlorocebus pygerythrus*) (L'Allier, 2020). In that frame, evaluating how the males' samples already available can help respond to aspects like physiological state (cortisol, testosterone) shortly before, shortly after, and time after (compared to baseline accumulated) levels using urine samples would be an interesting contribution to the field of behavioural endocrinology.

To conclude, I attempted to study infant-handling behaviours by non-mother females in 2019 but failed due to the massive infant mortality registered during a rather unusual dry season (Hulsman, Savenije and Hrachowitz, 2021). Following the initial intent of my PhD, I intended to evaluate the potential linkage between stress hormones and unwanted baby handling by third parties. Despite not managing my goal due to unsurmountable complications, I managed to observe plenty of behaviours that perhaps deserve future testing. To date, two studies support that non-mother female can achieve infant handling opportunities through grooming provisioning (crab-eating macaque *Macaca fascicularis* in Gumert, 2007; and vervet monkeys and sooty mangabeys *Cercocebus atys* in Fruteau, van de Waal, van Damme, & Noë, 2011).

Although the logic of the biological markets appears solid and the alleged declining function of the baby value with the age and the number of babies appears logical, my observations in the field invite different thinking. My observations during 4 years (27 months of fieldwork as a PhD and 10 months as a research assistant) helped me witness baby-handing behaviours extensively. Albeit, the testing of my hypothesis appears rather complicated, that is, that non-mother females offer longer grooming services that will invite the grooming mothers (with babies in body contact with them, as if babies are more independent they can be directly stolen by capricious non-female mothers) to relax and offer different body parts. In my eyes, recipient mothers are sometimes taken aback by non-usual non-mother-very-willing females that offer unusually good grooming bouts. Such a scenario seems to elicit a form of initial distrust (grooming recipient mothers do not offer different body parts and keep body contact, or hand contact to their babies). However, non-mothers could have perfected their technique by "persuading" or "convincing" their grooming partners by offering a somewhat atypical grooming service. During my last field trip in the "baby season" of 2019, I aimed to collect behavioural data that could help contrast this hypothesis, given that fruits were scarce and females would spend most of their active time on the ground lifting stones and searching for old fallback seeds. As a result, it would be feasible to collect the exact number of mouth to body contact during the grooming interaction that the non-mother groomer offers, the number of hand "clearing" displays that they do to visually detect parasites, the total duration of the grooming, the number of times the groomer eats a parasite as a count of the number of parasites being removed, and I considered the number of different body parts as done by (Allanic *et al.*, 2020).

Moreover, it appeared to me that the non-mother groomers' decision to take the baby and infant-handle it can be displayed in several fashions: i) seemingly agreed and consented one (that would fit the logic of the Biological Market Theory), ii) "give and take": non-mother stops grooming and profits the sudden carelessness or slip-up of the mother to pick up the baby to which the mother rapidly responds claiming it back, to which the non-mother consents, iii) "sneaky robbery": when non-mothers are not willing to give back the baby. This scenario would be worth investigating, if possible with the additional hormone component, also integrating the rank and bond relationship of the female dyad. As a result, such a detailed study could challenge the notion that baby handling, especially while the babies are younger than three months old when they are most vulnerable and more dependent (personal observation) fits the Biological Market Theory, as I believe there may more to it and if there is lack of consent, non-mothers are not entering a market but either using trickery or directly benefiting from their superior rank to cheat deceived mothers with grooming subterfuges. Regardless, it seems reasonable to catalogue the list of strategic behaviours as a form of tactical deception and therefore a manifestation of Machiavellian abilities (Whiten and Byrne, 1988; Byrne and Whitten, 1997). As it appears, it would be very interesting to challenge whether BMT can fully explain the tactical "cheeky" grooming that around subtle "sneaky" robberies or if additional explanations are needed. This particular context has important potential because biological markets appear to enter in action (if they are not present while non-mothers attempt accessing a baby) once the mothers have lost access to their babies. This new scenario may well make use of strategic "trickery" but this time the refinement of the trickery may need to adopt slightly subtler or smoother forms since "disposed mothers" are usually lower ranking than "non-mother stealers". Such instances seem to present "exaggerated" benign intent that attempts to hide the real interest (having the baby back) just as much as the robbers may do. As it appears, the social life of vervet monkeys is ripe with strategic decisions around cooperation and conflict that need more investigations combining experimental approaches with carefully collected (and rich in detail) opportunistic observations.

D.3. References

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