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Comportement de coopération chez les singes vervet: une approche expérimentale

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Thesis Abstract

Introduction

A number of theoretical papers have investigated the mechanisms by which cooperation may evolve but very few studies have examined cooperation in natural animal populations under experimental conditions. These studies usually consider cooperation (or working together) as achieved by dyads of individuals to get a reward. In social groups more than two individuals normally cooperate to obtain rewards useful to the community. In this project I study multi-player cooperative events under natural conditions.

Over the course of three years, I performed field experiments with three groups of wild vervet monkeys (*Chlorocebus aethiops*) in South Africa. The experiments involved two or more individuals in a group repeatedly operating feeders to get access to limited quantities of food. I established two fictitious social classes, and I subsequently assigned all individuals in a group to one of these classes: a small class containing only two individuals, and a large class formed by the remaining members of the group. Criteria to administer rewards were subsequently linked to the assignment of class: a reward was only administered if cooperation partners were of a different class.

The first aim in the experiments was to see whether cooperation at the feeders was appearing in our study groups. I subsequently studied strategic choice of cooperation partner. Firstly I predicted the individuals to select each other based on their relatedness. Secondly, using the established classes, I studied the consequences that cooperation had on the structure of the social groups. The prediction, based on the market effect, was that the law of supply and demand would modify the exchange of social behaviours across the classes of cooperative partners. The members of the small class, who were in demand and in an advantageous position for cooperation, would show an increase of beneficial behaviours directed at them.

Results

After a training phase during which the monkeys became accustomed to the feeders, I induced cooperation by way of food rewards. I analysed partner choice of members handling the feeders together. During the training phase I calculated proximity networks based on distances of nearest neighbours and social networks using behaviours such as grooming, contact-sitting and social play. The recurrent partner associations observed during training only partly predicted the forming of cooperative partnerships during the cooperation phase.

While most of the tested subjects cooperated with different partners, they preferred to do so with specific combinations of individuals and tended not to mix with group members outside these preferred partnerships. This caused the relatively homogeneous networks I observed before the experiment to differentiate since the cooperation partners selected each other limiting their choice. Interestingly neither sex nor age class explained the specific partner matching. Kinship could not explain this matching either. Rather cooperation partners were chosen based on social rank, where higher ranking individuals cooperated with other higher ranking ones, and lower ranking ones with others of lower rank.

To test market theory models, I analysed whether the distribution of exchange of beneficial behaviours had changed due to the reward criteria based on assigned class. During the cooperation phase, the monkeys became able to discriminate between the values of the contribution to the cooperation across classes. Because one class was less numerous than the other, its members acquired a privileged status and became in demand as cooperation partners. This was shown by a change of sociopositive behaviours in favour of the smaller class.

Discussion

This study reveals the key role of dominance rank when food resources are patchy and need to be accessed by multiple partners. Individuals belonging to same hierarchical categories (more dominants or more subordinates) segregated in a rank-related nepotistic manner.

Because of the found key role that the dominance status plays for this augmented social differentiation, I can emphasise that cooperation increases discrimination among group members. In addition, after cooperating the monkeys adjusted social behaviours' exchanges in favour to the smaller class of cooperators. They therefore adapted to the law of supply and demand as predicted by biological market theories.

I recommend the implementation of this cooperation experiment in the field with other primate species and other mammals to confirm our results on rank related social differentiation and the presence of a social modification predicted by supply and demand.

Thesis abstract in French - Résumé de Thèse

Question posée et approches expérimentales

De nombreux articles ont abordé, de manière théorique, les mécanismes d'évolution de la coopération, mais peu d'études ont examiné les phénomènes de coopération survenant naturellement dans les populations animales. Ces études s'intéressent généralement aux actes de coopération, effectués par des couples d'individus cherchant à obtenir une récompense de nourriture. Ces expériences sont habituellement réalisées en laboratoire, par des animaux captifs, et à l'aide d'une récompense de nourriture que les individus doivent se partager.

Dans la présente étude, nous nous sommes intéressés aux actes de coopération survenant entre de multiples acteurs, en conditions naturelles. En effet, il arrive fréquemment dans les sociétés animales, que plus de deux individus s'associent afin d'obtenir de la nourriture.

Durant trois années, nous avons réalisé des expériences sur le terrain avec trois groupes de singes vervet (*Chlorocebus aethiops*) dans une réserve naturelle en Afrique du Sud. Ces expériences faisaient intervenir au moins deux individus qui actionnaient spontanément des distributeurs contenant de la nourriture, ceci de manière à en libérer une petite quantité.

L'objectif de ces expériences était de tester si des actes de coopération et de partage de la nourriture provenant des distributeurs, allaient apparaitre dans les groupes étudiés. Dans un second temps, nous avons cherché à connaitre les stratégies de choix des partenaires adoptées par les individus qui coopéraient. Enfin, nous avons analysé les conséquences et répercussions que cette expérience et les actes de coopération qui y sont survenus, ont pu engendrer au niveau des comportements sociaux et des liens qui unissent les individus du groupe.

Résultats

Après une période d'habituation des singes aux distributeurs de nourriture, les trois groupes étudiés ont été capables de coopérer pour accéder aux récompenses.

Chaque groupe de vervets a été divisé en deux sous-groupes, les distributeurs devant être actionnés simultanément par au moins un membre de chaque sous-groupe pour que la nourriture à partager soit rendue accessible. Le choix des partenaires (membres composants chaque sous-groupe) a été déduit en fonction des associations spontanées observées dans ces groupes. Avant les expériences, nous avons analysé deux paramètres : les réseaux de proximité, basés sur les distances des plus proches voisins, et les réseaux sociaux, basés sur les comportements de toilettage, de « contact-sitting » et les jeux sociaux. Les associations récurrentes de partenaires observées avant l'expérience n'ont prédit que partiellement la formation des partenaires de coopération lors de la phase expérimentale. Avant les expériences de coopération, la majorité des sujets testés avaient plusieurs partenaires « privilégiés » et n'avaient que peu d'interactions avec d'autres membres du groupe. Suite aux expériences, on a observé des modifications au niveau du réseau social, celui-ci ayant été relativement homogène auparavant. Ces modifications sont vraisemblablement dues à la sélection limitée des partenaires pouvant obtenir une récompense lors des expériences réalisées. Singulièrement ni le sexe ni la classe d'âge ni même les liens de parenté n'ont pu expliquer la sélection des partenaires. En revanche, les individus dominants des groupes ont coopéré avec d'autres individus dominants et les individus subordonnés avec d'autres individus subordonnés.

Après la phase expérimentale, et afin de tester la théorie des marchés biologiques, nous avons analysé si les réseaux sociaux s'étaient modifiés de manière conséquente aux évènements de coopération. Durant la phase de conditionnement, les singes ont été capables de comprendre que, pour obtenir une récompense de nourriture, il était nécessaire que deux individus de sous-groupes différents s'associent. De plus, les sous-groupes comportant un nombre différent d'individus, ceux appartenant au sous-groupe le plus petit sont devenus des partenaires de choix pour actionner le distributeur.

Conclusions et perspectives

Cette étude a mis en évidence le rôle clé de la hiérarchie sociale lorsque les ressources de nourriture sont limitées et que plusieurs individus doivent s'associer pour la rendre accessible. Chacun des trois groupes de vervets ont coopéré de façon népotique : les individus appartenant à la même catégorie hiérarchique (dominants ou dominés) se sont séparés et ont effectué les actes de coopération entre eux. Ces résultats sont en accord avec les modèles sociaux écologiques qui décrivent les groupes despotiques se nourrissant de ressources limitées.

Pour conclure, on peut souligner que la coopération accroit la discrimination entre les membres d'un groupe à cause du rôle clé des statuts hiérarchiques.

D'autres études sur le terrain avec d'autres espèces de primates ou de mammifères devront être réalisées afin de confirmer ces observations.

Acknowledgments

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Chapter 1 – General Introduction

Introducing cooperation

Reaching an understanding of the mechanisms underpinning cooperation in both human and non-human evolutionary biology has been one of the significant scientific challenges in recent decades. The transition from selfish behaviour to social behaviour, and eventually to the level of complexity apparent in coordinated behaviour with partners, indicates that adaptation by natural selection favours the advent of cooperative acts where beneficial both in relatively simpler as well as more complex organisms.

Cooperation is often portrayed as a domino like cascade of events stemming from relatively uncomplicated origins that go on branching out. These events can lead to the formation of associations and interactions amongst many actors giving rise to a more complex state of order. Behavioural strategic factors, such as partner choice and partner switching, form a central role within this network of interactions. Such factors influence this network and provide the cues for the developmental dynamics that will eventually shape the life of social living group. These dynamics frequently are not evident to the human eye, and remain unknown unless routinely observed and recorded.

It is common sense to think that the same idea at the base of the phenomenon of cooperation is taking place not just in complex organisms, but also at any step forming life. The evolution of agents of increasingly complex form, such as molecules, cells, prokaryotic and eukaryotic organisms, and social groups, is due to a form of cooperation and development of the components forming the preceding level.

Studying cooperation at all levels of life in addition to comparing different species living under different social or ecological circumstances, will shed light on the evolution of cooperation. In particular, studying cooperation in primates helps us to understand how human cooperation has originated at the species level most proximate to us.

The function (or adaptiveness) of cooperation is not immediately obvious. The theory of evolution predicts that under natural selection, only genetic factors that lead to physiological or behavioural advantageous traits are maintained in a population. Being cooperative appears to be costly at times to one of the cooperative partners.

In this introduction I will first outline the definition of cooperation in animal behaviour. I will subsequently review the evolution of cooperation, summarising the main theories proposed to explain cooperation. Finally, in the last section I will introduce the aims of this study, its experimental field approach, and provide some details on data collection not presented elsewhere in this thesis.

Definition of cooperation with a few examples

Instances of cooperative behaviour have been found between members of the same species and between individuals of different species. Researchers in diverse fields have attempted to advance theories to explain why cooperation is so common in humans. Fehr & Fischbacher (2003) account much of the experimental evidence of the ubiquity of human altruism (but see also the recent West et al. 2011).

Cooperation can be observed not just in humans, but also in animals, in plants, in fungi, etc., as well as amongst species belonging to different kingdoms. It is important to note that cooperative actions do not necessarily require a high level of cognition. In fact cooperative interactions are also found at a molecular or cellular level (see Szathmáry & Maynard Smith 1995 for a review).

Cooperation is a general term used for a wide range of phenomena. A typical dictionary definition is "*the interactions simultaneously beneficial to all its participants*" and "*the behaviour of the participants in such interactions*" (Noë 2010).

More specifically, in the framework of the behavioural sciences, the interaction is considered as cooperative if it provides a benefit to another individual and if it has in some way evolved because of this benefit (West et al. 2007a). Focussing more on the economic sense of the definition, interactions are cooperative when on average result in net gain for all participants while potentially incurring in the risk of insufficient returns by some participants (Noë 2006a).

Association between two species are called 'symbioses' and 'mutualism'. I give examples to highlight the difference between the two. Both mycorrhizal relationships and plant-pollinator relationships are long term and obligate symbiotic relationships, whereas facultative interactions such as animals eating the fruits of a tree and, as a consequence, dispersing the seeds, are called mutualisms.

In animal species, cooperation can take various forms. For example allofeeding or providing support to a conspecific during an agonistic encounter are examples of altruistic behaviours. In primates, allogrooming is another example. While offering grooming the actor in fact spends time not feeding and decreases its vigilance against predators. While being groomed, on the other hand, the recipient is relieved from its external parasites.

One of the principal examples of apparent cooperation consists of species having helpers who babysit offspring at their nests. Meerkats have been most intensively studied for this aspect of their social life. For the helpers, attending other group members' nests has a cost in terms of not feeding at the same rate as others. It has been demonstrated that because of attending the nests over a day period, babysitters lose 1.3% of their body weight while other group members gain 1.9% of weight (Clutton-Brock et al. 1998).

Another example of cooperation can still be found in meerkats sentinel guarding. Clutton-Brock and colleagues (1999) suggest that in meerkats, guarding may be an individual's optimal strategy if no other animal is on guard. This is an example of providing help for predator-prey related interactions. Similarly, during social conflicts, the supporter expends energy and risks to be injured.

Blood sharing in vampire bats represents a classical example of cooperation by means of food sharing. When vampire bats fail to find food, they are often fed by successful roost-mates (Wilkinson 1984). These mates incur in a loss of food intake while sharing food with others and an increase in energy expenditure during foraging activity.

An example of cooperation by multiple individuals, is provided by communal territorial defence by lions (Grinnell 2002). Both male and female lions rely on the defence of their territory for their survival, hunting and raising their offspring. It is therefore advantageous to all members to ensure a safe habitat by guarding it together.

Evolution of cooperation

From an evolutionary standpoint, behaviours are social if they involve actors as well as recipients who become affected by the former. Some actions may be beneficial whereas others may be costly for one or all interactants. When beneficial, they increase the direct fitness of the individuals, that is their probability of survival and reproduction (West et al. 2007b). Following Hamilton's (1964a) terminology, behaviours beneficial to the actors but costly to the recipients are selfish, behaviours costly to the actors but beneficial to the recipients are altruistic. When beneficial to both actors and recipients are mutually beneficial (West et al. 2007a), whereas when having negative fitness impact to both actors and recipients are spiteful (Hamilton 1970). Different from mutually beneficial behaviours, altruistic cooperation does not entail direct fitness benefit for the initiator of the altruistic action (not even in the long term).

Often, being cooperative or altruistic looks as if being costly to the initiator and beneficial to the receiver. Performing an altruistic act in fact induces a cost with potential negative effects on the survival or on the reproduction of the initiator. Under natural selection and without any form of compensation, non-cooperative individuals (also called defectors or free-riders) would outcompete cooperators by avoiding the energetic cost of the cooperative action, while attaining the benefits. The higher fitness of defectors would then lead to the disappearance of cooperative individuals.

Since cooperation is found at many levels of life, several theories have been brought forward to explain its occurrence despite these outlined problems.

The kin selection theory

The concept of inclusive fitness introduced by Hamilton (1964a) provided a novel and the most established explanation for the evolution of altruistic behaviour in kin-related individuals. Hamilton suggested that the consequences of an altruistic trait are to be found not just in the recipient of altruism but also, indirectly, in all individuals that share the same genes and have been affected by such cooperative behaviour. According to Hamilton's rule, we can expect altruistic behaviours to evolve when the benefit of the recipient multiplied by its relatedness with the actor exceeds the cost of the altruistic individual. This theory, also known as kin selection (after Maynard Smith 1964), was a major breakthrough and explained altruistic traits through a simple evolutionary mechanism of common descent.

However, according to kin selection, animals should preferentially allocate their cooperative behaviour to interacting kin over non-kin. If individuals do not have the possibility to differentiate kin from non kin, there is no way to choose appropriately the correct recipient for the altruistic act so that a fitness return gain will be achieved.

Examples of cooperative actions directed to non-related individuals have been described in animals. These examples cannot be explained by kin selection and therefore other theories and explanations have been suggested.

The reciprocal altruism theory

Trivers (1971) proposed the theory of reciprocal altruism to explain cooperation in subjects not sharing genes through descent. The principle of the theory is simple in its essence. Any individual can help another if there is a future expectancy and likelihood of the former to receive help in return. This idea is based on the principle that these types of dyadic interactions can be repeated over time and that the benefits received by the partners can be asynchronous in time (Trivers 1971). For it to work, it is a requirement for the reciprocating partners to recognise each other during their social interactions and to remember these interactions. Moreover the immediate costs must be less than the expected future rewards. Individuals that do not return favours to previously acquired partners need to be excluded from future cooperative exchanges. If all these conditions are met, reciprocal altruism may become fixed in a population as a stable strategy. Reciprocal altruism is seen as one of possible mechanisms that could propagate the emergence of cooperation between unrelated partners (Lehmann & Keller 2006; Sachs 2004; West et al. 2007b). It has been argued however to be unlikely to occur in species other than humans (Clutton-Brock 2009), because it requires certain cognitive restrictive elements (e.g. Hammerstein 2003; Stevens et al. 2005). In his review (2009), Clutton-Brock sees the expressions of cooperation in animal species as the outcome of selfish interests and he could not find truly altruistic forms of reciprocity as found in humans.

The theoretical development of the principle of reciprocal altruism gave an input for further work on the subject by both theorists and empiricists. Sachs (2004) gave a review to show various different attempts made to design models that could explain the occurrence of cooperative behaviour in unrelated partners.

Some models focussed on how ‘players’ in a game could exert control over their partners in case of defection through immediate sanctions (Connor 1995; Roberts & Sherratt 1998). Other models (Batali & Kitcher 1995; Bull & Rice 1991; Noë & Hammerstein 1994; Noë et al. 1991) focussed on the presence of multiple players rather than dyads and their choice rather than control for cooperating with (Bshary & Noë 2003).

The biological market theory

In the 1990’s, Noë and Hammerstein (1994, 1995) brought forward a more comprehensive theory to explain cooperation in animals.

The theory of biological market tries to fill the gap left by missing or non-clear elements in reciprocal altruism. This latter theory does not give details on what happens in terms of costs and benefits of the interacting players during cooperation. Moreover, as Noë says “*a relationship of an individual with one partner is not independent of the relationship that individual has with other partners*” (Noë 1989). That is to say that often, in the real world, we cannot take into consideration simple dyadic interactions, especially when these become more complex to the level of iterating in time, as acknowledged in the reciprocal altruism theory.

Contrary to what Trivers did (1971), Noë and Hammerstein include partner choice as key factor in their theory to explain cooperation. This was in fact left out by previous theories which focussed more on partner control exerted a posteriori over successive social interactions. Any individual can chose to stop cooperating with a given partner and switch to another if found more convenient. And the economic idea of convenience is the key aspect brought forward by the biological market. Microeconomic aspects are to be found in the actions performed by the interacting individuals attempting to increase their reciprocal fitness. As a consequence, the market players negotiate their behaviours as a function of the supply and demand of such behaviour at any given time and space in a social group.

By forming a larger network of relationships, market players gain fitness rewards in terms of an attainment of more and/or better quality relationships.

Noë (2001) describes five general properties of biological markets common to human economic markets.

A biological system influenced by market selection must consist first of all of individuals that have tradable commodities (i.e. valuable social acts) similarly to market economies of human beings, where services and goods are exchanged amongst various classes of traders. Examples of such commodities traded are grooming in exchange of: tolerance (e.g. Barrett et al. 1999), mating (Gumert 2007b), coalition support (Noë 1992), infant handling (Henzi & Barrett 2002), and access to food (Fruteau et al. 2009).

As a second point is that cooperation should be seen as an exchange of acts by different trading classes of individuals (Bowles & Hammerstein 2003; Noë & Hammerstein 1995). The access to valuable commodities may differentiate in a market, leading to a fluctuation in price of such commodities depending on their availability during trading (e.g. Fruteau et al. 2009).

A third point focuses on the fact that the partners trading commodities are selected from individuals competing among them to gain these social partners. As seen, within a social market individuals chose their partner as to maximize their payoff from mutual trading. Their choice of partner should yield the most profitable relationships and a gain in profit from this cooperative social exchange. Profit could be measured in the number and the quality of commodities received. It follows that competition for the best partners will render the value of attractive partners higher.

The fourth point is the key element that allows this theory to combine microeconomics with evolutionary biology. The price of a commodity is determined by supply and demand. If in the market the commodity is rarely found and highly demanded, its value will become very high.

Following microeconomics, advertisement is a strategy found also among ‘biological’ market traders. When advertisers succeed in their displaying effort, they should gain a higher payment and a general greater demand.

Loskopdam Nature Reserve

I carried out this study between 2007 and 2009 in South Africa, 180 km northeast from Pretoria, at Loskop Dam Nature Reserve, in the Mpumalanga province at the border with Limpopo (Figure 1). The reserve includes an artificial dam. The building of the Dam was completed in the early 1940’s to supply the agricultural communities of Groblersdal and Marble Hall with water for irrigation. Loskopdam Nature Reserve is a protected area that is managed by the Mpumalanga Tourism and Parks Agency. The reserve ranges 23,000 ha of predominantly mixed bushveld. Loskopdam is fed by the Olifants and Wilge Rivers going to the Indian Ocean through Mozambique.

Thanks to prior research projects, the monkeys I studied had been partly habituated to the presence of researchers. This gave me an advantage when introducing the new experiments to the primates.

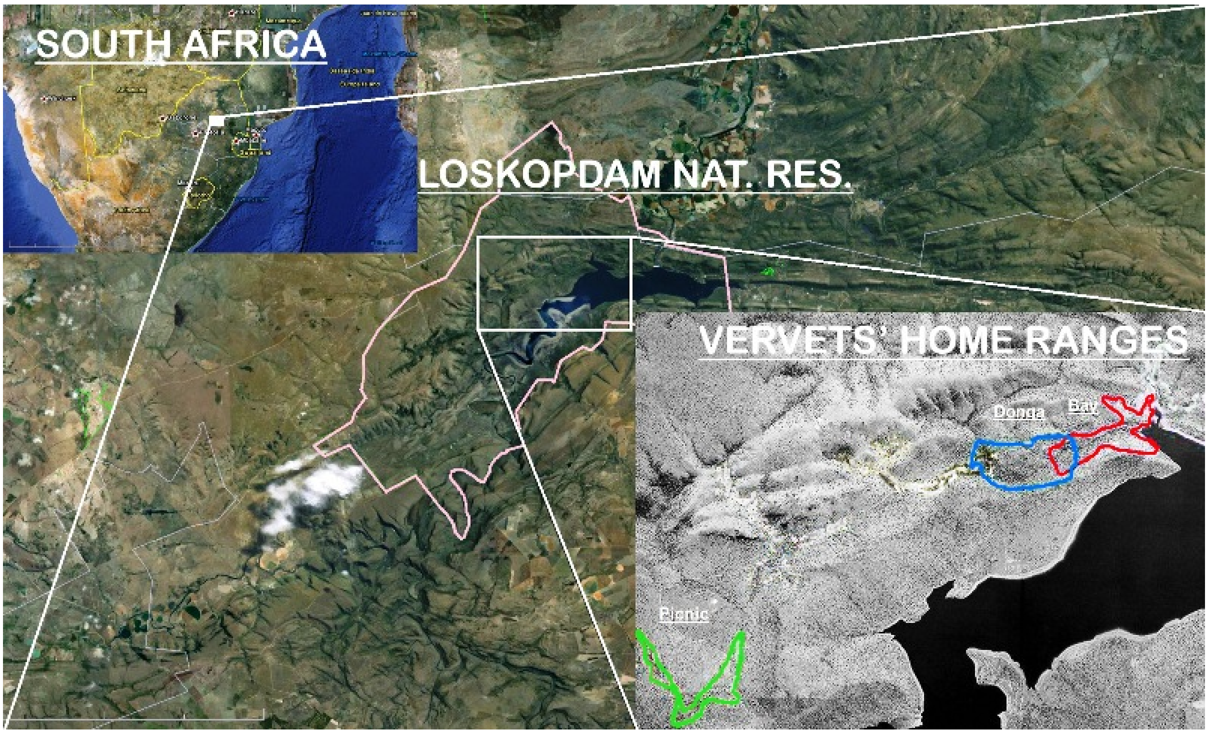

Figure 1 – Position of Loskopdam Nature Reserve and localisation of the three groups’ home

ranges: (1) Picnic in green, (2) Donga in blue, and (3) Bay in red (home ranges adapted from Borgeaud 2008).

Vervets as a study system

In Loskopdam, I studied three groups of wild vervet monkeys, *Chlorocebus aethiops*.

The vervets' social groups usually encompass an average of less than 20 individuals in the reserve, but in other sites they can be more numerous (Cheney & Seyfarth 1990). The females are organised in a normally stable hierarchy, with mothers passing on their rank status to the offspring. Males instead migrate from group to group and their rank fluctuates. These social groups have a rough sex-ratio of 1.5 adult females per adult males (Cheney & Seyfarth 1990).

In particular, the studied groups were: (1) the Picnic group with a total of 10 individuals, found in an area of the reserve with a picnic rest; (2) the Donga group with 19 individuals, located adjacent to (3) the Bay group with 17 individuals. Their home ranges stretched for about 1 km^2 each (Figure 1).

The experiments to induce the monkeys to cooperate

The experiments were designed to enhance instrumental cooperative behaviour in vervet monkeys. I used food contained in feeders as a reward to the individuals attempting to cooperate (Figure 2). In this way, I induced the individuals to stand in front of these machines, operate them and as an ultimate step, share food. Food sharing is a behaviour observed in several species of primates in nature (Brown et al. 2004) as well as in other species (Stevens & Gilby 2004).

Figure 2 – Two of the toasted rice feeder containers handled by a dyad of monkeys during the cooperation phase of the experiment. I assembled the feeders from plastic tanks inside which I installed the mechanism to release food. This was controlled by a push/pull lever button on top which could be activated by remote control when the correct individuals stood in front of the tanks.

The feeders were designed to dispense small quantities of food. Similar to a reinforcement-based conditioning task, access to food was granted only when the monkeys would operate a push/pull button on top of the machines, triggering the food release mechanism. I designed the feeders with the feeling that the subjects could learn the cooperation task specifically giving the chance to repeat the task several time a day. At each button release attempt a handful of toasted rice cereal was dispensed.

During an initial pilot feeding test, I checked which food items were preferred by the monkeys. I looked for a food type different from fruit, with the specific purpose of having the smaller possible impact on their diet. In addition, I had to match the food type with the proper functioning of the feeders. These bare an electronic mechanism in it which could have been impaired by leaking of juice. I therefore chose to use toasted rice cereal because of its low specific weight, large volume, and resulting low caloric impact. I could observe that at turns, when not having access to the feeders, the monkeys kept on foraging from the trees and on the ground, throughout the experimental sessions. This was an indication that the subjects did not become dependent on the artificial food resource.

The experiment was implemented in two phases to prompt the monkeys to cooperate (Figure 3): (1) a training phase to trigger a learning process in the individuals willing to habituate to the feeders and to become aware of their cooperation class (see below), and (2) a cooperation phase during when individuals acted together to obtain food. On average, each experimental session lasted three hours, during which several monkey partners could attempt to operate the feeders repeatedly (see next section for details on these apparatuses), both on their own (during training), and together (during cooperation).

(1) **The training phase** was necessary to get the vervets used to the feeders and their functioning. The feeders were secured on the ground and they could be accessed by one or more individuals. During this phase single animals learned the mechanism providing access to food. The division in two cooperator classes of different size was implemented during this training phase (Figure 3). This distinction was made to generate predictions of the biological market relating to supply and demand. Due to the law of supply and demand the monkeys of the smaller cooperation class (N=2) were expected to gain a privileged status compared to the rest of the group members. In each group, a smaller class was comprised of those two individuals who became used to have access to the feeding resources only if contained in feeders of black colour. The functioning of the correct feeder with the correct monkey class was possible with remote controls that activated and deactivated the push/pull trigger on top of the feeders. These two individuals of the smaller class were assigned and chosen in such a way as to be representative of the other larger class and the entire group. In this respect, the smaller class comprised of two individuals with a particular combination of age, sex and rank position. That is to say, one male and one female, one of them adult and the other juvenile, one relatively higher ranking the other of relatively low social rank. All the remaining individuals formed the larger class and learned that the only feeders functioning with them were those white coloured (with the same shape and dimension of the black ones).

The training phase terminated once at least half of the monkeys of each group became able to use the feeders of the correct colour. I evaluated this ability, once each of the trained monkeys could independently activate the food releasing mechanism.

(2) During **the cooperation phase** the same feeders were used, but this time they were joint, one black and one white together, distanced a few metres away from another pair of black

and white feeders. The feeders were releasing the rice reward together at the same time, as long as at least one monkey from each cooperator class was standing in front to the machines trying to operate them. The individuals were free to associate in any desired combination giving the opportunity to the system to work not only with dyadic combinations, but also in presence of multiple partners.

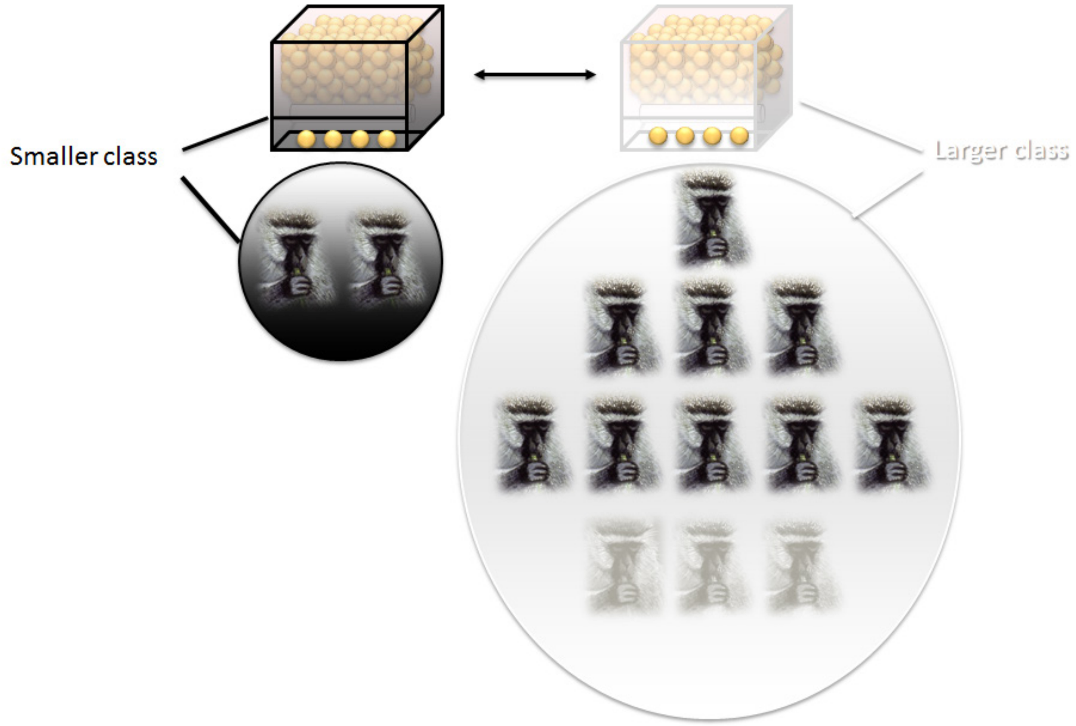

Figure 3 – Schematic representation of the experiment. From the training to the cooperation phase the feeders get joined to induce the two classes of monkeys of different size to cooperate. The feeders were 4 in number; here only two are drawn.

Overview of the thesis

The main topic of the thesis is cooperation and economic behaviour in vervet monkeys.
After the current introductory chapter, I include two draft papers which incorporate the majority of the field results and the thesis itself. Other data that were collected in the field are attached in the form of **appendixes** at the end of the manuscript. These data have not been analysed yet since they do not deal directly with the cooperation context of this thesis
This thesis concerns the sociodynamics of three monkey groups once cooperation is established for accessing artificial food.

Chapter 2 highlights what happens during the cooperation phase of the experiment. The question tackled by this chapter concerns the establishing of preferred partners for cooperating. During cooperation the monkeys were requested to operate the feeders according to a number of combinations of partners. Allowing the vervets to combine and cooperate, as long as at least one member of each of the cooperation classes was present, allowed me to score partner choice preferences in the three groups. To analyse these data I mostly made use of network analysis, an exploration I found most appropriate to shed light on type of relationships arising by partners having to associate and interact together with the same aim.

Chapter 3 presents the data on what happened as a result of the cooperation experiment, in terms of a modification in social behaviours exchanged after having cooperated at the feeders. This paper makes reference to the supply and demand part of the biological market theory of Noë and Hammerstein and shows how differently social behaviours were exchanged across the two cooperator classes. The question tackled by this chapter concerns whether the monkeys abide to supply and demand law. Specifically the monkeys were divided into two cooperator classes of different sizes. The purpose of the experiment was therefore to test whether one of these two classes, the smaller in size, assumed a privileged status as a consequence of becoming in demand given it being rare.

Chapter 4 highlights the significant findings of both of the preceding papers in economics terms and synthesises them.

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Chapter 2 – The partner choice

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Title

Induced cooperation to access a shareable reward increases the hierarchical segregation of wild vervet monkeys

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Abstract

Until now cooperation experiments in primates have paid little attention to how cooperation can emerge and what effects are produced on the structure of a social group in nature. I performed field experiments with three groups of wild vervet monkeys in South Africa. I induced individuals to repeatedly approach and operate food containers. At least two individuals needed to operate the containers in order to get the reward. The recurrent partner associations observed before the experiment only partly predicted the forming of cooperative partnerships during the experiment. While most of the tested subjects cooperated with other partners, they preferred to do so with specific combinations of individuals and they tended not to mix with other group members outside these preferred partnerships. Cooperation therefore caused the relatively homogeneous networks I observed before the experiment to differentiate. Similar to a matching market, the food sharing partners selected each other limiting their choice. Interestingly neither sex nor age classes explained the specific partner matching. Kinship could not explain it either. Rather, higher ranking individuals cooperated with other higher ranking individuals, and lower ranking also matched among the same rank. This study reveals the key role dominance rank plays when food resources are patchy and can only be accessed through sharing with other individuals.

Keywords: partner choice, association pattern, dominance hierarchies, network analysis, social differentiation, matching market

Introduction

One of the key elements in evolution is the potential of individuals to act together in cooperation. Cooperation allows many individuals to achieve goals that can often not be achieved by single individuals. Specifically, I define cooperation as any act jointly carried out so that there is a net gain for all individuals involved (following Noë 2006a). In mammals, events such as being able to identify feeding resources more easily and warn group members for predators are examples of evolutionary stable cooperation strategies.

After kin selection theory and the concept of inclusive fitness had proposed (Hamilton 1964b), the theory of the evolution of cooperation amongst unrelated individuals was further explained through reciprocal altruism. Reciprocal altruism focuses on the future benefit return of the cooperative act (Trivers 1971). Being able to assess the outcome of repeated interaction is central when individuals can choose to cooperate or defect at turns among a range of partner options. The iteration of the cooperative act is a key element in the maintenance and stabilization of cooperation (Axelrod & Hamilton 1981).

With this study, I am interested in why partners are chosen in relation to the investment required in the cooperative act (as formalised in biological market theories, Noë & Hammerstein 1994, 1995). The choice individuals make to find suitable partners should be based on the quality of honest signals, indicating the qualities of potential partners. The evaluation of potential partner quality a posteriori can also occur through some sort of trial interaction. If cooperation with specific individuals does not produce a convenient outcome, partner switching should take place so to favour a search for the profitable combination of partners (Bshary & Bronstein 2011; Bshary & Noë 2003). This perspective allows generalising further, because it takes into consideration the strategies accounted by multiple interacting individuals. Examples of animal societies applying multi-partner cooperation are many, but scant has been the specific analysis of these strategies under a game theoretical approach. The few, non-experimental models developed comprise lions defending their territories (Heinsohn & Packer 1995) and male dolphin alliances (Connor 2010).

Following kin selection theory, animals living in a group are expected to cooperate taking into account kinship relationships and broad family bonds (Hamilton 1964b). An example is provided by species of birds and mammals breeding cooperatively with multiple helpers attending the same nest (e.g. Komdeur et al. 2008). Cooperation in unrelated individuals, instead, may be rarer to observe even when the subjects belong to stable social groups (as recently reviewed by Clutton-Brock 2009).

Studying cooperation in any model species is of special concern when framed within the species' ecological context. Among other communal actions, accessing food as a group can be seen as a cooperative act that social species repeat several times on a daily basis. Communal food search should be a strategy worth to be adopted when the feeding resources are limited (Oates 1987). A relatively complex case of cooperation is food sharing. If it occurs, animals act together and make joint use of food resources that could in principle be used and monopolised by single individuals (Stevens & Gilby 2004). If cooperation is a stable strategy, food sharing is favoured over exclusive control over the resources.

In this study I induced wild vervet monkeys to cooperate in order to access to food. In my paradigm, the resources do not necessarily need to be offered by one individual to the other (as e.g. with offspring feeding by meerkats, Brotherton et al. 2001), but they are rather accessed by the animals at the same time (as with captive hyenas, (Drea & Carter 2009) for experiments with captive rooks, where the resources are both offered and accessed at the same time, see (Scheid et al. 2008)). I first analyse the ability of the tested subject to learn the cooperation task. Subsequently, I assess if the social network of the individuals modifies due to the induced cooperation. I did so by scoring how partners selected each other according to particular factors influencing their partner choice. Partner preferences should appear according to the individuals' choice to cooperate with specific group members as in a matching market (Sotomayor 2004).

The questions to investigate were: were preferred partners before and after the cooperation experiment the same, or did new combination of partners arise? Moreover, what were the factors inducing new combinations of individuals: sharing the same sex, the same age class, or similar rank? If the monkeys cooperate according to kin selection theory, the prediction is that they would combine taking into account relatedness.

The analysis of how preferred partnerships form is often missing in literature. This study represents a first step in answering this question and provides the first results concerning cooperative problem solving in primates in the field with experimental manipulation.

Materials and Methods

Study subjects

I carried out this study in South Africa, 180 km northeast from Pretoria, at Loskop Dam Nature Reserve, in the Mpumalanga province. The reserve extends for 23,000 ha and consists mainly of 'bushveld' (some trees where the monkeys are most regularly found, thick acacia bushes and tall grasses). I studied three groups of wild vervet monkeys, *Chlorocebus aethiops*. Their social groups usually comprise an average of less than 20 individuals in Loskop Dam (Barrett et al. 2010; Fruteau et al. 2009; van de Waal et al. 2010), but in other sites they can be more numerous (Cheney & Seyfarth 1990). The females are organised in a stable hierarchy, with mothers passing on their rank status to the offspring. Males instead migrate from group to group and their rank fluctuates. These social groups have a rough sex-ratio of 1.5 adult females against adult males (Cheney & Seyfarth 1990).

The studied groups were: (1) the Picnic group with a total of 10 individuals (4 males and 6 females; 6 adults and 4 juveniles); (2) the Donga group with 19 individuals (8 males and 11 females; 11 adults and 8 juveniles); and (3) the Bay group with 17 individuals (11 males and 6 females; 10 adults and 7 juveniles. I define as juveniles as individuals of 4 years of age or less who have normally not bred yet. The infants younger than 1 year of age did not cooperated actively and were not included in the observations of this paper. They are therefore not listed in this demography. Their home ranges extended for about 1 km^2 for each group. The Donga and the Bay group had adjacent home ranges; the Picnic group was at 6 km distance from the other two.

All three groups were habituated to human observers before the start of these experiments (Barrett et al. 2010; Fruteau et al. 2009; van de Waal et al. 2010).

Outline of the experiment

After an initial observational period with the three groups, I started offering feeders to monkeys (for details on the feeding protocol see Supplementary material). Similar to a reinforcement-based conditioning task, access to food was provided only when individuals would operate a push/pull button on top of the machines. This triggered the food release mechanism. I provided the feeders to the monkeys during several days. An experimental session or trial is defined as a day during which the feeders where provided to the monkeys. Two phases were implemented and followed to induce the monkeys to cooperate: (1) a training phase and (2) a cooperation phase.

(1) The training phase was necessary to get the vervets used to the feeders and their functioning. The feeders were secured on the ground, and they could be accessed by one or more individuals indiscriminately. The individuals of a group were divided by me into two "cooperation-classes": a small and a large cooperation-class. The smaller class was comprised of the same two individuals who became used having only access to black feeders. All the remaining individuals formed the larger class and learned that the only feeders functioning for them were coloured white (with the same shape and dimension of the black ones). The functioning of the correct feeder with the correct monkey class was possible with remote controls that activated and deactivated the push/pull trigger on top of the feeders. The two individuals of the smaller class were assigned and chosen so to be representative of the larger class and the entire group. The small class individuals thus had a predetermined combination of age, sex and rank position. They comprised one male and one female, one of these was adult and one juvenile, and one had a relatively high rank and the other a low rank.

(2) The cooperation phase was subsequently implemented. Couples of feeders, one black and one white, were now joined together (Figure 1). During this phase individuals of one class could not access the feeding resources unless waiting for the presence of members of the other class in front of the feeders. I therefore define cooperation in this specific experiment as the act of being at proximate distance and standing in front of the feeders by dyads or multiple partners. In the Supplementary material I report data on normal foraging behaviour of these vervets. These data show that their foraging proximity distances were superior to the unnatural adjacent manifestations at the feeders.

Taking an economic perspective, the cooperation phase was designed to create a matching market (Roth & Sotomayor 1992; Sotomayor 2004) whereby individuals coming from the mixed classes (at least one from the smaller and at least one from the larger) had to match and cooperate among each other in order to have access to food. The combinations possible at the feeders were limited in number and apparent from the asymmetric matrix made up by the two individuals of the smaller class joining with the individuals of the larger class. More importantly, and distinct from a traditional matching market, the individuals could combine with others, but at a following stage they could re-assort in other combinations.

The short side of the market was formed by the members of the smaller class as these individuals became in demand for cooperation (given their limited availability in number as compared to the larger cooperator class).

Behavioural data collection

The monkeys were observed during the daytime from 7 to 15 hours. Scan samples from all visible individuals (except the infants) were collected at 10 minutes intervals. In addition, an all-occurrence sampling technique was used. It consisted of the whole group being observed by more than one observer (with inter-rate consistency tested a priori). One observer (R. Pansini) continuously monitored the feeders, recorded all cooperation interactions and agonistic behaviours. At the same time, one or two assistant-observers recorded all-occurrence and scan behaviours of the rest of the monkeys not present at the feeders.

Recording of affiliative behaviours was done with all-occurrence sampling. The affiliative behaviours comprised allogrooming, contact sitting and social play. The agonistic interactions were collected to determine the relative rank of all individuals and consisted of recording all aggressive and submissive behaviour bouts started within 5 m radius from the feeders. Behavioural bouts were considered to have ended if these ceased for 5 or more seconds, replaced by another behaviour or a partner exchange. For each behavioural data point, the information recorded consisted of: (1) the starting time, allowing to infer the frequency of each bout (and not the duration in this case); (2) the time when the behaviour occurred – if before, during or after the experiment; (3) the identity of the individuals involved; (4) the direction of the behaviour when this was social (actor and recipient); (5) the distance place in relation to the feeders (when present) of where the bout took; (6) and the identity and the distance of the nearest neighbour individual (if present within 10 m distance). The software Noldus Pocket Observer 2.1 and Pendragon Forms 5.1 were used for the collection of data in the field with Pocket PC's.

Statistics of association and interaction data and network structure

The several analyses produced are split in this section with roman numerals.

I use social network analysis to describe proximity and social relationships amongst the individuals. I define associations in terms of proximity distances; interactions, such as allogrooming are instead social behaviours exchanged by partners (following Whitehead 2008a).

For producing the statistics of association and interaction data and to structure the networks, I obtained (a) social differentiation indexes, (b) affiliation and cooperation rate indexes, and (c) standard errors of social differentiations.

i) The social differentiation index describes how varied the social system is (Whitehead 2008a). It is an estimate of the coefficient of variation of the proportion of sampling periods dyads spend together, calculated by removing an estimate of the sampling variance from the coefficient of variation of the estimated association indices (calculated in the appendix of Whitehead 2008b). As a rule of thumb, Whitehead imputes to a value of less than 0.3 a society that can be considered rather homogeneous (displayed in a sociogram, the individuals forming the nodes are on average all well connected to the others); to a value between 0.5 and 2.0 well differentiated societies (sub-units of individuals start to clump together well); and to a value higher than 2.0 extremely differentiated societies (Whitehead 2008a, 2009).

To infer the change in the social differentiation of the groups across the conditions of proximity, affiliative behaviours' exchange and cooperation, I compared the social differentiations with (c) standard errors calculated via bootstrapping 10,000 random replicate matrices of the collected data. The first matrix produced, showed the preferred associations of monkeys found in space. This network carried the identity of each monkey with the one of its nearest neighbour, as long as this latter monkey was estimated within a maximum distance of 10 meters from the former. In this case, to avoid the spurious influence of the artificial food offered, both these individuals had to be further than 10 meters radius from the feeders. The second network was formed by the interactions of partners engaged in allogrooming, contact sitting and social play both during the training and cooperation phases. This matrix measures preferred and recurring partners exchanging affiliative behaviours. The third network was formed by behavioural interactions of individuals cooperating at the feeders. These interactions consisted in simply coming together to the feeders and sharing food.

ii) I made use of tests for preferred/avoided associations (Whitehead 2008a) to test how individuals associate for cooperating at the feeders. These tests compare the real matrices formed by the occurrences of cooperators at each experimental session in repetition with 10,000 randomly generated matrices of dyads or more individuals shuffled (variation of Bejder et al. 1998) (by Whitehead 2008a), keeping as a constant their actual presence in the nearest surroundings during the experimental sessions. If an individual could not be found that day in the surroundings of the feeders, then I would not include that individual in the permuted matrix. In the text that follows and in the legends for figures and tables, I specify the permutations with the adjective 'semi-random' which represents the non-complete random shuffling of the individuals.

iii) Thereafter, I constructed Mantel Z-statistics models for each group. These tests were used to investigate cooperation patterns depending on individuals' attributes (sex, age, rank, and relatedness).

The same Mantel analyses were performed on feeding proximity occurrences. This was done to see whether these proximity data could predict preferred partnership during the experimental phase. These proximity data were collected during scan samples taken during the training phase comprising foraging behaviours from natural food sources of nearest neighbours.

At each comparison, the Mantel tests calculate whether there is a linear relationship between the cooperation formed by partners, whose reciprocal interactions are summarised in a matrix, and 10,000 of other permuted matrices of semi-random, dummy cooperation events. The correlation between the matrices was tested only on that part of the dataset that included the cooperation between the individuals of the smaller class (operating the black feeders) and the individuals of the larger class (white feeders). This was done not to bias the result with non-relevant cooperation events taking place between the fractions of individuals belonging to the same class of cooperators (when more than 2 individuals were then cooperating at the same time). In the Result section I provide, in addition, the matrix correlation coefficients (MCC), a descriptive measure of correlation between non-diagonal elements of the test matrices.

Linear mixed effect modelling was performed with SPSS 19. Network analysis and all related statistics were performed with SOCPROG 2.4 (Whitehead 2009).

Results

The Groups' Social Differentiation

To interpret the gradual social change in the groups' differentiation structure across the conditions of proximity, affiliative behaviours' exchange and cooperation, I compared the three social differentiation estimates for each group. Their standard errors were calculated via bootstrapping. The social differentiation estimates for the three groups are reported in Table 1, together with the relative standard errors and other parameters of accuracy.

All the three groups showed a tendency of increase in the social differentiation when looking at proximity in space as compared to the exchange of social behaviours. Social exchanges occurred on average with a lower number of preferred companions than the frequency of meeting other individuals at least within 10 meters distance. A more significant result was the one provided by the comparison of the social differentiation indexes of proximity associations and affiliative interactions together, with the social differentiation value of cooperation. This result may be partly induced by the experimental design with the individuals of different classes having to join for cooperating. Still, all the three groups, when challenged with the cooperation experiment, reduced the number of partners (as witnessed by the increase of social differentiation, Figure 2 and Table 1). This result provided an indication that the process of selection of partners for sharing food to cooperate with was stricter than the one for sharing the same space and for exchanging social behaviours.

Pattern of association preferences

An initial analysis that shows how the individuals increased their selective choice for cooperating is reported in Supplementary material.

Applying a preliminary test for preferred/avoided associations (variation of (Bejder et al. 1998) by (Whitehead 2008a)), I rejected the null hypothesis that individuals associate randomly for cooperating at the feeders. The Picnic group showed a real association index of 9.0, s.d. = 7.615, significantly different ($p \leq 0.001$) from a random, permuted association index of 12.34, s.d. = 7.517. Similarly, the Donga group displayed a real association index of 5.893, s.d. = 7.289, significantly different ($p \leq 0.001$) to a random association index of 7.045. The individuals of the Bay group did not ($p = 0.001$) associated randomly either (association index of 6.469, s.d. = 3.193) but gave a real association index of 4.714, s.d. = 4.286.

These tests suggest that there may be an underlying pattern of cooperation of preferred cooperation partners. I therefore tested my observation in this direction. In Supplementary material I report results which show that the cooperation pattern within and between classes is different across the three groups. Finally, to find out whether the individuals' partner choice was dependent on intrinsic characteristics of the individuals preferring to share food together, I performed a partner choice analysis.

Social units of cooperative partners

Two social units of cooperating individuals split from each of the three groups. The two members of the smaller class gathered around themselves other individuals from the larger (Figure 3). The preferred partners of each subunit did not mix with individuals of the other subunit. This was shown by the very low cooperation rates at which the two subunits of individuals cooperated with each other (Figure 3, Cooperation phase as opposite to Habitual foraging). The two subunits clumped around the two individuals of the smaller class indicating (together with the following partner choice analysis) that the larger class members did not switch between individuals at the black feeders.

For the Donga group, the two social units arising from the feeding experiment were less distinct (lower cophenetic correlation coefficient of 0.62 for the Donga then the other two groups of 0.97 for Picnic and 0.79 for Bay, calculated from cluster analysis, Figure 3). This was probably due to the fact that in this Donga group the two members of the smaller class of cooperators belonged both to the higher ranking individuals (individual 02 presenting dominance indices of +55 David's Scores and individual 15 with David's Scores of +40. The second individual was chosen to belong still to the smaller class after her lower dominant sister that was chosen at first disappeared from the group). This group seems therefore to differentiate less than the other groups.

Partner choice

The cluster analysis of Figure 3 shows the subunits of partners cooperating at the feeders (cladograms on the right side). Compared to habitual foraging, the Picnic group maintained in general the same preferred partners during the two conditions. Only individual number 7, a juvenile female, changed preferred partners. The Donga group in general did not conserve the preferred associating partners between normal foraging and feeding at the feeders. Also in the Bay group, in general, preferred foraging partners did not conserve their preferred association during cooperation. The (less defined) cluster formed by two juvenile male partners foraging often together became more distinct during cooperation including also other subordinate individuals.

To investigate the causing factors for the occurrence of non-random cooperation, I looked at whether there was a correlation between the recurring cooperators and their identity in terms of sex, age class, rank, and relatedness. In addition, relatedness was also tested, controlled at the same time for the matriline and sibling strains. Since the matriline is generally known to the monkeys, this control allowed to test whether relatedness is taken into account by the subjects outside the members of the same matriline. The same analyses were performed on feeding proximity occurrences to check whether they could predict food sharing during cooperation. The Mantel Z-tests are reported in and they show the correlation between the matrices formed by dyads or more individual cooperating and their sex, age, rank and relatedness type.

During normal foraging, the individuals cooperated without a given pattern choice of same or different sex attribute, age class, rank, or relatedness. On the other hand, a specific trend appeared during the cooperation condition. During this phase, males cooperated with females indiscriminately and vice versa (Table 2). This holds true in the Picnic and the Donga, but not in the Bay group where, because of a large predominance of males, a same-sex preference was found. In the three groups, adults cooperated indiscriminately with juveniles, and juveniles with adults, except in the Picnic group where a mixed sorting was found. Conversely, in all the three groups, higher ranking individuals cooperated consistently more with other higher ranking individuals, and lower ranking individuals with other lower ranking individuals (Table 2).

Was this due to genetic similarities, given the small size of the groups? One would in fact expect matriarchal vervet individuals that are related, also to bear similar dominance index, leading to a correlation between rank preference and genetic similarity. Although individuals belonging to the same matriline tended to stand on similar dominance positions, I did not find the null hypothesis of cooperation among kin individuals to be met. The individuals of the three groups cooperated irrespective of their relatedness. Although the limited genetic variability found in these monkeys often belonging to few matrilines within each group, I did not find a tendency of kin partners to share food (with a p-values that would have gradually moved from the random value of 0.5 to the related one of 1 – Table 2). In contrast, the two groups of the Donga and the Bay gave values tending towards the remarkable conclusion of preference for matching to unrelated partners. The occurring partners at the feeders were thus more often coming from more distantly related family lineages, at least limiting the genetic relatedness analysis to the two classes of cooperators. This finding was not as strong as to provide significant p-values at a 0.05 significance level. All specific p-values of the models testing for partner preference are found in Table 2.

Discussion

The current study shed light on the modified social dynamics that arose in three wild primate groups when an experiment to elicit cooperation was set up in the field. The limited and patchy resources were offered to couples or multiple monkeys, side by side, operating a food releasing mechanism.

Firstly, the monkeys did succeed cooperating with other individuals. The partners in fact adapted to the sharing food condition by becoming able to cooperate (more over time, as shown in Supplementary material). I therefore demonstrate that vervets can in general cooperate in the field.

Due to the cooperation condition, the individuals congregated together more heterogeneously when co-feeding. Thus cooperation increased the groups' social segregation tendency. Associations of proximity distances and interactions of affiliative behaviours exchanged before the experiment did not predict the interaction pattern during cooperation. That animals and humans cooperate with preferred partners is not a new element in the literature (e.g. Berghänel et al. ; Croft et al. 2006; Harrison et al. 2011). What is new here is that social networks previous to cooperation did not predict occurring ones during cooperation. What we found is an indication that the process of selection of partners to cooperate with became stricter than the one for sharing the same area (up to 10 m apart), or for exchanging affiliative behaviours. This result could be explained by the availability of possible partners to match with at the feeders and individuals' preferences for matching (as in a matching market, (Sotomayor 2004), with limited number of partners joining together). Providing the monkeys with limited and patchy resources caused agonism at the feeders. It is therefore possible that some individuals opted to approach the feeding resources when preferred partners were present and avoided approaching at other times not to get involved into conflicts with other group members. Hence the three groups of vervets moved from presenting rather homogeneous societies to increasing their social differentiation and becoming more segregated when cooperating. The prediction of a resident-nepotistic strategy, in which rank differences are strongly enforced (Sterck et al. 1997) was therefore met in an artificial setup as this one.

With the help of network analysis (of particular interest in primate behaviour studies, (Sueur et al. 2011) and (Kasper & Voelkl 2009)) I could quantify the social differentiation of group across different conditions.

With these field experiments I was able to show that monkeys cooperate at the feeders choosing specific preferred partners. The preferred partner combinations did not tend to change during following experimental sessions. In fact dyads or multiple individuals were observed consistently at the feeders as shown by their consistently repeated cooperation rates. To check for the reason of preferred sub-units of individuals, I tested multiple explainable variables describing the status of each monkey within each group. I thus constructed models to test sex, age class, rank, and relatedness as affinity for partner choice. Across the three groups, the monkeys preferred cooperating at the feeders in arbitrary combinations of sex and age class. Surprisingly, I did not find that the monkeys preferred to share food with related individuals. Significantly, I found a consistent discriminant of dominance of the cooperators. Dominant individuals preferred cooperating with other dominants and subordinates with other subordinates.

Recently Jaeggi and colleagues (2010) have shown the importance of rank in the context of reciprocal food sharing. This study, however, was done in captive chimps and bonobos and without the constrained cooperation condition enforced.

My result suggests the key role that social rank has in vervet monkeys, when constrained to access and share limited resources in a limited space. These primates showed heterogeneous social networks and rank-related nepotistic behaviours which prevented individuals of very different rank statuses mixing together for cooperating. The strategy applied by the test subjects may be an evolutionary stable one. If we assume that it is convenient to avoid conflicts between higher and lower ranking individuals, these vervets seem avoiding mixing these two rank categories as to avoid conflicts for accessing and sharing food together.

The effect of rank on cooperation may be also justified in terms of tolerance: dominants tolerate other dominants and subordinates other subordinates.

Finally, looking at kinship, these monkeys did not show an association trend confirming the common theory that related individuals would preferentially support each other in cooperation (Clutton-Brock 2009). These study groups would have been likely candidates for showing cooperation among kin individuals, given the limited genetic variability in these small groups. Nevertheless this expectation was not met, and the monkeys cooperated irrespective of their relatedness, with a tendency to find partners from a different family.

Most significantly we see that dominance status plays a key role in this augmented social differentiation and gets exacerbated under a condition with two cooperation classes. It can be argued that the division of the groups into two classes of skewed size causes the clumping of the individuals around the two individuals of the smaller class. I chose the size of the smaller class to be as small as comprising two individuals to test whether the smaller class gets rewarded, after the experiment, for its influential commitment in cooperation (see Chapter 3.). The reduced class size does not explain however why partner choice was attained with determined partners so strictly and no exchanges occurred throughout the cooperation phase.

In summary, monkey partners preferred to cooperate with other partners of similar rank status.

In order to test whether cooperation induces other social groups to differentiate, I recommend the implementation of this experiment in other primate species and mammals.

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Figures

Figure 1 – The setup of the experiment in the field. The picture was taken during the cooperation phase in July 2008 with the Picnic group. It shows two dyads of vervet monkeys cooperating and sharing food from the two joined feeders. The reward consisted of toasted rice cereal and was accessed by operating push/pull lever triggers on the top side of the boxes.

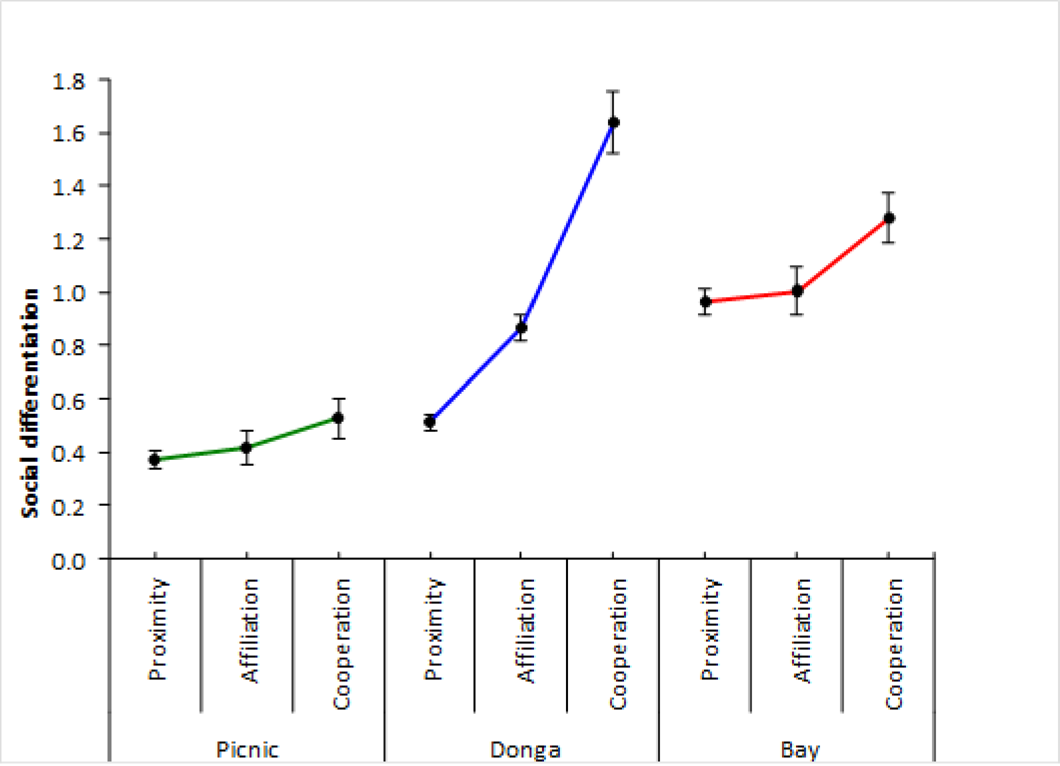

Figure 2 – The social differentiation of the three vervet groups across conditions. For each group the social differentiation estimate was extracted during both training and cooperation from: (1) proximity distances of nearest neighbour individuals not at the feeders collected during scan intervals; (2) affiliative interactions of allogrooming, contact sitting and social play among individuals not at the feeders recorded on an all-occurrence basis; and (3) all-occurrence recordings of cooperation attempts from dyads or more individuals operating the feeders. Standard errors were calculated with bootstrapping procedure permuting 10,000 semi-random replicates of each type of matrix data from associating individuals. The dataset plotted in this graph is reported in full in Table 1.

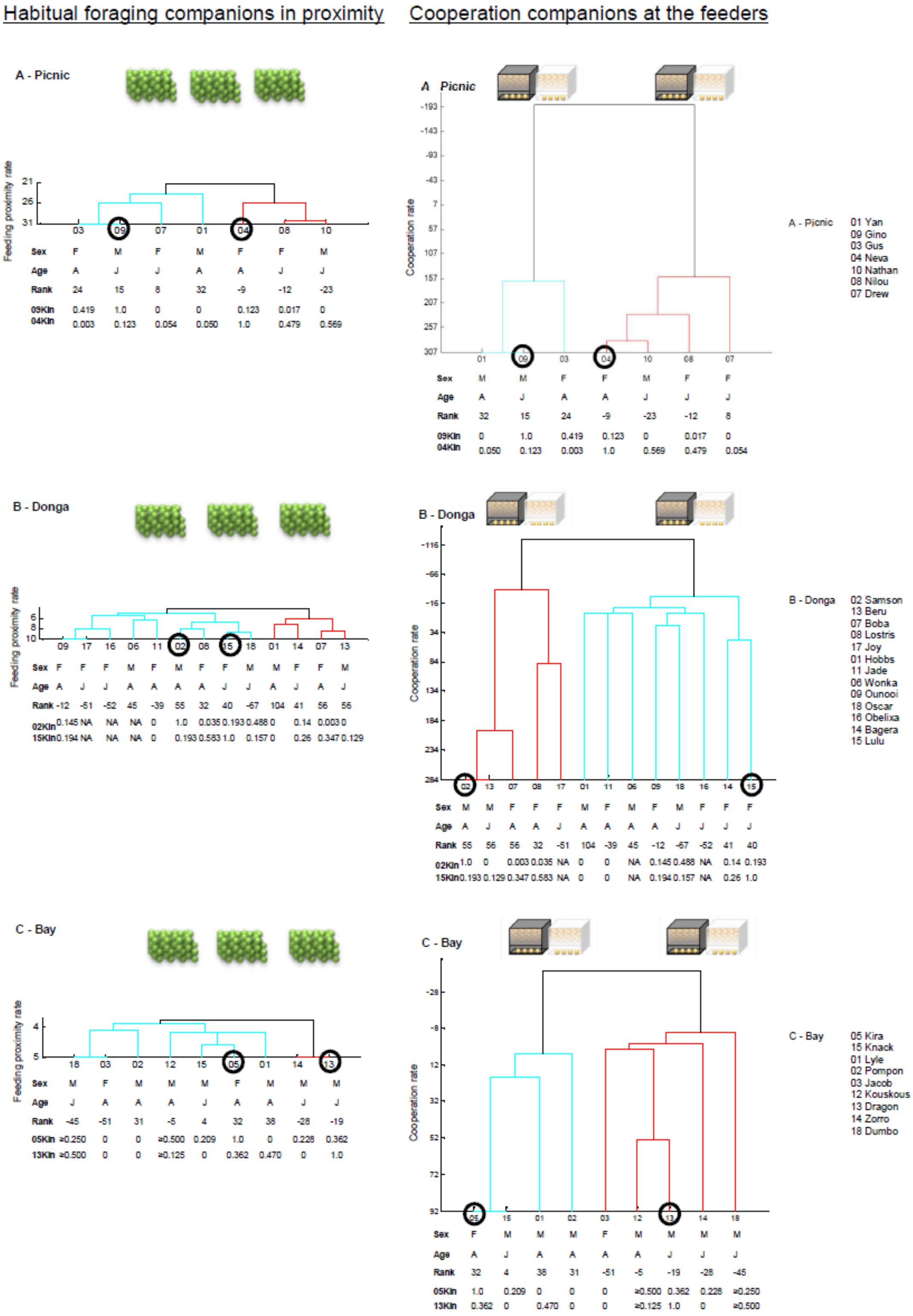

Figure 3 – Dendograms of the social clusters of the three groups of wild vervet monkeys. The diagrams (inferred from cluster analysis using the Ward linkage coefficient) show the sub-units of companions during habitual foraging from natural sources and companions cooperating at the feeders during the experiment. Differently than during the habitual foraging activity, the monkeys discriminated and chose their cooperation companions at a

higher rate. The clusters of preferred cooperation partners are more distinct during cooperation. The different colours (light blue and red) are assigned to the clusters by using the method of the modularity of Newman (2004). This method assigns the same colour to the clusters including the individuals who preferentially clumped together. Set the summed cooperation rates of the different individuals, the individuals' clustering is calculated by the difference between the observed and expected proportion of the total cooperation rates (y-axis). The probability of finding partners of different clusters interacting during cooperation is lower during cooperation. The feeding and cooperation rates on the y-axes were calculated by the sum of all cooperation attempts among individuals sharing food resources. The individuals marked with a black circle represent the smaller cooperator class able to operate the feeders in combination with at least one other member of the larger class (all the remaining individuals of each group). For the Picnic and Bay group (A and B), each one of these individuals was found most of the times in combination with a subset of preferred partners (either light blue or red coloured clusters). In the Donga group (C), this did not happen as distinctly (interaction rates of individual 15 proximate to 0) because of the discussed relatively high-ranking position of individual 15. On the x-axes the individuals are tagged with their sex, age class of whether adults or juveniles, dominance rank estimated with the David's Score (rounded to its closest integer, see Supplementary material for further description), and the relatedness coefficient of Queller & Goodnight. The relatedness coefficients reported refer only to the relations of the two individuals of the smaller class with all the others of the larger class. A 0.5 coefficient means first order generation (e.g. son), 0.25 is relatedness at second order (grandson). The coefficients of three individuals from the Donga group could not be reliably extracted and are therefore not available, missing as well the relatedness of two individuals from the Bay group (id 12 and 18); I was able to partially infer them through the known maternity link and from genotyped siblings (see Supplementary material for further description). The Ward's linkage method used to build the clusters can bear negative values of the ordinate as it uses the increase in the total within-cluster sum of squares because of joining two clusters at a time (the within-cluster sum of squares is defined as the sum of the squares of the distances between all objects in the cluster and the centroid of the cluster). According to the extracted cophenetic coefficients, the two A and C dendograms give a faithful representation of the social structure of the three groups: 0.97 for A and 0.79 for C. The social representation of the monkey group B is less faithful to reality, with a coefficient of 0.62. A cophenetic coefficient of 1.0 means a perfect fit of the dendogram with the data and 0.8 is generally taken as good estimate (Whitehead 2008a).

Tables

Group	Condition	Individuals	Mean individuals identified per sampling period	Sampling period (days)	Number of associations or interactions	Social differentiation	SE
Picnic	Proximity	10	9.59	46	4281	0.3680	0.0340
	Affiliative interactions	10	9.13	33	2313	0.4145	0.0655
	Cooperation	7	6.35	20	763	0.5260	0.0740
Donga	Proximity	18	16.14	51	5457	0.5110	0.0290
	Affiliative interactions	18	13.97	51	3161	0.8650	0.0510
	Cooperation	13	7.20	25	784	1.6390	0.1160
Bay	Proximity	17	12.13	31	1468	0.9630	0.0480
	Affiliative interactions	18	10.36	28	930	1.0040	0.0910
	Cooperation	9	6.38	13	284	1.2770	0.0940

Table 1 – Values of social differentiation of the three groups according to the three conditions of (1) proximity in space of the nearest neighbour individuals within 10 m distance from each other, (2) between partners' display of affiliative behaviours of allogrooming, contact sitting and social play, and (3) display of the cooperative behaviour at the feeders. The standard errors of the social differentiation indexes were calculated via bootstrapping, with 10,000 semi-random permutations. The social differentiation values with their standard errors have been plotted in Figure 2.

Group	**Identity**	**Individuals of the smaller / larger class**	**Feeding proximity** Mantel Z-test p-values	**Feeding proximity** Matrix Correlation of Mantel tests	**Cooperation** Mantel Z-test p-values	**Cooperation** Matrix Correlation of Mantel tests
Picnic	Sex	2 / 5	0.896	-0.650	0.493	0.161
	Age class	2 / 5	0.902	-0.382	0.999	-0.976
	Rank	2 / 5	0.114	0.531	**0.041**	0.685
	Relatedness	2 / 5	0.999	-0.627	0.853	-0.514
	Relatedness controlling for matriline and siblings	2 / 5	0.896	-0.308	0.455	-0.017
Donga	Sex	2 / 11	0.914	-0.097	0.695	-0.224
	Age class	2 / 11	0.651	-0.097	0.510	0.038
	Rank	2 / 11	0.630	-0.040	**0.045**	0.323
	Relatedness	2 / 7	0.352	-0.093	0.091	0.462
	Relatedness controlling for matriline and siblings	2 / 7	0.317	-0.012	0.156	0.370
Bay	Sex	2 / 7	0.999	0	0.999	-0.267
	Age class	2 / 7	0.665	-0.098	0.348	0.131
	Rank	2 / 7	0.283	0.202	**0.043**	0.538
	Relatedness	2 / 7	0.227	0.257	0.273	0.173
	Relatedness controlling for matriline and siblings	2 / 7	0.146	0.343	0.233	0.207

Table 2 – Multiple matrix analyses from feeding proximity and cooperation interactions of

the three groups with their members' identity in terms of sex, age class, rank, and relatedness. In addition, the cooperation interactions were further compared to the relatedness controlling the former for matriline and sibling identity apparent to the monkeys. The relatedness coefficients of three individuals from the Donga group are missing, and two from the Bay were partially inferred through the known maternity link and deducing them from fingerprinted siblings. The tests were performed between the mixed cooperator classes and the total number of individuals of each class is displayed. Even though during normal foraging activity the monkeys it was not imposed any class distinction, in order to compare the two conditions, the class distinction was also imposed to these normal behaviours excluding interactions from same class partners. Mantel Z-tests are reported together with their matrix correlation coefficients (the correlation between non-diagonal elements of the test matrices). The p-values significant are bold typed.

Supplementary material

Supplementary Methods

Data collection

For the Picnic group, I collected training and cooperation data from May to July 2008 and from September to November 2008. From the other two groups of the Donga and the Bay, the data were collected at the same time on rotated days from May to September 2009. The training phase stretched for 26 sessions with the Picnic group, 26 sessions with the Donga, and 18 with the Bay. The cooperation phase instead was repeated during 20 sessions with the Picnic, 25 sessions with the Donga, and 13 sessions with the Bay.

Feeding Protocol

During an initial pilot feeding test, I checked which food items were preferred by the monkeys. I chose to use toasted rice cereal (even if different from some more natural fruit items) because of its low specific weight, large volume, and resulting low caloric impact (3.9 cal/gr). The feeders were designed in a way to dispense small food provisions. Their volume was 0.0035 m3each and their size 20x20x13 cm.

To avoid over-habituation to the food type and to limit the impact on their natural behaviour, I tended not offering artificial food to the same group on successive days. Even if the food offered was appreciated by the monkeys, the experiment did not have a serious impact on their natural feeding habits. At turns, when not having access to the feeders, they used to forage from the trees and on the ground, throughout the day and before, during and after the experimental sessions. At each button release attempt a handful of toasted rice cereal was dispensed. The monkeys became habituated to access food several times during an experimental session (see Video 1 for an example of the subjects feeding during the cooperation phase).

On average, each experimental session lasted three hours, during which several monkey partners could attempt to operate the feeders both on their own (during the training phase) and share food (during the cooperation phase).

During the training phase of the experiment the individuals of each of the three groups were divided in two classes. For the smaller class (the one comprised of two individuals), in the Picnic group one individual was a juvenile male higher ranking, and the other was an adult female lower ranking. In the Donga, one adult male higher ranking, and one juvenile female lower ranking. In the Bay group, one adult female higher ranking, and one juvenile male lower ranking. During the training phase, these white feeders were positioned in the same area at 2-3 meters distance from the blacks. The training phase terminated once all the individuals of the black class and at least half of the monkeys of the larger class became able to use the feeders of the right colour. I assessed this ability as accomplished once each of the trained monkeys could independently activate the food releasing mechanism.

During the cooperation phase, the total number of feeders positioned on the ground was 4; that is to say two joint feeders at 2-3 meters distance from each other (Figure 1, main text). By the use of remote controls, one observer (R. Pansini) could activate or deactivate the triggers and hence allow the right combination of monkey classes to feed (if the monkeys were pressing the activated trigger on their own). With the monkeys releasing the triggers, we can specify cooperation as a work of active food producing (same emphasis as in the 'active' food sharing of (Stevens & Gilby 2004)). In fact, by operating the buttons the monkeys were releasing the food reward on their own. The operable triggers on the joined feeders were two (one on top of each single box) and the individuals feeding were dyads or more individuals. So as long as one monkey was activating one trigger, both feeders were providing food to all in front. The previous training phase had a long lasting effect on the monkeys and the individuals of the smaller class were still operating the triggers of the black feeders, and those of the larger the white feeders.

Estimation of Individuals' Hierarchy

The hierarchical rank of the monkeys was computed by examining submissive behaviours at the feeders. They consisted of a 'looking-away' or a 'walking-away' behaviour, displayed to avoid the individual that would approach and/or take the position of the submitted individual. These behaviours were collected during the training phase of the experiment, as a result of agonism within 5 m radius from the boxes, and when the feeders were not joined.

Rank values were assigned in the form of David's Scores (David 1987) which calculate cardinal, non-linear rank indices for each individual. Thanks to these scores I can quantify, and not just order, the differences in ranks among all individuals participating in contests. The scores are based on an unweighted and weighted sums of the individuals' dyadic proportions of wins, combined with unweighted and weighted sums of their dyadic proportions of losses (David 1987). The scores provide a heavier weight to winning a contest with a high-ranking animal compared to defeating a low-ranking animal. This induces known advantages (Gammell et al. 2003; Hemelrijk et al. 2005) that make them robust descriptors of unbalanced contest data. With these scores, the higher ranking individuals tend to bear positive coefficients, whereas lower ranking have negative values. I also calculated an alternative to the David's scores, the Normalized David's Scores (de Vries et al. 2006) (no statistics shown here). These latter were recently shown as suitable measures in case of contests around feeding resources (Bissonnette et al. 2009) and they confirmed the output of the statistics of the David's Scores (reported in the Result section). The rank scores were obtained with the MATLAB programs SOCPROG 2.4 (Whitehead 2009).

Estimation of Relatedness

Coefficients of maternal relatedness of most of these monkeys were known from demographic records thanks to previous studies (Barrett et al. 2010; Fruteau et al. 2009; van de Waal et al. 2010). To establish full relatedness including patrilines of both juveniles and adults, genetic analysis was performed from faecal samples. Forty-three faecal samples from individuals of the three groups were collected in parallel with the behavioural observations. An average of two samples per animal was taken preferably during the dry season, so to aim at finding a higher concentration of intestine cells in the specimens. Directly after defecation, the faecal samples were preserved in RNAlater solution and a copy set in ethanol. Those in ethanol were desiccated three days later with silicagel for their longer preservation in time and subsequent lab analyses (Krützen & Goossens 2007).

Relatedness was measured among all pairs of individuals coming from the comprehensive pool of collected data of the three groups. A comprehensive matrix bearing a total of 42 monkeys was therefore produced with 903 extracted pairwise genetic distance coefficients. The relatedness estimator used was the one of Queller & Goodnight (1989) based in this case on 13 microsatellite loci. I double checked the results with the Wang estimator (2002) which confirmed consistency and robustness of the Queller & Goodnight genetic distances reported in results.

The relatedness coefficients of three individuals from the Donga group could not be reliably extracted and are therefore not available. For the statistics, I was still able to infer the coefficients of two individuals from the Bay group through the known maternity lineage and from genotyped siblings in common. Only two of these three individuals shared food (Figure 3C). Their relatedness indexes bear a '≥' symbol, meaning the estimated minimum relatedness coefficient with the individuals of the smaller class of cooperators. The value could be higher than the one shown in case the father(s) of these monkeys is (are) inbred with the mothers.

Increase in Cooperation Events

I made use of a linear mixed effect model to test whether the amount of cooperation events at feeders changed over the course of the cooperation phase across the three groups. Confidence intervals were kept at a 95% level for the standard deviation and residuals were checked for normality by plotting a q-q plot. The p-value reported originates from the minimal model (as indicated by lower AIC indexes) produced applying an autoregressive moving average covariance to the time series cooperation trials. I fitted this covariance structure given the longitudinal and repeated pattern of the experiment, iterated in consecutive days.

Social Differentiation

Association and interaction data were used to structure the networks and to infer (a) social differentiation indexes, (b) affiliation and cooperation rate indexes, and (c) standard errors of social differentiations.

Having collected the identity and proximity measure of individuals at within 10 meters proximity and when exchanging social behaviours (both affiliative interactions and cooperation), I extracted (a) social differentiation indexes from these three networks (plotted in Figure 1.

To perform statistical analyses, it was necessary to extract (b) interaction rate indexes which sum up the matrices of the repeated measures of relationships of dyads of individuals collected at each sampling session. The interaction rate index, used to calculate matrices of individuals associating among each other, is given by the sum of all the social exchanges among the individuals. This index estimates the proportional frequency of time each individual spend associated with somebody else (Whitehead 2008a).

The social differentiations were compared with (c) standard errors calculated via bootstrapping 10,000 random replicate matrices of the collected data. The bootstrapping procedure provides the most accurate method to date to obtain standard errors (Whitehead 2008a), as compared to those acquired from F-statistics. This procedure also allows a cross-comparison of the data taken at different time intervals (scan and all-occurrence samples).

Within and Between Classes Variation

In another analysis, I went deeper studying what happened during cooperation. I tested whether the interaction rates of cooperation events between and within the two classes of cooperators were different. The idea behind is to show whether interactions between classes, those of interest here, are different than interactions within the same class, usually across members of the larger class. As explained, during cooperation co-feeding could not take place if not both class members were present. During multiple-partner cooperation events, usually one monkey from the smaller class would feed with others, at least two or more members of the larger class. Mantel t-tests with 10,000 permutations were used to assess this null hypothesis of similar cooperative events across classes (Schnell et al. 1985).

Supplementary Results

A summary with the total data collected from the three groups is reported in Table 1. In there, are listed (1) the number of individuals followed, (2) the sampling sessions in days, (3) the mean individuals identified per sampling session, and (4) the total number of associations or interactions.

Natural foraging behaviour and nearest neighbour distances

I recorded instances of foraging behaviour in natural conditions from trees, lower vegetation and on the ground. I collected scan samples of these occurrences to assess habitual foraging companions and their distance in space. These data are the same as those reported in left cladograms of Figure 3 of the main text. The three groups showed similar recurring distances on average of foraging companions. These data included all individuals in the group, including dyads of mothers with the young offspring.

In the Picnic group the individuals foraged at 3.74 meters from each other (± 0.153) (N=213). In the Donga group the monkeys fed at 4.27 meters (± 0.212) (N=139). In the Bay at 4.48 meters (± 0.216) (N=129).

On the other hand, during the cooperation experiments, the individuals fed from the apparatuses at non-natural, adjacent position in space. This is an indication that the presence of the partners at such close distance is a manifestation of cooperation behaviour. Cooperation intended not as instrumental, but as task solving for being at such close distance in space. The distance was not manifested, on average, during normal foraging conditions.

The Increase of Cooperation Events

In the Picnic group 7 out of 10 individuals ended up cooperating; in the Donga, 13 out of 19; and in the Bay 9 out of 17.

I was expecting the monkeys to gradually learn that the food reward could be accessed as long as the two cooperator classes stood in front of the feeders together.

With the iteration of the experiment trials in the condition of cooperation the monkeys gradually increased their cooperation attempts. As plotted in Figure 4, the number of these cooperation events increased in frequency. This increase was found statistically significant when tested with a linear mixed model with the three groups included in the mixed model as random effects (estimate +0.205, SE = 0.040, $t_{3,58} = 5.073$, $p = 0.038$).

Within and Between Classes Variation

After I tested if, during the cooperation phase, the interaction rates of cooperation events between and within the two classes of cooperators were different. By doing so, I studied also the difference between co-feeding attempts of dyads (one individual in front of the black feeder and the partner in front of the white) against larger combinations of monkeys (usually one individual from the smaller class and two, three or more from the larger in front of the white feeders). Results are expressed with a t-value (with infinite degrees of freedom), a p-value (for 1-tailed test) for the analytical approximation, a permutation p-value (with 10,000 permutations set), and a matrix correlation coefficient. For all the three groups, cooperation rates between and within the classes of individuals were statistically different (Mantel t-statistics: Picnic: $t = -1.561$, $p < 0.0001$, Matrix correlation (MC) = -0.314; Donga: $t = -2.129$, $p < 0.0001$, MC = -0.369; Bay: $t = -2.761$, $p < 0.0001$, MC = -0.499).

The social differentiation test and the within and between classes one suggest that the monkeys chose each other according to a specific pattern of partner choice. This was tested with the analyses of partner choice (both in the main text and thereafter here), which finds out how rank plays a determinant role in the partner choice.

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Supplementary Figures

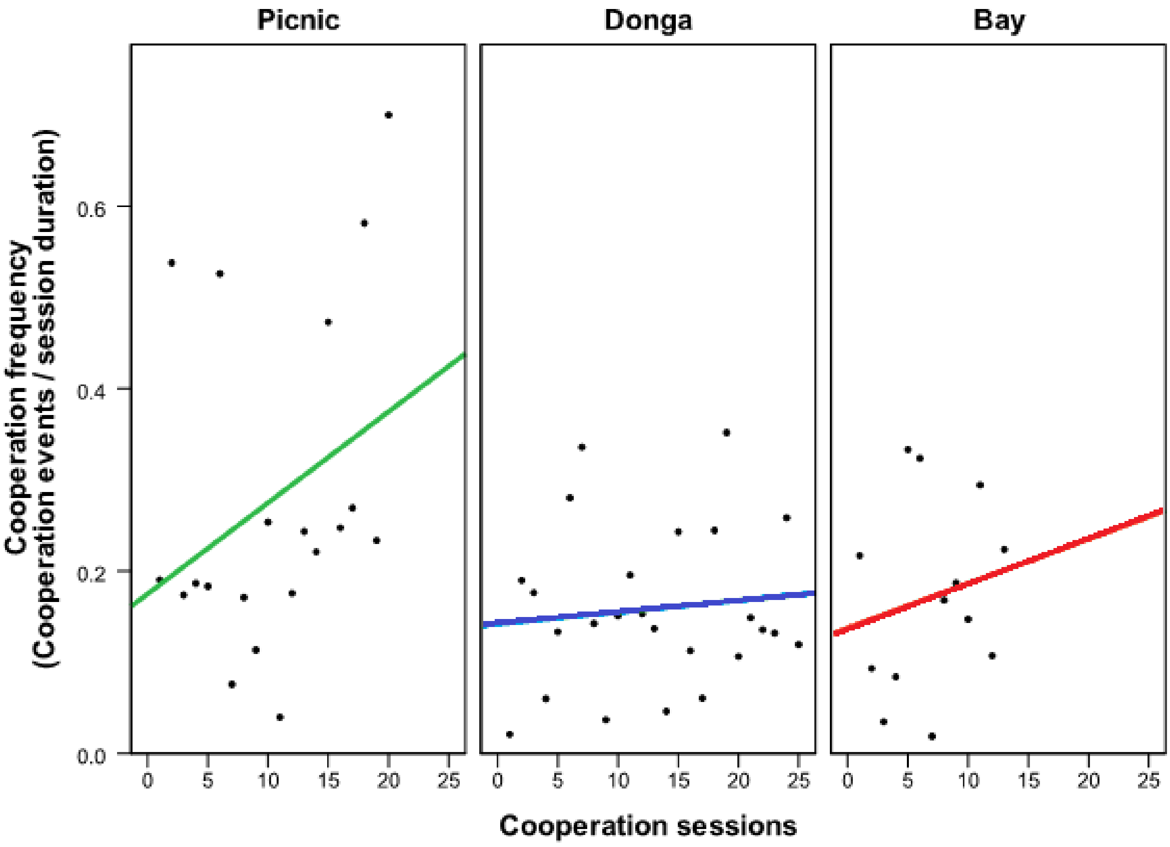

Figure 4 – The increase in cooperation events during the cooperation phase of the experiment. Dots represent total number of cooperation events by day divided by the duration of that experimental session in minutes. A linear interpolation line has been added to the data to show the increase of cooperation frequency at successive sessions. An experiment was considered as concluded when the monkeys would leave the experiment area after having fed for long enough.

Chapter 3 – The biological market effect

Manuscript in preparation

Title

The need of cooperation partners induces wild vervet monkeys to act according to supply and demand

Abstract

A number of theoretical papers have investigated the mechanisms by which cooperation may evolve but very few studies have examined the social setting in which cooperation naturally occurs. In this study we experimentally test the law of supply and demand in three groups of vervet monkeys engaged in a cooperation experiment.

In these experiments, individuals belonging to two classes of different sizes have to cooperate in order to obtain a food reward. I intentionally assigned the individuals to two fictitious classes, one comprised of two individuals and the other comprised of the remaining members of the group. Criteria to administer rewards were subsequently linked to the assignment of class: a reward was only administered if cooperation partners were of a different class.

I predicted that the value of the contribution to the cooperation of a member of the small class is relatively higher than the value of the contribution of a member of the large class. This should lead to an asymmetrical division of the reward and/or a shift in the exchange rates for 'social commodities', such as grooming or tolerance.

The experiment induced the monkeys to cooperate first at the feeders, and to exchange social behaviours differently after, as a result of having cooperated. To test market theory models, I analysed whether the distribution of exchange of beneficial behaviours had changed due to the reward criteria based on assigned class. Because one class was less numerous than the other, its members acquired a privileged status and became in demand as cooperation partners. After cooperating the monkeys adjusted social behaviours' exchanges in favour to the smaller class of cooperators. They therefore adapted to the law of supply and demand as predicted by biological market theories.

To date there has been no experimental evidence that clearly show the link between cooperation and the law of supply and demand. This study demonstrates that a high demand for cooperating with few individuals causes these latter to be rewarded with an adjustment of beneficial behaviours directed towards them. These results lend support to the theory of biological market.

Preface

In this chapter I experimentally test the law of supply and demand applied to monkeys after their engagement in the cooperation experiment. To attain cooperation and get a food reward, the tested subjects chose each other according to specific partner choice patterns (analysed in the previous chapter). The feeders were joined to induce the individuals to stand in front of them and share food. Different numbers of individuals were assigned to different feeders so to test whether a matching market was arising as a result of the reciprocal need of members of the two different classes to obtain the reward. From then on, after cooperating and sharing food, they exchanged social behaviours differently. I analyse here how differently social behaviours of affiliation were exchanged across cooperative partners. My expectation was that due to the law of supply and demand, the members of the small class would gain an advantageous position, visible in terms of sociopositive behaviours directed at the members of the small class by the members of the large class.

Introduction

The biological market theory of cooperation has modelled that cooperative exchanges in the natural world are similar to those in an economic market (Noë & Hammerstein 1994, 1995).

In a biological market specific behaviours are seen as commodities (goods and services) that can be traded or bartered (Noë 2006b). When individuals exchange commodities, they should do it according to economic rules and for their reciprocal benefit. Compared to human markets though, verbal negotiation is missing as well as written and binding contracts (Bowles & Hammerstein 2003).

Market dynamics are discernible when trading partners compete to find the most attractive ones in the form of an outbidding competition. The individuals with a common commodity will try to offer their ‘product’ at a lower price and more easily than other members with scarce amounts of this same product, in order to make themselves more favourable trading partners.

Scientific evidence presented during the last two decades has shown that a biological market can be found for several social systems (summarised in Barrett & Henzi 2006; but see also Schino & Aureli 2010). In primates, allogrooming has been the behavioural ‘currency’ best observed for this purpose. Valuable service to be sought, allogrooming has become exchanged beyond the functional use of removing foreigner bodies from the skin (for a review, see Dunbar 2008). This behaviour is customarily recorded since a direction from a groomer to a receiver is always evident. Firstly noted with baboons (Barrett et al. 1999; Barrett et al. 2000), grooming was found used as a currency for tolerance. Following these observations, other primate species were observed trading grooming for tolerance, food, handling of babies and mating (mangabeys, Chancellor & Isbell 2009; and Fruteau et al. 2011; vervets Fruteau et al. 2009; macaques Gumert 2007a; and Gumert 2007b; for partial evidence on chimpanzees Newton-Fisher & Lee 2011; sifakas, Norscia et al. 2009; and lemurs, Port et al. 2009). The hint that a biological market can potentially occur also outside the order of primates has been given by analogous observations in some other animal species (meerkats, Kutsukake & Clutton-Brock 2010; passerine birds, Radford & Du Plessis 2006; hyenas, Smith et al. 2007).

The emergence of cooperation among unrelated individuals poses dilemmas which have challenged both evolutionary biologists and economists. As in the previous chapter, I define cooperation as any act done together so that there is a net gain for all individuals engaged (Noë 2006a). The risk of overexploitation of individuals offering the services makes cooperation unstable at times. With this study I am interested in cooperative interactions beyond one-shot interactions, as those of the prisoner's dilemma game. Trivers (1971) hypothesized that interacting subjects might attain cooperation over a sequence of reciprocal acts by keeping track of the previous moves of their partners. This idea was later applied in models based on the iterated prisoner's dilemma (Axelrod 1984; Axelrod & Hamilton 1981). And this latter became the custom model used for studying reciprocity in repeated interactions (Dugatkin 1997).

Although reciprocal altruism has now for long proposed as an explanation for cooperation (Trivers 2006), further evidence has shown also the presence of a biological market. Yet almost no experiments were put in place to prove that markets really occur, with the exception of the models of the cleaner fish (Bshary 2001) and the vervets (Fruteau et al. 2009). Especially the second study is of particular interest to the current paper. In fact, the experiment here depicted was designed as a follow up to Fruteau et al. (2009), and includes the condition of cooperation to be tested within this model of the vervets. In Fruteau et al. (2009), two monkey individuals (called 'producers') of two wild vervet groups provided food to the rest of the group members. An orientation period was necessary to the rest of the monkeys to allow these special individuals to have control over the food resources, and the producers learned to be the only individuals able to open large food containers. On their own, these individuals with the monopoly over food production could provide access to food to the whole group. As a consequence to their food production, the selected monkeys got rewarded by receiving more grooming by the individuals that fed thanks to them. In the Fruteau et al. experiment, the ‘producers’ provided food to the rest of the group by simply opening the food containers. Differently, in my experiment I do not have specific ‘producers’, but the food is accessed by the action of multiple individuals working together. I did not limit the access to food only to dyads, but according to a more realistic cooperation layout, multiple individuals and combinations were let free to form at the feeders. To test the presence of a market, consisted of the exchange of commodities between trading classes, I recorded the exchange of social behaviours among partners. Chief social behaviour used in the past for this purpose has been allogrooming. Traditionally grooming has been recorded with focals, measuring the amount of time one individual is grooming another. Differently from previous studies, sociopositive and affiliative behaviours additional to grooming (hereafter referred altogether as SPB’s) have been recorded with the purpose of revealing the presence of a market (see Methods for more details on how the behaviours of contact sitting and social play were included in the analysis).

Making use of the same experiment depicted in the previous chapter, I focus in this chapter on what happened as a result of having artificially created two classes of different sizes. Since the individuals of the larger class outnumbered the two individuals of the smaller class, according to the law of supply and demand, the members of the smaller class are expected to become in demand for cooperation. Being the individuals composing the smaller class only two, their supply is limited compared to the demand for cooperating in multiple combinations with the individuals of the larger class. Because of this, their status in the group should become advantageous. As a first, general prediction, I checked whether the introduction of the cooperation experiment caused the monkeys to interact in affiliation differently than during the training phase. Afterwards, to test whether the law of supply and demand predicts a change in the direction of affiliative behaviours, I tested if on average the individuals of the smaller class received more of these behaviours. Having recorded frequencies and the direction from actors to recipients of these social behaviours, I predicted the smaller class will receive more often than offer affiliative behaviours.

Methods

Tested subjects

This study was performed as a follow up on the same animals engaged in the same experiment of the previous chapter. The groups I followed at Loskop Dam Nature Reserve were the Picnic, the Donga and the Bay. Of the 10 members of the Picnic group, 7 cooperated at the feeders. Of the 19 monkeys of the Donga 13 cooperated. Of the 17 of the Bay 9 cooperated. Since I concentrate on the effect that cooperation had on the exchange of social behaviours among cooperators, the non-cooperating individuals are not included in the analyses. The infants were also not included as they did not cooperate actively at the feeders and were always following the mothers.

Experiments

Again, the experiments I refer to in this chapter are the same feeding trials as those explained in the previous one. The experiment was divided in two phases. An initial training phase was needed for the monkeys to become accustomed to their division in two different classes of different sizes. The white feeders were allocated to the large class and the black feeders to the small class, which had two members in each of the three groups. During this training phase, the feeders were positioned at equal distances from each other (of 3-4 meters) and fixed to the ground. The angle they were disposed at gave the opportunity to the monkeys to see each other. I expected the monkeys to learn distinguishing each other as belonging to these two different classes gradually over time.

During the subsequent cooperation phase two joint feeders, each consisting of one black and one white box, where placed at about 3-4 meters from each other. These joint feeders only provided the reward when both (or all, if more than two) individuals from each class stood in front of their appropriate feeder waiting to obtain food. In addition food was released when at least one member of each class handled a feeder. In these specific terms then, cooperation is achieved when the monkeys are together expecting to receive the reward that can be shared.

Data collection and calculated variables

The data used in this chapter are restricted to observations made during the training and the cooperation phases of the experiment. At turns, during these sessions, the monkeys would be engaged in feeding from the apparatuses and would be involved in interacting socially. The sociopositive behaviours (SPB's) were recorded during the feeding sessions. SPB's are allogrooming, contact sitting and social playing. Due to the competition for obtaining food in proximity of the feeders, sociopositive behaviours usually occurred at 3 metres distance or more from the feeders.

SPB data can be collected when observed taking place in relation to an experiment setup and outside more natural settings (as of grooming for mating Gumert 2007b; or grooming for handling infants Henzi & Barrett 2002). A part from allogrooming, in contact sitting and playing a direction throughout the bout is not evident. They can nevertheless be considered as commodities to be exchanged. The direction is given by the initiator of the action. I provide two examples to clarify this.

In contact sitting, when individual A goes and contact sits with individual B, it means it is A who is looking for association partnership with B. In social play the initiator of playing is as well the individual who behaviourally shows the impulse to exchange ludic and social interactions. Since juveniles and not only adults interact in cooperation, social play becomes another important variable to include in the analysis. It is in fact known that juveniles tend to express affiliation to other juveniles not just with grooming but especially so with playing (e.g. Fagen 1993).

The aim of the data collection by the all-occurrence sampling method (Altmann 1974) was to keep track of the occurrence of all the SPB's performed by the individuals in the group. The data described here are frequencies given by each start of a social display. No durations have been collected (like focals of grooming) since it was not feasible to monitor the durations of social exchanges of all cooperating individuals in the group by a limited number of observers. Data were collected according to the following rules: if a monkey stopped displaying a specific social behaviour for longer than 5 seconds (meanwhile being vigilant or such), then I considered a new bout to have started.

I define (1) SPB aggregated data:

as the amount of SPB given plus those received per individual divided by the time of the experimental session in minutes by day. As said before, all SPB's were recorded during the experimental trials, and the time in minutes of the experimental trial reflects the sampling time by the observers. Not all trials lasted the same amount of time; by dividing the SPB's by the minutes of the trials I therefore weighted longer sessions against shorter ones.

I define (2) SPB ratios:

similar to Fruteau et al (2009) with the difference that frequencies and not durations are recorded. SPB ratios are calculated by dyads as times receiving SPB's minus times offering

SPB's divided by the total number of SPB's (the total is given by times receiving plus times offering SPB's). This ratio returns values set between -1 and 1 per dyad and per day. Negative values signify an individual offer SPB's more than receiving them, positive values signify the other way round.

Behaviours were gathered by two assistants and RP after inter-observer reliability tested a priori. The data were entered in Pocket PC's directly in the field through the software Pendragon Forms 5.1.

In addition to behavioural variables, I executed a social network analysis to understand the social change of certain individuals in relation to the whole group as a result of the introduction of the cooperation experiment. I calculated eigenvector centrality measures as suitable parameters (Kasper & Voelkl 2009; Whitehead 2008a) to infer the change in influence of the individuals of the smaller class. Eigenvector centrality is by definition proportional to the sum of the centralities of the monkeys' neighbours, so that an individual can acquire high centrality either by being connected to several other individuals or by being connected to others that themselves are highly central (Newman 2004).

Statistical models

Two models were applied on all the data coming from the three groups: (1) a linear mixed effects model on the SPB aggregated data and (2) a Mantel test on SPB ratios. Confidence intervals at a 95% level for the standard deviation were adopted in all the analyses. All p-values reported for significant terms (and non-significant ones, when relevant) originate from the appropriate minimal models (as indicated by lower AIC indexes). The alpha-levels were all set to 0.05.

1) SPB aggregated data

To find out whether all SPB data changed with the introduction of the experiment, I applied a linear mixed effects model. For this model I used the SPB aggregated data as the dependent variable to analyse the changes between the values of baseline and the follow-up measurements during cooperation. I used as fixed effects: (a) the cooperation condition, (b) belonging to either classes, and (c) whether the behaviours' exchange was taking place within the same class or between the two classes of different sizes.

The mixed model was used due to the pseudo-replication type of structure of the data. In fact, two observations made on two different groups are independent but two observations made on the same group are dependent. Another level of dependency is that two observations made on same group but for different individuals are less dependent that two observations involving the same individual.

The data of SPB total behaviours had to be box-cox transformed to apply the linear mixed effects model (Box & Cox 1964). This procedure computes the best power to apply to the SPB aggregated variable so that the residuals of the model follow a normal distribution (checked with a Q-Q plot).

Also the descriptors such as the sex, age class and rank of each subject were entered as fixed effects in a more comprehensive model. This was done to find out whether among the 6 individuals of the smaller classes there were some that due to their characteristics were consistently receiving and/or giving social behaviours at a different frequency. Nevertheless these descriptors were not found explaining the variation within the dataset (increasing the AIC's) and they were hence removed. It is possible that these factors do not show up as explanatory variables due to our limited sample size.

As a last step, including an autoregressive structure could not improve the fit on the data. The autoregressive structure checks whether the data points change significantly over time during the two experimental phases compared against each other and corrects the fit of the line to neighbouring data points averaged together. If the curves representing SPB ratios of each individual of the smaller classes of Figure 5 were changing according to this rule, then the autoregressive fit would have shown up as significant. After a graphical assessment on the change of behaviours given and received, if this was found occurring gradually in time, it could have been interesting to split the cooperation phase into different intervals. Since that was not the case, I limited the analysis to comparing the two phases without differentiating into smaller time intervals.

2) SPB ratios

To check whether the law of supply and demand predicted the direction of exchange of SPB's, I analysed the ratios of SPB offered minus those received divided by the total for the three groups together. The analysis was executed with three Mantel tests combining the values of the three groups together (29 monkeys). The dyadic interactions of SPB exchanged between groups remained disconnected, since the matrix to be computed did not presented values of between groups joining partners. Yet in this way the individuals of the smaller class – now six in number – could make up for degrees of freedom sufficient to provide p-value.

Mantel tests take into account the direction of offering and receiving by dyads. By doing so I consider that each social interaction is specific of a dyad and I account for the interdependency of the data. The matrices compared were those of SPB's exchanged during training and during cooperation. The null hypothesis to be rejected was that the SPB ratios were similar in both conditions.

I used Mantel Z-tests which, at each comparison, find whether there is a linear relationship between the SPB's exchanged by partners during training and cooperation. For each model, the sets of reciprocal interactions are summarised in two matrices that are in turn compared with 10,000 of other permuted matrices of random interactions. The permutation tests are done for the stepwise determination of significance. The correlations between these matrices were checked for the individuals of the smaller as well as the larger class.

Although it would have been better to control for the pseudoreciprocity of the interactions as in a mixed-model, to date no mixed effects matrix model exists that as random factors computes the individuals nested into dyads nested into groups. And dyad would be a key factor missing from the model.

The mixed models were fitted using the library nlme (Pinheiro et al. 2010) for R version 2.10.1 (R-Development-Core-Team 2010). Mantel analysis was performed with the MATLAB programs SOCPROG 2.4 (Whitehead 2009) and with PASSaGE 2.0 (Rosenberg & Anderson 2010).

Results

Cooperation induces a modification in the exchange of social behaviours

In this section I refer to the SPB aggregated behaviours predicted to modify as a result of the experiment. As expected, the cooperation experiment caused indeed a strong change in the amount of SPB interactions among the monkeys.

The full statistical output for the SPB aggregated behaviours by linear mixed models is reported in Table 3.

The frequency of SPB aggregated behaviours decreased significantly during the cooperation phase. From training to cooperation, the fact of belonging to either the larger or the smaller class caused marginal difference in the amount of SPB given and received (Cooperation by Class effect results in Table 3). Nevertheless, the amount of SPB's did vary if exchanged by members of the same class or members of different classes. What most relevant to the purpose of the experiment, the SPB's decreased significantly when cooperation was introduced compared to the smaller and larger class mixed exchanges. This might have been due to the more challenging cooperation phase and increase in competition, as I discuss later. Even though these social behaviours decreased in frequency, the less numerous members of the smaller class may have received more SPB ratios from the larger class as predicted by the market. I investigated this latter perspective in more detail with the subsequent analysis.

The commodities are exchanged as predicted by the market

In this section I refer to the modification of SPB ratios during the cooperation phase.

The SPB ratios during training were different than during cooperation per monkey dyad (observed $Z = 25.296$, matrix correlation = 0.716, $t = 12.029$, $p < 0.0001$). The three smaller classes of individuals increased their SPB ratios significantly $p = 0.0103$ (matrix correlation = 0.719). This result indicates that SPB ratios increased in favour of these monkeys and that the market effect holds true. From Figure 6 we can see what happened for each specific monkey during training and cooperation. Five out of the six individuals of the smaller class had their SPB ratio value modified according to our hypotheses of adjustment to the market. One individual of the first group instead, did not behave as expected (first graph of the six of Figure 6). Yet averaged with his other peers of the smaller class, this individual did not cause a modification of the general trend for this group.

In the Bay group, the two individuals belonging to the smaller class offered more SPB's than they received during both training and cooperation. Their SPB ratio values are in fact negative. During cooperation still, this negative ratio decreased in favour of the smaller class on average (last graph of the six of Figure 6).

The individuals belonging to the larger class of the three groups also modified their behaviour significantly during cooperation ($p < 0.0001$, matrix correlation 0.689). Yet a consistent trend across individuals and groups was not found (Figure 6, both individuals' and classes' plots), which does not allow us to infer what happened exactly. I can nevertheless assume that this last result is also a consequence of the strong modification of social behaviours given and received because of the cooperation condition, and comes as no surprise. All the monkeys had to adjust to a new social condition – cooperation – which induced the vervets to have a higher social participation and to combine in specific subgroups of individuals at the feeders (see previous chapter). As shown by the other analyses of this study, if the smaller class changed its SPB ratio, also the other class has responded to the change. After all these analysed behaviours were exchanged between classes so a change in one class should induce a related change in the other class.

Increased influence of the individuals of the smaller class of cooperators

I performed a simple network analysis to inspect whether the influence of the individuals of the smaller class changed as a result of the cooperation experiment. To do so, I calculated eigenvector centrality measures of the monkeys (Newman 2004; Sueur et al. 2011).

As expected, from the training phase to cooperation the individuals of the smaller class increased their eigenvector centrality measure in the network represented by SPB behaviours exchanged (Figure 7 with statistics reported in Table 4). This is a further sign that these vervets underwent to a change of social influence due to the cooperation condition and their smaller class size.

In summary, these results indicate that the vervets belonging to the smaller class were rewarded from the other group members with an increase in grooming, contact sitting and playing ratios because of the experiment.

Discussion

Fruteau and colleagues also published results testing the biological market theories with vervet monkeys (Fruteau et al. 2009). The study showed that SPB ratios limited to grooming shifted in favour of a female monkey chosen as provider of a large food resource. In a second phase of that experiment, the grooming paybacks dropped when a second female monkey provider was introduced, demonstrating the effect of the law of supply and demand in an experimental setup. The Fruteau et al. study (2009) proved a strong increase in the social value of these vervet providers, who received more grooming and/or offered it less to the rest of the group members. The focus of that experiment was on food providers and not, as in this case, on multiple partners cooperating to get access to the food resources. In this specific case, the manipulation to test the market was done (1) on the size of the two classes that shared limited amounts of food, and (2) on the repetition of the cooperation events during several experimental sessions.

I showed in the previous chapter that the vervets are capable of feeding from the joint apparatuses at very close distance from each other. The monkeys moreover consistently stood in front and operated their specific (class) side of the joint feeders (of different colours), an indication of their understanding of the need of specific partners to obtain together the reward. It is the need of specific partners though and the several combinations possible that are key of this study. As shown by my results, also the supply and demand law could be proved when examining the change in SPB ratios at a dyads' level.

The SPB (aggregated) levels decreased on average for all the individuals during the cooperation phase. I can interpret this result in view of the modified social condition the vervets underwent once the experiment switched from training to cooperation. At that point the monkeys interacted at the feeders gradually more in order to share food (see results of previous chapter). The time they passed at the feeders during a feeding session also increased in respect to the time they waited and interacted socially. Grooming, contact sitting and social play are behaviours displayed when the group is free from feeding and being vigilant, and gets relaxed before and after resting time (e.g. Dunbar 2008). I can assume that these SPB's decreased in general in response to the aroused condition at the feeders.

But are SPB patterns observed after the cooperation experiment at the feeders actually be interpretable as a cue of recompensing the smaller class of cooperators?

Not all individuals of the larger class offered more SPB's to the smaller class; some in fact received less SPB's. The individual of the larger class were probably accepting fewer amounts of SPB's from the smaller class due to the individuals' increased social value. This can be justified by the market dynamics of fluctuation in price. SPB's can be exchanged more, less: it's the ratio what counts.

I found that vervet monkeys adapt to the introduction of an experiment to induce cooperative behaviour by fluctuating the amount of social behaviour exchanged. I also found that the direction of SPB's exchanged differed in favour to the smaller class of cooperative partners, sign that the monkeys became able to discriminate between the values of the contribution to the cooperation across classes. These results support biological market theories and show that the law of supply and demand applies to primates' cooperative behaviour.

Figures

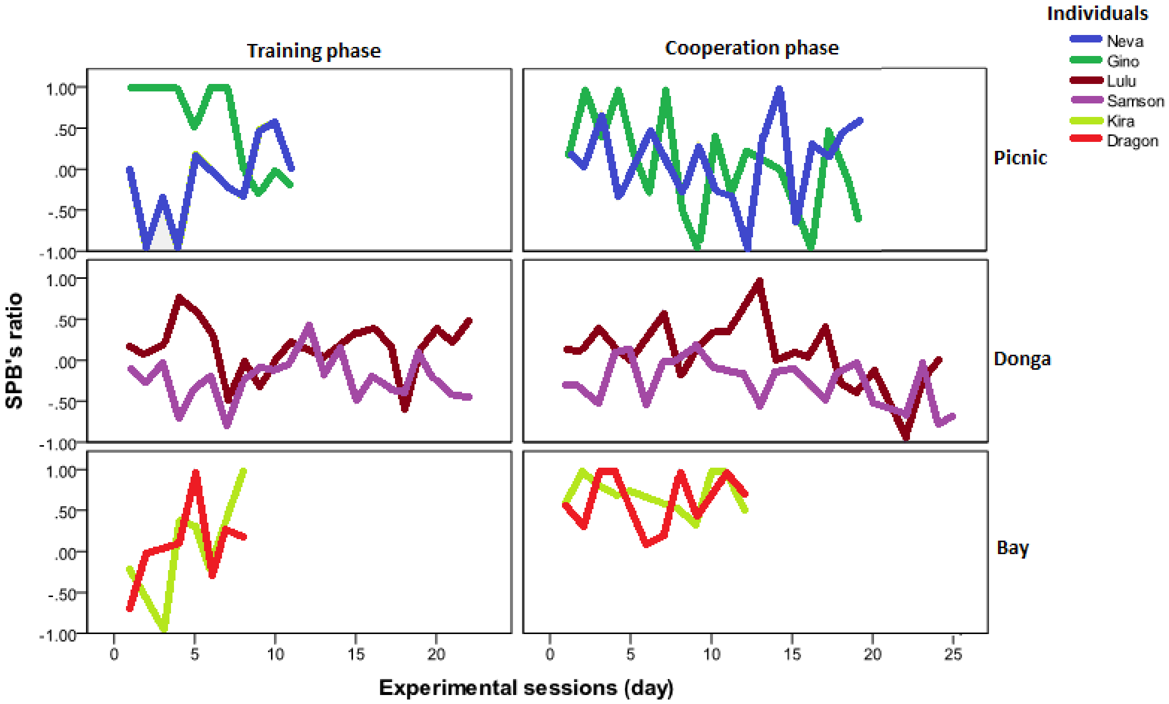

Figure 5 – Fluctuations in sociopositive behaviour (SPB) ratios during training (left) and cooperation (right) conditions. The lines show the difference in social behaviours received and given for each of the two individuals of the smaller class of cooperators of the three tested groups. The analysis performed with Mantel tests takes into account the difference in SPB ratios by dyads that this graph does not show.

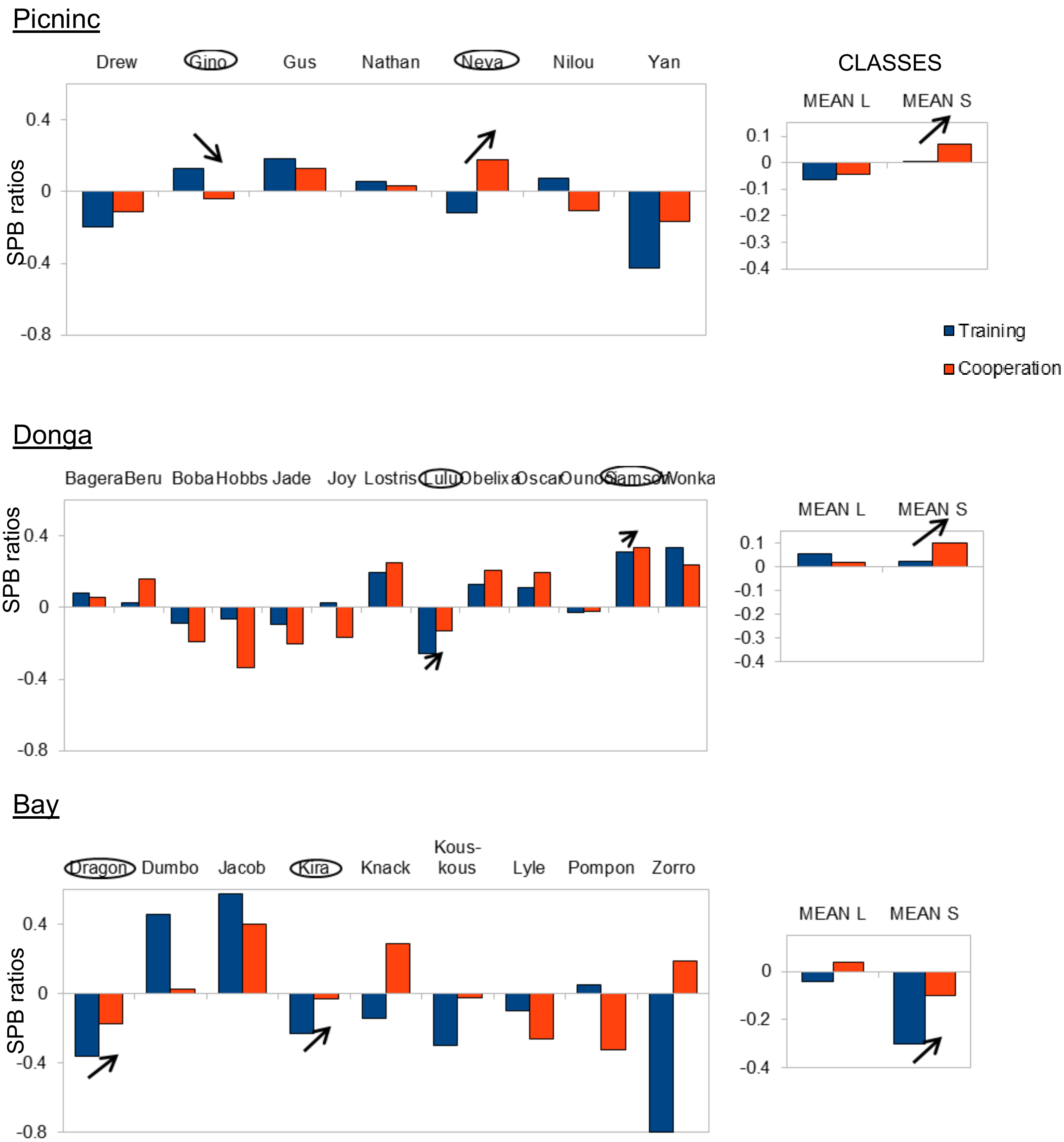

Figure 6 – Histogram plots of averaged sociopositive behaviour (SPB) ratios during training (blue bars) and during cooperation (red bars) per each individual of the three tested groups. Individuals belonging to the smaller class are marked with black circles. SPB ratios are defined as SPB's offered minus received divided by the total of the two. On the right, the smaller graphs show the difference combined by class (Large and Small – the graph shows the mean values of the two individuals). Errors bars are not reported for graphical clarity. In

the Picnic group one individual, Gino, did not follow the expectation of increase in SPB ratio. Yet the mean value of SPB still increases when combined with his same class member. For the Bay group the two individuals belonging to the smaller class offered more SPB's as compared to receiving them, during both training and cooperation. Yet the market was confirmed decreasing the amount of SPB's offered on average by dyads during cooperation.

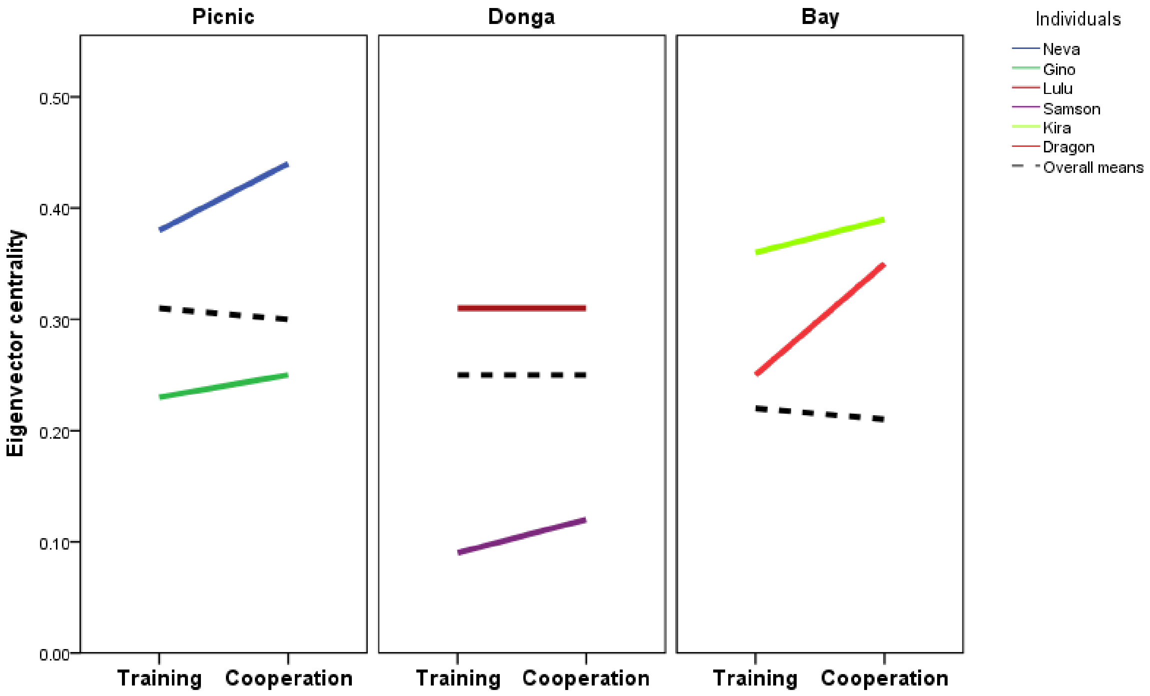

Figure 7 – From training to the cooperation, each of the two members of the smaller class of cooperators increased their eigenvector centrality measure (except for Lulu in the Donga group that remained the same). Conversely, the centrality of the mean of all individuals of the group (dashed lines) slightly decreased or remained the same. SE have been omitted since all giving a value between 0.01 and 0.02. The values are reported in Table 4.

Tables

Effects on SPB aggregated	Value	SE	df	t	p
(Intercept)	0.702	0.158	3385	4.444	< 0.0001
Cooperation	-0.062	0.012	3385	-4.927	< 0.0001
Class	0.241	0.056	43	4.286	0.0001
Mixed class interactions	0.101	0.012	3385	7.881	< 0.0001
Coop by Class	0.071	0.036	3385	1.993	0.0463
Coop by Mixed	-0.028	0.017	3385	-1.593	0.1111
Mixed by Class	-0.423	0.037	3385	-11.419	< 0.0001
Coop by Class by Mixed	-0.146	0.050	3385	-2.898	0.0038

Table 3 – Values of linear mixed models statistics of the three groups according to the two experimental phases of training and cooperation. The dependent variable is SPB's aggregated, that is the sum of sociopositive behaviours of allogrooming, contact sitting and social play both offered and received.

Group	Ids	Condition	Eigenvector centrality	SE	Strength	SE
Picnic	Gino	*Training*	0.23	0.01	0.52	0.03
		Cooperation	0.25	0.01	0.54	0.02
	Neva	*Training*	0.38	0.02	0.78	0.03
		Cooperation	0.44	0.02	0.59	0.02
	Overall means	*Training*	0.31	0.01	0.73	0.01
		Cooperation	0.30	0.01	0.62	0.01
Donga	Lulu	*Training*	0.31	0.01	0.59	0.02
		Cooperation	0.31	0.01	0.57	0.03
	Samson	*Training*	0.09	0.01	0.31	0.02
		Cooperation	0.12	0.01	0.25	0.03
	Overall means	*Training*	0.25	0.01	0.46	0.01
		Cooperation	0.25	0.01	0.45	0.01
Bay	Dragon	*Training*	0.25	0.01	0.69	0.02
		Cooperation	0.35	0.02	0.92	0.02
	Kira	*Training*	0.36	0.02	0.81	0.03
		Cooperation	0.39	0.02	0.74	0.03
	Overall means	*Training*	0.22	0.01	0.53	0.01
		Cooperation	0.21	0.01	0.51	0.01

Table 4 – Values of eigenvector centrality and strength determined through social network analysis. For each of the three groups the values were calculated distinctly for the two individuals, part of the smaller class of cooperators, and on average for all the group members during each of the two experimental conditions. SE's have been generated with 10,000 boostrapped permutations.

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Chapter 4 – Concluding remarks

The results obtained

I organise this final section following the order of the results as acquired in the field and presented in this thesis. I first point at the effects of partner choice presented in chapter 2, and move on to the exploration of the market presented in chapter 3.

I focus on the partner choice results according to the matching market paradigm, concisely highlighted in economic terms in chapter 2.

I briefly discuss then the results of chapter 3, in light of the theory of microeconomic markets.

The matching market paradigm

The cooperation experiment performed in South Africa was designed to induce the vervets to combine as in a matching market. Once the monkeys learned to respond in accordance with their assigned cooperator classes, partners were consistently found joining into preferred combinations of either higher ranking individuals or relatively low ranking ones.

The idea of the matching market comes from a simple mathematical problem that tries to solve several real-world settings given by having to match individuals as in a matrix (for a recent review see Gale 2001; original theory in Gale & Shapley 1962). In 1962 Gale and Shapley successfully found the algorithm for solving the conundrum of matching all the possible partner combinations. The examples they presented for the applicability of their algorithm was for colleges having to match with the right student candidates and for women having to match with the right combination of male partners. The principle followed by the contenders in the market is that both parties will attempt to match with partners of high value. The problem is solved, in summary, only when the combination of partners of very similar quality is found (quality as per best qualified students and most attractive men). The matching problem is related to the other problem of cooperation, as envisaged under economic terms by the theory of the biological market (of Noë & Hammerstein 1995). Multiple individuals with the opportunity to cooperate will continuously attempt to form the right and most valuable partner choice. In an imaginary case, where the total number of partners to join with is unlimited, the combinations will also be unlimited. The partners will continuously attempt to find other partners of high quality – possibly of better quality than themselves. The game modifies however once (1) the number of partners to join are limited and (2) they can be matched with only one possible combination. These were the conditions behind my field experiments with the proviso that I allowed the monkeys to combine not just in dyads, but also in combinations of multiple individuals at the feeders (as theoretically proposed in Sotomayor 2004) and to subsequently recombine after, during following cooperation trials.

Although it cannot be ascertained specifically from the data whether it was the monkeys from the smaller class looking for the best partners of the larger class, or vice-versa, on the basis of my observations one could approximately distinguish the order in which choices were made. Initially the most dominant individuals would approach the positioned feeders, irrespective of their class. Then the higher ranking individual of the small class would approach the feeders, and in succession the other higher ranking monkeys of the larger class would join with the initiator. After all relatively dominants individuals would have fed, the subordinates would take ther turn and access the feeders starting with the low ranking individual of the smaller class. I can therefore generally say that the individuals of the larger class matched themselves to the ones of the smaller class: first the dominants and subsequently the subordinates.

The combinations possible at the feeders were limited in number and apparent from the asymmetric matrix made up by the two individuals of the smaller class joining with the individuals of the larger class. More importantly, and distinct from a traditional matching market, the individuals could combine with others, but at a following stage they could re-assort in other combinations.

The individuals go through three stages in order to find a stable matching system (adapted from Gura & Maschler 2008).

(1) Every individual of the larger class (l_1, $l2$, … l_x in order of dominance) turns to the individual of the smaller class (s_1 or s_2) who is first on his list, and tries to cooperate with it. Given the results of chapter 2 and my observational evidence, we can assume that s_1 selects those higher ranking and ‘favourite’ l individuals. Since each of the two individuals of the smaller class has several contenders, it selects its favourite partner from among those who propose cooperation.

(2) Those l_x monkeys not interested in joining s_1 will attempt joining s_2.

(3) If s_2 rejects them they are excluded from cooperating. This selection procedure stops here since no other combinations can be made (being the s partners only two in number). Other combinations of partner choice can nevertheless be attempted on other successive cooperation trials. Given the results of chapter 2 (Table 1), it is known that in all three groups not all members ended up cooperating, but some (those l_x most subordinates) were constantly excluded. This may well be further evidence that a selection mechanism and partner choice

process is taking place with the vervets.

The assumption I made prior to the monkeys joining at the feeders concerned the need for the players to join several times before a more or less stable preference emerged. Stability of this matching system follows the definition given by Gale and Shapley for the marriage matching problem: "*a matching system is called stable if a pair of a man and a woman cannot be found that are not paired but who prefer each other to their actual mates*". I therefore assumed that several food sharing trials and experimental sessions were necessary prior to the experiments so individuals could adjust their choice of preferred partners.

Although the results of partner choice preference provided in chapter 2 are statistically significant, I cannot tell whether the number of trials I allowed to the monkeys for cooperating were sufficient for them to display a stable partner choice preference.

Stable partner choice preferences are not necessarily those in which every individual is satisfied with its choice. In other words, a stable market does not necessarily serve the interests of all community members (Gura & Maschler 2008).

A likely indication that more trials had to be attempted in order to reach stability is provided by the partner choice analyses showing the division in two subunits of cooperative partners. Even though a preferential pattern of sex, age class or kinship was not found, it is possible that once stability is reached, these other factors come into play further modulating the choice of preference. To investigate this further, it would be interesting to replicate these experiments with larger sample sizes. In any case, dominance rank appears to be an overruling element for choice of cooperation partner in vervet monkeys in a food reward context.

Once this experimental setup will have been applied to other species and in cooperative conditions other than food sharing, it will be interesting to see whether rank will remain predominant element affecting choice of cooperation partner.

It is necessary to note that the design of this experiment can be changed to improve its significance for partner choice analysis. The idea behind skewing the size of the two cooperator partners is that the limited supply of the smaller class should predict its higher demand, and this was shown in chapter 3. This might have inevitably caused an effect on the partner choice itself, even though I specifically chose the members of the smaller class to be representative of the whole group. A design that should be implemented is to impose no class size at all, but let the partners combine freely and observe emerging natural partner choice.

Economic and biological markets

In chapter 3 I tested the value of monkey individuals in the market. I presented some evidence that the monkeys adjust to the limited size of the smaller class of cooperator partners by increasing the price these individuals need to be paid with. This is an indication that their cooperative behaviour adapts to and obeys the law of supply and demand, as the theory of biological market predicts (Noë & Hammerstein 1995). But are the vervets acting according to conventional economic markets? Some relevant ideas for discussing this parallel have emerged (Bowles & Hammerstein 2003). They contrast the two types of market models, the standard human market and the biological one.

Classical economics models concerning human maximisation of subjective expected utility involve complex cognitive processes that take into account the multiple strategies of the market players, our past experiences, etc. The biological market theory, on the other hand, considers population-wide dynamics for the maximisation of individual fitness (Bowles & Hammerstein 2003). Non-human primates will be more severely constrained cognitively, compared to humans. For instance simple organisms almost certainly do not cooperate according to markets with intention, but they are more likely to only apply rules of thumb that maximise their fitness. In the case of humans, instead, both intent and unconscious processes are involved.

In the case of the vervets, we can assume that their cognitive abilities in general are not as limited as those of more simple organisms. It is therefore conceivable that the vervets do somehow keep account of past experiences. It would be interesting to compare market related behaviour across mammals and relate this to relative neocortex size as has been done for deception rate in primates (Byrne & Corp 2004).

Clearly significant differences exist between human economic markets and biological markets. Biological markets focus to a larger degree on partner interactions, and individual reputation, whereas economic markets, including the stock market are much more complex and based on reputation of organisations and corporations and bound and constrained by centralised interference such as contracts, price determinations and other regulations (see also Bowles & Hammerstein 2003). However, these differences aside, the present study establishes that simple factors modifying the value of participants in cooperation have the ability to modify the market accordingly and influence the benefits accumulated by participants with increased value.

The comparative framework applied to Institutional Economics

In modern institutional economics, issues concerning emerging markets and the relationship with rank hierarchies of the market's players have received considerable attention (Gellner 1999).

The organisation of the rank in the female phylopatric vervet monkeys is different between the males and the females. Since females are permanently resident in the group their rank is inherited from the mothers (see Introduction chapter). This hierarchy is therefore based on an 'aristocratic-inheritance' system of ranking for females. The males instead need to conquer their rank position gradually. This system can then be seen as 'bourgeois-conflict' based for the males (who at certain age migrate to other groups).

The two male and female genders in the vervet can be compared for its characteristics to human agrarian and industrial societies. They can in fact be seen as a mix between these two hierarchies, whereby the two models (female-aristocratic and male-capitalist) are bound between each other by a relationship of institutional complementarity. The work of Ernest Gellner, (reviewed by Pagano 2003) has been a the relevant reference for showing how agrarian societies and industrial societies self-reinforce their respective institutional equilibriums.

If the experiment had a higher impact on the social relationships of the cooperating individuals, it would have been interesting to assess whether market effect is equally strong on the hierarchies of the two genders, or whether market de-stabilises one hierarchy more than another. It could have happened in fact that only the hierarchy of the males gets affected by the market. On the other hand it may have been plausible to think that is more difficult to have market destabilising the inherited hierarchy of the females.

This thesis shows that similar issues found in human societies are relevant when considering market forces on the vervets' primate society. The data I have presented point towards the direction that the prevailing hierarchy can shape cooperation patterns and, in turn, cooperation can re-shape hierarchy by enhancing the status of scarce skills cooperators in an implicit biological market.

Although the feeding experiment with the vervets did not have an impact to the extent to modify the internal groups' hierarchies, it is envisaged that natural events of a certain impact can influence the hierarchical power of specific individuals, if they become influential in the group. If we work out the computation of rank adding to the outcomes of contests also the modification of certain affiliative behaviours (e.g. O'Keeffe et al. 1983), we can imagine that a more invasive experiment could modify the rank structure more or less temporarily.

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Appendix

Faecal samples' data collection

I collected faecal samples in the field with the purpose of determining full relatedness of the monkey individuals. Besides genetics, I employed collaborations with other colleagues to fully use the biological information contained in the samples. This information will become useful for one or two other papers to be published without the purpose of studying cooperation.

Methods

Faecal samples were collected during behavioural observations whenever defecation was observed and the individual could be identified. To extract the hormones, ethanol was added to the faecal samples transferred to a polypropylene vial. After 48 hours, one third of the ethanol was extracted and transferred to a glass vial which was then dried. The residual faecal matters were frozen for DNA analysis. Another fraction of the residual was stored in formaldehyde and stored for parasite analysis.

The method for this DNA extraction is unpublished but generally follows Krützen & Goossens (2007).

The method for parasite extraction is from Muller-Graf and collaborators (1996) adapted by Hernandez and colleagues (2009).

Relatedness estimates

1_Picnic	4	3	7	2	8	5	9	10	6	1
4		0.003	0.054	-0.122	0.479	-0.010	0.123	0.569	0.166	0.050
3	0.003		-0.047	-0.127	-0.022	0.046	0.419	-0.149	0.235	-0.212
7	0.054	-0.047		0.121	0.453	0.097	-0.020	-0.046	0.093	-0.152
2	-0.122	-0.127	0.121		0.177	-0.065	-0.224	0.009	0.029	-0.070
8	0.479	-0.022	0.453	0.177		0.031	0.017	0.133	0.224	0.010
5	-0.010	0.046	0.097	-0.065	0.031		0.012	0.061	0.534	-0.080
9	0.123	0.419	-0.020	-0.224	0.017	0.012		-0.049	0.227	-0.160
10	0.569	-0.149	-0.046	0.009	0.133	0.061	-0.049		0.163	0.593
6	0.166	0.235	0.093	0.029	0.224	0.534	0.227	0.163		-0.019
1	0.050	-0.212	-0.152	-0.070	0.010	-0.080	-0.160	0.593	-0.019	

3_Bay	1	2	5	14	15	13	3
1		-0.018	-0.187	0.340	-0.174	0.470	-0.256
2	-0.018		-0.321	-0.223	0.238	-0.092	0.090
5	-0.187	-0.321		0.228	0.209	0.362	-0.234
14	0.340	-0.223	0.228		0.004	-0.122	-0.093
15	-0.174	0.238	0.209	0.004		-0.200	0.121
13	0.470	-0.092	0.362	-0.122	-0.200		-0.171
3	-0.256	0.090	-0.234	-0.093	0.121	-0.171	

Table 1, 2 and 3 – The relatedness coefficients extracted from the monkeys' faecal samples. The estimators are those of Queller & Goodnight (1989). The samples were analysed in collaboration with the Anthropological Institute of the University of Zurich.

2_Donga	**1**	**2**	**12**	**10**	**18**	**20**	**3**	**9**	**19**	**15**	**13**	**8**	**7**	**14**	**11**
1		-0.022	-0.131	-0.153	-0.210	0.431	-0.219	-0.356	-0.010	-0.134	0.471	-0.008	-0.172	-0.132	-0.278
2	-0.022		0.019	0.054	0.488	-0.139	0.107	0.145	0.566	0.193	-0.074	0.035	0.003	0.141	-0.044
12	-0.131	0.019		0.357	-0.156	-0.214	0.263	-0.058	-0.008	-0.033	-0.247	0.185	-0.051	0.065	0.064
10	-0.153	0.054	0.357		-0.080	0.096	0.171	-0.059	0.339	-0.053	-0.097	0.169	0.182	0.336	0.205
18	-0.210	0.488	-0.156	-0.080		-0.133	0.071	0.623	-0.018	0.157	-0.043	0.153	0.129	0.215	0.071
20	0.431	-0.139	-0.214	0.096	-0.133		0.002	-0.092	0.001	-0.268	0.270	-0.107	0.029	0.092	0.247
3	-0.219	0.107	0.263	0.171	0.071	0.002		0.071	0.021	0.227	0.014	0.240	0.347	0.025	0.200
9	-0.356	0.145	-0.058	-0.059	0.623	-0.092	0.071		-0.114	0.194	-0.139	0.288	0.211	0.303	0.072
19	-0.010	0.566	-0.008	0.339	-0.018	0.001	0.021	-0.114		-0.051	-0.135	-0.072	-0.061	0.131	0.081
15	-0.134	0.193	-0.033	-0.053	0.157	-0.268	0.227	0.194	-0.051		0.129	0.583	0.347	0.263	-0.059
13	0.471	-0.074	-0.247	-0.097	-0.043	0.270	0.014	-0.139	-0.135	0.129		0.223	0.554	0.288	-0.090
8	-0.008	0.035	0.185	0.169	0.153	-0.107	0.240	0.288	-0.072	0.583	0.223		0.556	0.372	-0.218
7	-0.172	0.003	-0.051	0.182	0.129	0.029	0.347	0.211	-0.061	0.347	0.554	0.556		0.557	0.061
14	-0.132	0.141	0.065	0.336	0.215	0.092	0.025	0.303	0.131	0.263	0.288	0.372	0.557		0.065
11	-0.278	-0.044	0.064	0.205	0.071	0.247	0.200	0.072	0.081	-0.059	-0.090	-0.218	0.061	0.065	

Cortisol estimates

A - Picnic

Date	Individual	Sex	Age	weight (gr)	72 T ng/g
07/07/2008	Drew	Female	Juvenile	0.8	2048.00
13/07/2008	Drew	Female	Juvenile	1.5	3044.80
16/07/2008	Drew	Female	Juvenile	1.3	1571.08
25/07/2008	Drew	Female	Juvenile	1.1	1234.91
21/10/2008	Drew	Female	Juvenile	1.5	1812.27
15/07/2008	Francis	Male	Adult	1.6	985.00
13/09/2008	Francis	Male	Adult	1.4	1625.43
19/09/2008	Francis	Male	Adult	0.9	959.56
10/10/2008	Francis	Male	Adult	1.3	612.62
12/10/2008	Francis	Male	Adult	1.4	721.43
14/07/2008	Gino	Male	Juvenile	1.4	914.29
16/07/2008	Gino	Male	Juvenile	1.5	1225.60
18/07/2008	Gino	Male	Juvenile	1.6	1921.50
19/07/2008	Gino	Male	Juvenile	1.5	1485.60
21/07/2008	Gino	Male	Juvenile	1	945.60
22/07/2008	Gino	Male	Juvenile	1.2	857.00
26/07/2008	Gino	Male	Juvenile	1	1437.60
14/10/2008	Gino	Male	Juvenile	1.2	680.67
30/10/2008	Gino	Male	Juvenile	1.3	842.77
14/07/2008	Gus	Female	Adult	1.4	890.57
26/07/2008	Gus	Female	Adult	1.5	1334.13
10/09/2008	Gus	Female	Adult	0.4	1318.00
13/09/2008	Gus	Female	Adult	1.1	989.09
15/09/2008	Gus	Female	Adult	1.4	1137.43
08/10/2008	Gus	Female	Adult	1.3	1448.62
12/10/2008	Gus	Female	Adult	1.1	1116.00
19/07/2008	India	Female	Adult	1.3	881.54
25/07/2008	India	Female	Adult	1.5	970.93
10/09/2008	India	Female	Adult	1.2	980.00
12/10/2008	India	Female	Adult	1.2	424.00
24/10/2008	India	Female	Adult	1.6	570.75
31/10/2008	India	Female	Adult	1.6	994.00
14/07/2008	Isis	Female	Adult	1.1	940.73
19/07/2008	Isis	Female	Adult	0.6	1071.33
19/07/2008	Isis	Female	Adult	1.5	440.80
25/07/2008	Isis	Female	Adult	1.6	461.75
13/09/2008	Isis	Female	Adult	1.1	809.09
27/10/2008	Isis	Female	Adult	1.6	2046.00
14/07/2008	Nathan	Male	Juvenile	1.2	919.67
15/07/2008	Nathan	Male	Juvenile	0.9	648.00

22/07/2008	Nathan	Male	Juvenile	1.4	1028.29
25/07/2008	Nathan	Male	Juvenile	0.9	906.67
26/07/2008	Nathan	Male	Juvenile	1.6	1531.75
24/10/2008	Nathan	Male	Juvenile	1.4	1142.57
14/07/2008	Neva	Female	Adult	1.4	811.14
16/07/2008	Neva	Female	Adult	1.2	1162.67
17/07/2008	Neva	Female	Adult	1.2	1458.00
19/07/2008	Neva	Female	Adult	1.6	1048.50
10/09/2008	Neva	Female	Adult	0.9	1591.11
07/07/2008	Nilou	Female	Juvenile	1.4	934.86
14/07/2008	Nilou	Female	Juvenile	1.3	1757.54
16/07/2008	Nilou	Female	Juvenile	1.3	1736.62
25/07/2008	Nilou	Female	Juvenile	1.5	1956.00
26/07/2008	Nilou	Female	Juvenile	1.2	1148.33
26/07/2008	Nilou	Female	Juvenile	1.6	1174.75
30/10/2008	Nilou	Female	Juvenile	1.5	516.53
07/07/2008	Yan	Male	Adult	1.4	794.29
14/07/2008	Yan	Male	Adult	1.5	954.93
18/07/2008	Yan	Male	Adult	1.5	736.53
19/07/2008	Yan	Male	Adult	1.6	578.75
26/07/2008	Yan	Male	Adult	1.6	1464.25
10/09/2008	Yan	Male	Adult	0.9	688.89

B - Donga

Date	Individual	Sex	Age	weight (gr)	72 T ng/g
13/07/2009	Agathe	Female	Adult	1.4	8073.21
29/07/2009	Aztec	Male	Adult	1.3	4754.38
06/08/2009	Aztec	Male	Adult	1.8	3920.56
07/09/2009	Aztec	Male	Adult	1	5305.50
27/09/2009	Aztec	Male	Adult	0.8	3513.25
07/08/2009	Beru	Male	Juvenile	1.2	8190.25
21/09/2009	Beru	Male	Juvenile	1.3	7288.46
07/08/2009	Boba	Female	Adult	1.1	10681.09
09/09/2009	Boba	Female	Adult	1.1	6941.82
26/07/2009	Hobbs	Male	Adult	1.5	1607.40
05/08/2009	Hobbs	Male	Adult	1.7	2298.76
19/09/2009	Hobbs	Male	Adult	1.1	8854.73
21/09/2009	Hobbs	Male	Adult	1	6373.60
16/07/2009	Jade	Female	Adult	1.6	6919.75
21/07/2009	Jade	Female	Adult	1.5	9501.27
09/09/2009	Jade	Female	Adult	1.1	7597.55
28/07/2009	Jedi	Male	Juvenile	1	6458.97
24/07/2009	Lostris	Female	Adult	1.3	4394.69
27/09/2009	Lostris	Female	Adult	0.9	3968.44
16/07/2009	Lulu	Female	Juvenile	1	2615.16
25/07/2009	Lulu	Female	Juvenile	1.7	6876.65
21/09/2009	Lulu	Female	Juvenile	1.1	5112.91
16/07/2009	Obelixa	Female	Juvenile	0.7	4748.07
16/07/2009	Oscar	Male	Juvenile	1.4	7618.86
20/07/2009	Oscar	Male	Juvenile	1.2	6675.12
21/09/2009	Oscar	Male	Juvenile	1	2918.63
27/09/2009	Oscar	Male	Juvenile	1.1	4532.64
07/08/2009	Ounooi	Female	Adult	1.1	6356.86
05/09/2009	Ounooi	Female	Adult	1.3	7607.08
28/09/2009	Ounooi	Female	Adult	0.7	4187.66
20/07/2009	Samson	Male	Adult	1.7	9033.29
28/07/2009	Samson	Male	Adult	1.2	2435.83
07/08/2009	Samson	Male	Adult	1.4	6703.21
28/09/2009	Samson	Male	Adult	1.3	2728.38
09/07/2009	Wonka	Male	Adult	1.6	2044.88
16/07/2009	Wonka	Male	Adult	1.6	3322.25
25/07/2009	Wonka	Male	Adult	1.3	6240.15
05/08/2009	Wonka	Male	Adult	1.7	3146.12
07/08/2009	Wonka	Male	Adult	1.8	4615.56
08/09/2009	Wonka	Male	Adult	1.3	4354.00
28/09/2009	Wonka	Male	Adult	1.4	5495.50

C - Bay

Date	Individual	Sex	Age	weight (gr)	72 T ng/g
10/08/2009	Dragon	Male	Juvenile	1.3	1220.32
13/09/2009	Dragon	Male	Juvenile	1	5816.40
05/08/2009	Dumbo	Male	Juvenile	0.8	10225.43
04/09/2009	Dumbo	Male	Juvenile	1.3	3791.46
15/07/2009	Jacob	Male	Adult	2.1	3288.62
10/08/2009	Jacob	Male	Adult	1.8	3552.61
10/09/2009	Jacob	Male	Adult	1.1	8721.18
04/09/2009	Kephria	Female	Juvenile	0.7	3696.53
26/09/2009	Kira	Female	Adult	1.2	3093.75
27/07/2009	Kous-Kous	Male	Juvenile	1.5	702.08
19/07/2009	Lyle	Male	Adult	1.9	3180.37
09/08/2009	Lyle	Male	Adult	1.5	2215.33
26/09/2009	Lyle	Male	Adult	1	3050.60
15/07/2009	Zorro	Male	Juvenile	1.1	1486.19
26/09/2009	Zorro	Male	Juvenile	1	4374.23

Table A, B and C – The cortisol values extracted from the monkeys' faecal samples. Cortisol levels are expressed in ng of glucocorticoid metabolite (72T) per gram of faecal weight. Faecal glucocorticoid metabolite extracts were analysed for glucocorticoid immunoreactivity by using an 11-oxoaethiocholanolone enzyme immunoassay (Palme & Möstl 1997). The analyses were carried out in collaboration with the Physiology Institute of the Vienna Veterinary University.

Parasite estimates

1 - Picnic

Date	Id	Sex	Age	Weight (gr)	Strong.	Ascar.	Trichur.	spp.
07/07/2008	Drew	Female	Juvenile	0.75	0.00	13.33	33.33	2
21/10/2008	Drew	Female	Juvenile	0.60	0.00	0.00	0.00	0
13/09/2008	Francis	Male	Adult	0.41	0.00	0.00	0.00	0
10/10/2008	Francis	Male	Adult	0.65	0.00	0.00	0.00	0
14/07/2008	Gino	Male	Juvenile	0.42	0.00	0.00	0.00	0
14/10/2008	Gino	Male	Juvenile	0.61	0.00	0.00	8.20	1
03/07/2008	Gus	Female	Adult	0.65	0.00	0.00	30.77	1
26/07/2008	Gus	Female	Adult	0.50	0.00	0.00	20.00	1
05/07/2008	India	Female	Adult	0.57	0.00	0.00	35.09	1
25/07/2008	India	Female	Adult	0.57	0.00	0.00	35.09	1
14/07/2008	Isis	Female	Adult	0.51	0.00	0.00	19.61	1
25/07/2008	Isis	Female	Adult	0.72	0.00	13.89	6.94	2
14/07/2008	Nathan	Male	Juvenile	0.62	0.00	0.00	24.19	1
24/10/2008	Nathan	Male	Juvenile	0.60	8.33	0.00	25.00	2
05/07/2008	Neva	Female	Adult	0.43	0.00	0.00	0.00	0
19/07/2008	Neva	Female	Adult	0.61	0.00	0.00	0.00	0
03/07/2008	Nilou	Female	Juvenile	0.56	0.00	0.00	26.79	1
30/10/2008	Nilou	Female	Juvenile	0.55	0.00	9.09	9.09	2
07/07/2008	Yan	Male	Adult	0.56	8.93	26.79	0.00	2
26/07/2008	Yan	Male	Adult	0.69	0.00	14.49	14.49	2

2 - Donga

Date	Id	Sex	Age	Weight (gr)	Strong.	Ascar.	Trichur.	spp.
13/07/2009	Agathe	Female	Adult	0.95	0.00	31.58	0.00	1
17/07/2009	Aztec	Male	Adult	0.92	0.00	54.35	32.61	2
27/09/2009	Aztec	Male	Adult	0.64	0.00	23.44	23.44	2
07/08/2009	Beru	Male	Juvenile	0.91	0.00	16.48	0.00	1
21/09/2009	Beru	Male	Juvenile	0.66	0.00	7.58	0.00	1
07/08/2009	Boba	Female	Adult	1.02	0.00	0.00	0.00	0
09/09/2009	Boba	Female	Adult	0.55	0.00	9.09	0.00	1
26/07/2009	Hobbs	Male	Adult	0.87	0.00	63.22	0.00	1
19/09/2009	Hobbs	Male	Adult	0.69	0.00	7.25	0.00	1
16/07/2009	Jade	Female	Adult	0.89	0.00	5.62	0.00	1
09/09/2009	Jade	Female	Adult	0.86	0.00	5.81	0.00	1
24/07/2009	Lostris	Female	Adult	1.04	0.00	0.00	0.00	0
27/09/2009	Lostris	Female	Adult	0.85	0.00	0.00	0.00	0
25/07/2009	Lulu	Female	Juvenile	0.89	0.00	0.00	0.00	0
21/09/2009	Lulu	Female	Juvenile	0.66	0.00	0.00	7.58	1
16/07/2009	Obelixa	Female	Juvenile	1.12	0.00	0.00	0.00	0
16/07/2009	Oscar	Male	Juvenile	1.11	0.00	9.01	0.00	1
27/09/2009	Oscar	Male	Juvenile	0.77	0.00	19.48	0.00	1
07/08/2009	Ounooi	Female	Juvenile	0.80	0.00	12.50	6.25	2
28/09/2009	Ounooi	Female	Juvenile	0.50	10.00	10.00	0.00	2
28/09/2009	Samson	Male	Adult	0.74	0.00	6.76	0.00	1
20/07/2009	Samson	Male	Adult	0.68	7.35	14.71	0.00	2
09/07/2009	Wonka	Male	Adult	0.93	0.00	16.13	16.13	2
28/09/2009	Wonka	Male	Adult	0.67	0.00	14.93	7.46	2

C - Bay

Date	Id	Sex	Age	Weight (gr)	Strong.	Ascar.	Trichur.	spp.
13/09/2009	Dragon	Male	Juvenile	0.82	0.00	18.29	27.44	2
05/08/2009	Dumbo	Male	Juvenile	1.11	0.00	20.27	6.76	2
15/07/2009	Jacob	Male	Adult	0.85	0.00	17.65	0.00	1
10/08/2009	Jacob	Male	Adult	0.98	7.65	0.00	0.00	1
04/09/2009	Kephria	Female	Juvenile	0.80	0.00	0.00	0.00	0
26/09/2009	Kira	Female	Adult	0.55	0.00	0.00	0.00	0
15/07/2009	Kous-Kous	Male	Juvenile	0.58	0.00	12.93	12.93	2
27/07/2009	Kous-Kous	Male	Juvenile	0.83	0.00	0.00	0.00	0
19/07/2009	Lyle	Male	Adult	0.83	0.00	9.04	27.11	2
09/08/2009	Lyle	Male	Adult	0.91	0.00	0.00	24.73	1
26/09/2009	Lyle	Male	Adult	0.75	0.00	30.00	0.00	1
15/07/2009	Zorro	Male	Juvenile	1.00	0.00	0.00	7.50	1

Table A, B and C– The parasites' estimates calculated from the vervets' faecal samples. A total of 3 parasite types appear in these samples. All parasites have a direct life cycle. Two (an ascarid egg type and a trichurid egg type), have a life history where the hosts ingest eggs that contain embryos while eating contaminated foods, or while putting contaminated hands to their mouths. When the eggs are first shed in the faeces, they contain embryos that complete development outside under the right temperature and moisture conditions (Anderson 2000). Work in collaboration with the Center for Infectious Disease Dynamics from The Pennsylvania State University.

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Riccardo Pansini

Cooperation and economics behaviour of wild vervet monkeys: an experimental approach.

Thesis Abstract

A number of theoretical papers have investigated cooperation but only a very few studies have examined the evolution of cooperation in natural animal populations under experimental conditions. Over the course of three years, I performed field experiments with three groups of wild vervet monkeys (*Chlorocebus aethiops*) in South Africa. The experiments involved at least two or more individuals repeatedly operating feeder; that is to cooperate to get access to food. The purpose of the experiments was to test partner choice strategies and the modified social structure after the experiment.

The recurrent partner associations observed before the experiment only partly predicted the forming of cooperative partnerships during the experiment. Most subjects cooperated with specific and recurring combinations of partners. Interestingly sex, age and kinship did not explain the specific partner matching. Rather, higher ranking individuals cooperated with others higher ranking, and lower ranking ones with others of lower rank.

To test biological market theory models, I thereafter analysed whether the social networks modified because of the cooperation events. During the training phase, the monkeys became able to discriminate between the values of the contribution to the cooperation across classes. Because one social class was less numerous than the other, its members acquired a privileged status.

To test whether cooperation increases discrimination among group members I recommend the implementation of this experiment in the field with other primate species and other mammals.