

Direct and generalized reciprocity in the cooperative exchanges of free living *Rhesus macaques* on Cayo Santiago



Submitted by
William O'Hearn

To the University of Exeter as a thesis for the degree of
Masters by Research in Psychology
March 2019

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

Abstract

Direct reciprocity is the most cited explanation for the evolution of cooperation between unrelated individuals. Yet, few studies have examined generalized reciprocity as an alternative mechanism, despite generalized reciprocity's minimal cognitive demands and capacity to explain the same patterns of cooperation as direct reciprocity. Studies of direct reciprocity tend to explore reciprocal exchange across either individual interactions or long periods of time, rarely studying both at once. In addition, most studies of reciprocity only account for maternal relatedness between cooperative partners, failing to rule out the effect of kin selection through paternal relatedness. In this thesis we investigated the role of direct and generalized reciprocity in female rhesus macaque cooperative exchanges. We modified a classic playback experiment and explored the effect of both recent and repeated grooming interactions on females' willingness to provide coalitionary support to other adult females. We conducted this study using the rhesus macaques at the Cayo Santiago field station, where maternal and paternal relatedness is known for all study subjects. We found no evidence of direct or generalized reciprocity in the exchange of grooming for coalitionary support. Our results contradict the findings of similar playback experiments but are consistent with correlational studies in species that are despotic like rhesus macaques. The despotic nature of our study system, combined with our finding that females' willingness to provide support declined as the number of infants in their matriline increased, could suggest that grooming is not a sufficient price to pay to acquire coalitionary support from unrelated rhesus macaques. We propose by-product mutualism and kin-selection may play a larger role than has been previously appreciated in decisions regarding who to support in agnostic encounters, and we highlight the importance of investigating multiple cooperative mechanisms when studying of the evolution of cooperative behaviours.

Acknowledgments

This thesis would not have been possible without the efforts of a vast multitude of people.

I would like to thank my advisory team, Dr. Lauren Brent and Dr. Saffi Darden for the chance to be involved in this project, and for all of their advice and support throughout the many twisting paths this project took. I would like especially to thank Lauren for her patients during the many many times I walked into her office with a small question that turned into a 45-minute impromptu meeting. Few students of any kind are fortunate to have a teacher as giving as you.

A big thank you to my field assistant Emma McNamara for all of her help conducting an unforgiving and difficult playback experiment surrounded by often hostile monkeys. I would like to thank the team of research assistants on Cayo Santiago, Dany Phillips, Josue Negron, and Joel Glick that collected and continue to collect such excellent behavioural data. Also thank you to everyone at the Caribbean Primate Research Center for your help navigating Cayo and Puerto Rico in general.

I would like to extend a special thank you to my fellow post graduate students and research assistants on Cayo Santiago January to September 2017. Thank you, Sam Jackson, for keeping me sane by being insane. Thank you, Erica Dunayer, for your friendship and advice on how to be a good supervisor. Thank you, Christina Walker, Leah McCormick, Dave Massey, Jade Brooks, Francesca De Petrillo, and Madeleine Andrews, for your support, friendship and constant good cheer. And thank you to Bonn Aure and Nicole Compo for taking me into your respective homes in

each of the two hurricanes we weathered. Nicole thanks for helping me stay calm during the hurricane hangover after Maria.

I am grateful to everyone in the CRAB research group at Exeter for putting up with incessant questions about how to science. I greatly appreciate all of your attempts to educate me and your patients when it turned out to be harder than you thought. Thanks particularly to Dr. Sam Ellis for his counsel early on when I arrived without any idea what I was doing.

A big thanks to PhD office family that were my social fishbowl for a year and a half including Ellis, Sylvia, Pip, Chloe, Rachel, Christine, Kaitlyn, Andy, Katie, Theo, Paul and Michael for being there to talk out problems and solutions, complain about statistics and generally make the whole process seem more doable. Thanks especially to Michael Weiss for his statistical knowledge that he was ever willing to dole out when I was in trouble, accompanied by a sardonic wit.

Lastly, I am grateful to my friends and family who were willing to support me from across the pond while I completed my masters. Thank you as well to the friends I made in Exeter that made a year and a half fly by.

Table of Contents

Title Page.....	1
Abstract.....	2
Acknowledgments	3
Table of Contents	5
List of Figures.....	7
List of Tables.....	8
Author’s Declaration.....	9
Chapter 1: General Introduction	10
1.1 The Puzzle of Cooperation	10
1.2 Inclusive Fitness.....	10
1.3 Cooperation between Non-Kin: Direct Fitness Benefits	11
1.4.1 By-product Mutualism and Pseudo-reciprocity.....	12
1.4.2 Reciprocity	13
1.4.2.1 Direct Reciprocity.....	13
1.4.2.2 Indirect Reciprocity	15
1.4.2.3 Generalized Reciprocity.....	16
1.4.2.4 Comparing Reciprocal Mechanisms	18
1.4.2.5 Time Component of Reciprocity	19
1.5 Reciprocity in Non-Human Primates.....	20
1.6 Study System: Rhesus macaques	27
1.7 Study Goals	28
Chapter 2: Direct and generalized reciprocity in the cooperative exchanges of Rhesus macaques	30
2.1. Introduction	30

2.2 Methods.....	36
2.2.1 Study Site and Subjects.....	36
2.2.2 Determining Relatedness Between Subjects	38
2.2.3 Long-Term Behavioural Data.....	39
2.2.4 Call Collection	41
2.2.4.1 Stimuli Selection.....	42
2.2.4.2 Call Editing.....	43
2.2.5 Experimental Procedure	44
2.2.5.1 Measuring Responses to Playbacks.....	46
2.2.6 Experimental Conditions.....	49
2.2.7 Statistical Analyses	54
2.2.7.1 Comparing experimental conditions.....	54
2.2.7.2 Other Predictors	56
2.3 Results	63
2.3.1 Does recent grooming predict willingness to support?	63
2.3.2 Do past social relationships predict willingness to provide support?	67
2.4 Discussion	70
2.4.1 Summary of Findings	70
2.4.2 Does recent grooming predict willingness to provide support?	70
2.4.3 Do social interactions experienced over longer periods of time predict willingness to provide support?	76
Chapter 3: General Conclusion.....	82
References.....	86
Appendix.....	102

List of Figures

- Figure 2.1.** Examples of the five rhesus macaque recruitment call or scream classes.....- 43 -
- Figure 2.2.** Diagram of Condition Types.....- 51 -
- Figure 2.3.** Subjects' responses to playback stimulus plotted against the date of the playback trial across the study period.....- 59 -
- Figure 2.4.** Female's mean a) latency to look and b) duration of looking in the direct of the playback stimulus divided by condition types: Combined Grooming Condition (Groomed), Social Control Condition (Social), and Null Control Condition (Null)..- 64 -
- Figure 2.5.** Female's mean a) latency to look and b) duration of looking in the direction of the playback stimulus, divided by condition types: Direct Reciprocity Condition (Direct), Generalised Reciprocity Condition (General), Social Control Condition (Social), and Null Control Condition (Null).....- 66 -
- Figure 2.6.** Female's mean a) latency to look and b) duration of looking in the direct of the playback stimulus, divided by condition types: Long-Term Direct Reciprocity Condition (Long-Term Direct) and Null Control Condition (Null).....- 68 -

List of Tables

Table 2.1. Candidate models used to explore the relationship between trial date and latency to look.....- 60 -

Table 2.2. Candidate models used to test the relationship of trial date on the duration of looking.- 61 -

Table 2.3: Description of the predictor variables used to assess responses of female rhesus macaques to playback stimulus.....- 62 -

Table 2.4. Does recent grooming predict social response to vocal stimuli?.....- 64 -

Table 2.5. Does the identity of a recent grooming partner predict response to their vocal stimuli?- 66 -

Table 2.6. Does grooming history predict social response to a past partner's vocal stimuli?- 67 -

Author's Declaration

All chapters were written by William J O'Hearn with comments provided by Dr. Lauren Brent and Dr. Saffi Darden.

Experimental data collection was performed by William J O'Hearn, Emma McNamara, and Daniel Phillips. The long-term behavioural data was collected thanks to the hard work and dedication of Daniel Phillips, Jose Negron, and Joel Glick. The census and genetic database were created and maintained by the staff members of the Caribbean Primate Research Centre (CPRC).

Chapter 1: General Introduction

1.1 The Puzzle of Cooperation

A cooperative behaviour provides direct benefits to individuals other than the performer of the behaviour (West, Griffin, & Gardner, 2007). To explain the evolution of cooperative behaviours we must therefore ask why an individual would perform a behaviour for the benefit of another (Hamilton, 1964). Individuals that perform behaviours that only benefits others should experience reduced fitness and should, by consequence, be removed from the population by natural selection. Yet, this is not the case - cooperative behaviours are rife within the animal kingdom (Dugatkin, 1977). Understanding how cooperation evolved and is maintained in animal societies has thus resulted in more than a century of research (Dugatkin, 1977).

1.2 Inclusive Fitness

The first theoretical framework put forward to understand cooperation came from Hamilton's 1964 paper on inclusive fitness. Inclusive fitness theory states that there are two ways an animal's behaviour can result in fitness benefits: 1) it can act in manner that enhances its survival and reproductive success (direct fitness benefits), or 2) it can act in manner that results in the enhanced survival and reproductive success of those who share similar genes to the animal, thus increasing the prevalence of those genes in future generations (indirect fitness benefits). Indirect fitness is often referred to as kin selection because the simplest way to gain indirect fitness benefits is for an individual to provide assistance to related individuals (Maynard, 1964; West et al., 2007). Hamilton created a simple formula, referred to as Hamilton's Rule, for calculating how animals might accrue indirect fitness benefits. Hamilton's rule states that a behaviour will be favoured by selection when $rb > c$, where (r) is the degree of relatedness between the behaviour's actor and its

recipient, (b) is the behaviour's benefit to the recipient, and (c) is the behaviour's cost to the actor (Hamilton, 1964). Put more simply, cooperative behaviours will be favoured when the benefit to the recipient, weighted by the degree of relatedness between recipient and actor, is greater than the cost of the behaviour to the actor. Hamilton's rule predicts that cooperation between kin will be most common between partners with a high degree of relatedness (r), or when the cooperative behaviour provides a large fitness benefit (b) for a low fitness cost (c) (Hamilton, 1964). However, Hamilton's rule only provides a solution to the problem of cooperation between kin, cooperation between non-kin requires another set of solutions.

1.3 Cooperation between Non-Kin: Direct Fitness Benefits

Where cooperation between relatives can be somewhat costly to the actor, cooperation between non-relatives must be mutually beneficial to evolve. That is, actors who direct costly cooperative behaviours toward non-relatives must receive a fitness benefit above and beyond the cost of their original investment in return. The direct fitness benefits for non-kin cooperation fall into two main categories. The first category includes behaviours that benefit the actor automatically (by-product mutualism), or as a by-product of a recipient's self-interested act (pseudo-reciprocity) (West et al., 2007). The second category includes behaviours in which actors provide a costly benefit contingent on receiving a benefit of equal or greater magnitude in return (reciprocity) (West et al., 2007). Both categories are described in more detail below.

1.4.1 By-product Mutualism and Pseudo-reciprocity

By-product mutualism occurs when an individual receives a direct fitness benefit simply from being in the presence of other individuals performing self-serving behaviours (J. L. Brown, 1983; West-Eberhard, 1975). It is the “simplest” form of cooperation, requiring the fewest conditions to evolve (Clutton-Brock, 2009). By-product mutualism does not require kinship between actors, a facilitating group structure, or specific cognitive conditions (Clutton-Brock, 2009). Examples of by-product mutualism include cooperative hunting in African wild dogs and other canids, and group augmentation effects for territory defence like those found in meerkats (Clutton-Brock, 2002). Pseudo-reciprocity is similar to by-product mutualism and can be described as “investing in by-product mutualism.” In pseudo-reciprocity an actor performs a costly behaviour that promotes a recipient’s self-serving behaviour, which in turn benefits the original actor (Connor, 1986, 1995a; Leimar & Connor, 2003). For example, colonial nesting swallows that feed on difficult to track swarms of insects give out calls while feeding. These calls draw conspecifics to the swarms who in turn give their own feeding calls, allowing the first caller to track the swarm and increase their own feeding time (Brown, Brown, & Shaffer, 1991). As long as the returned benefit is greater than the initial investment, the cooperative behaviour will be favoured. It differs from by-product mutualism in that it requires a costly investment, and differs from reciprocity in that the recipient’s returned behaviour is self-serving and so guaranteed (Bergmüller, Johnstone, Russell, & Bshary, 2007; Leimar & Hammerstein, 2010).

1.4.2 Reciprocity

Although by-product mutualism and pseudo-reciprocity may be prevalent in nature, the explanation for cooperation between non-kin that has received by far the most attention and amassed the largest body of theoretical and empirical evidence is reciprocity (Clutton-Brock, 2009; West et al., 2007). Reciprocity involves a reciprocal exchange between two partners that take turns performing behaviours that are costly to the actor, but beneficial to the recipient. Reciprocity assumes that the benefits gained by the recipient are greater than the costs paid by the actor so that by taking turns, individuals balance the costs and benefits of the cooperative behaviour, overall leading to a gain in net benefits for both partners (Axelrod & Hamilton, 1981; Trivers, 1971).

The difference between reciprocity and other forms of cooperation is that the invested cost and returned benefit occur over two distinct behaviours, the first giving, the second receiving. This means that reciprocity almost always has a built-in time lag between invested cost and returned benefit that can be abused by cheaters. As a result, cooperation in reciprocal exchanges can only be maintained so long as animals have a way to select which partners to cooperate with, or a way of encouraging partners to be more cooperative (Clutton-Brock, 2009; West et al., 2007). Indeed, three main forms of reciprocity have been proposed, which differ in the criteria individuals use when deciding which individuals to cooperate with: direct, indirect, and generalized reciprocity.

1.4.2.1 Direct Reciprocity

In direct reciprocity individuals are more likely to cooperate with those that have cooperated with them in the past, following the simple rule “help those that

have helped you”. This form of reciprocity was first suggested by Robert Trivers in 1971 who gave it the name “reciprocal altruism.” This term is still widely used in the cooperation literature but has been the centre of debate for decades (for a full discussion see (Carter, 2014)), resulting in multiple terms referring to the same process: reciprocal altruism, reciprocal cooperation, contingent cooperation, and direct reciprocity. To avoid confusion, we will refer to this form of cooperation as direct reciprocity.

Since the inception of the theory there has been debate about the number of examples of direct reciprocity that exist in nature (Stevens & Hauser, 2004). Many examples of direct reciprocity have been presented. For example, humans reciprocate when they are the recipients of cooperative acts, and overtime build successful cooperative relationships (Melis & Semmann, 2010; Rand, Ohtsuki, & Nowak, 2009). Many non-human primate species appear to exchange grooming reciprocally between female partners (Schino & Aureli, 2008), and also to exchange grooming for other commodities, such as social tolerance (Tiddi et al., 2011), access to infants (Barrett et al., 1999b), and coalitionary support (Cheney, 1977; Cheney & Seyfarth, 1990; Seyfarth, 1980). Outside of primates, direct reciprocity has been used to explain blood donations in vampire bats (*Desmodus rotundus*) (Carter & Wilkinson, 2013), nest defence in pied fly-catchers (*Ficedula hypoleuca*) (Krams, Krama, & Igaune, 2008), sentinel behaviour in dwarf mongoose (*Helogale parvula*) (Kern & Radford, 2018), predator inspection in sticklebacks (*Gluteroneu aculeatus*) (Milinski, 1987), and turn-taking in migratory bird formations in northern bald ibis (*Geronticus eremita*) (Voelkl et al., 2015). The examples provided indicate direct reciprocity is present in exchanges of benefits between individual interactions (Majolo, Schino, & Aureli, 2012; Molesti & Majolo, 2017), but also across repeated

interactions with common partners (Schino, Di Sorrentino, & Tiddi, 2007; Schino & Pellegrini, 2009). However, some authors contend that direct reciprocity is unimportant outside of humans, pointing to a number of examples that have been contested and to the availability of alternative explanations (Dugatkin, 1977; Hammerstein, 2003). A commonly stated argument against direct reciprocity is that it requires complex cognitive processes (Stevens & Hauser, 2004). By which they mean that in order to perform direct reciprocity an animal must be able to identify individual groupmates, and keep track of the outcomes of past cooperative exchanges, which may be beyond the abilities of most non-human animals (Dugatkin, 1977; Stevens & Hauser, 2004). However, less cognitively demanding mechanisms by which direct reciprocity could be maintained have been proposed (Noë, 2006; Raihani & Bshary, 2011; Schino, Di Giuseppe, & Visalberghi, 2009) and the long list of reciprocal exchanges in nature that could represent direct reciprocity continues to grow (Schino & Aureli, 2009, 2010a, 2010b).

1.4.2.2 Indirect Reciprocity

The second form of reciprocity, indirect reciprocity, is based on the idea of reputation, where individuals use the rule “help those who help others.” In other words, individuals should be more likely to cooperate with a partner who has a history of cooperating with others (Bshary & Grutter, 2006; Leimar & Hammerstein, 2001; Nowak & Sigmund, 2005). Indirect reciprocity is advantageous because it can be used when animals lack first-hand experience with a potential partner but have observed that individual interacting with others (Nowak & Sigmund, 1998, 2005). Indirect reciprocity also incentivizes individuals to themselves be cooperative, because doing so increases the likelihood that others will select them as a future

cooperative partner (Nowak & Sigmund, 1998, 2005). Indirect reciprocity has been supported by theoretical evidence from game theory models under varied conditions (Nowak & Roch, 2007; Nowak & Sigmund, 2005), and by empirical evidence from humans, where reputation has been shown to promote cooperation (Sommerfeld, Krambeck, Semmann, & Milinski, 2007; Sylwester & Roberts, 2010), song sparrows (*Melospiza melodia*), which practice mutual restraint with territorial neighbours (Akçay, Reed, Campbell, Templeton, & Beecher, 2010), and from cleaner wrasse (*Labroides dimidiatus*), that modify their behaviour in the presence of an audience (Redouan Bshary, 2002).

1.4.2.3 Generalized Reciprocity

The third form of reciprocity is termed generalized reciprocity and can be described by the rule “help if you are helped.” Receiving cooperation should therefore make an individual more likely to cooperate with all others, including their most recent partner (Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005). Because it includes an actor’s most recent partner, generalized reciprocity therefore encompasses direct reciprocity (Hamilton & Taborsky, 2005; Nowak & Roch, 2007). While both direct and indirect reciprocity assume individual recognition and some tabulation of social exchanges, generalized reciprocity does not require either and individuals can base their decision to cooperate solely on the outcome of their last cooperative interaction. (Pfeiffer et al., 2005; Rankin & Taborsky, 2009). For this reason, generalized reciprocity is assumed to be less cognitively demanding than either direct or indirect reciprocity (Stevens & Hauser, 2004). Theoretical models have shown that generalized reciprocity is evolutionarily viable, demonstrating that stable levels of cooperation can be established when individuals choose whether or

not to cooperate based solely on the outcome of their most recent interaction, regardless of the identity of their present cooperative partner (Pfeiffer et al., 2005). These theoretical results have been supported by recent empirical evidence from laboratory-based experiments on humans and non-human animals. For example, a study of 4-year-old humans and capuchin monkeys (*Cebus apella*) found that individuals in both species paid forward the positive and negative outcomes of an identical testing apparatus (Leimgruber et al., 2014). Laboratory experiments using dogs (*Canis familiaris*), rats (*Rattus norvegicus*), and guppies (*Poecilia reticulata*), have also shown that individuals are more cooperative toward conspecifics after they receive cooperation themselves (Edenbrow et al., 2017; Gfrerer & Taborsky, 2017; Rutte & Taborsky, 2007, 2008). In addition to laboratory-based experimental work, a small number of observational studies have investigated generalized reciprocity in captive and wild primates. Two studies examining the reciprocal exchange of grooming for grooming in long-tailed (*Macaca fascicularis*) and Barbary macaques (*Macaca sylvanus*) (Majolo et al., 2012; Molesti & Majolo, 2017) as well as two studies examining the exchange of grooming for food in chimpanzees (*Pan troglodyte*) (Brosnan et al., 2009; De Waal, 1997) all found no evidence that generalized reciprocity was mediating cooperative exchanges. Although experimental evidence is the gold-standard of studies of cooperation – allowing causation to be distinguished from correlation – experimental studies of generalized reciprocity have thus far been limited to laboratory-based experiments, and thus whether or not generalised reciprocity exists in naturalistic systems amongst individual interacting spontaneously and repeatedly remains unclear.

1.4.2.4 Comparing Reciprocal Mechanisms

Direct, indirect and generalized reciprocity are not mutually exclusive. All three forms of reciprocity could theoretically be present in the same species and used in combination with one another. Actors could use past cooperative interactions with a partner to determine whether to cooperate with that partner again. But in the absence of past direct interaction, an actor could use social information to assess the reputation of a potential partner. Finally, in the absence of any information on a partner, an individual could choose to cooperate based on the outcome of their most recent cooperative interaction. Indeed, a small number of studies have compared multiple forms of reciprocity within a single study system. In chimpanzees, individuals that received grooming shared more food with their recent grooming partner, but not with any other groupmates (De Waal, 1997), suggesting exchanges operate according direct but not generalized reciprocity. Laboratory rats cooperated more towards known partners that previously cooperated with them compared to unknown partners that provided the same cooperation, suggesting that direct reciprocity generates more cooperative tendencies than generalized reciprocity (Rutte & Taborsky, 2008). A study of grooming patterns generated over three months of observations of long-tailed macaques found correlational evidence in support of direct reciprocity, weak evidence for indirect reciprocity, and no evidence for generalized reciprocity (Majolo et al., 2012). When the same researchers looked for short-term temporal relationships between grooming bouts they found evidence for direct but not indirect or generalized reciprocity (Molesti & Majolo, 2017). Overall, when comparing types of reciprocity in the same system, all studies to date found evidence of direct reciprocity, but no evidence of generalized or indirect reciprocity. However, this conclusion comes from the results of a handful of studies that are

either observational studies of spontaneous natural behaviour, or laboratory-based experiments of instrumental helping tasks. Future studies of reciprocity are therefore needed that investigate multiple forms of reciprocity use experimental methods in a single natural study system.

1.4.2.5 Time Component of Reciprocity

There are two times scales over which the exchange of behaviours via reciprocity can occur (three really – immediate exchange is the third). One incidence of cooperation can be followed by another after a short-term temporal period (a few minutes or hours) or can be separated by longer periods of time (a few days, weeks, months). Short- and long-term temporal scales manifest themselves differently in direct, indirect, and generalized reciprocity. In direct reciprocity based on short-term exchange, animals would be most likely to cooperate with their more recent cooperative partners, while in the long-term individuals would cooperate most often with partners that cooperate most with them. In the short-term, indirect reciprocity would be expected to result in animals that cooperate with the individual that cooperated with others most recently, and in the long term would result in individuals that cooperate most with individuals that provide the most cooperation overall. Finally, in the short-term, generalised reciprocity would be expected to result in animals that direct cooperation to a groupmate shortly after receiving cooperation, and in the long-term would be expected to result in the animals that receive the most cooperation overall would provide the most cooperation to others. Thus far, studies have investigated all three forms of reciprocity operating over short temporal periods (Bshary, 2002; Getty et al., 2004; Rutte & Taborsky, 2007), but only direct reciprocity has been examined to determine whether it operates over longer periods of

exchange (Schino & Aureli, 2010b). Future studies of reciprocity are therefore required that simultaneously examine the existence of multiple forms of reciprocity in the same study system, and that include exchanges of cooperative behaviours that occur over both short and long periods of time.

In this thesis, I investigate direct and generalized reciprocity expressed over both short and long periods of interaction. In particular, I examine the exchange of grooming for coalitionary support between adult female rhesus macaques. Below I provide a brief overview of reciprocity in non-human primates, outline previous evidence for the exchange of grooming for coalitionary support in non-human primate females, and provide a general description and justification for the use of the rhesus macaque as a study species in this context.

1.5 Reciprocity in Non-Human Primates

Group-living primates make especially excellent subjects for the study of reciprocity because they possess many of the characteristics required for reciprocity to evolve (Trivers, 1971). Primates recognize one another as individuals (Pfefferle, Ruiz-Lambides, & Widdig, 2015; Pfefferle, Ruiz-lambides, & Widdig, 2014; Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2001) and live in stable social groups where individuals interact repeatedly with their groupmates (Campbell, 2011). There is also evidence that group-living primates monitor the activities of their groupmates and modify their behaviours in response to that information (Fruteau, Voelkl, van Damme, & Noe, 2009; Pfefferle, Heistermann, Hodges, & Fischer, 2008).

Primates direct most cooperative behaviours towards their kin, but cooperation between non-kin has also been widely documented (Schino & Aureli, 2010b; Silk, 2005, 2013). Of the relatively large number of cooperative behaviours in

which non-human primates engage, two have received the most attention: allogrooming, hereafter called grooming, and coalitionary support (Silk, 2005).

Grooming is a behaviour performed by pairs of individuals where one partner picks through the fur of the other, removing dead skin, dirt, and parasites (Hutchins & Barash, 1976). It is the most common social behaviour in primates, comprising 20% of individuals' daily activity budget in some species (Dunbar, 1991). Grooming has played a central role in the study of reciprocity because it is unmistakable, easily documented, and has an inherent reciprocal structure; where individuals take turns repeatedly grooming one another within a single grooming bout (Brosnan & Waal, 2002; Cheney, 2011; Henzi & Barrett, 1999; R. Seyfarth, 1977; Silk, 1982; Wu et al., 2018).

One reason grooming has received so much attention in the study of reciprocity is that primates exchange grooming for a number of social currencies, such as food (De Waal, 1997), tolerance (Borgeaud & Bshary, 2015; Henzi & Barrett, 1999; Silk, 1982; Tiddi et al., 2011), and coalitionary support (Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; Hemelrijk, 1994; Palombit, Seyfarth, & Cheney, 1997). Of these, the exchange of coalitionary support for grooming has received the most attention, potentially as a result of the costly nature of coalitions. Coalitionary support occurs when an individual intervenes in on behalf of one of the participants in an agonistic conflict (Chapais, 1995). It is particularly costly because the supporting individual risks sustaining an injury or becoming a target of redirected aggression from the unsupported combatant (Chapais, 1995). This is particularly true in more despotic and aggressive species, where conflicts are more likely to escalate to physical violence (Chapais, 1992; Kaplan, 1978). Coalitionary support is found in a wide range of primate species [chimpanzees, *Pan troglodytes* (de Waal, 1982),

baboons *Papio ursinus* (Cheney, 1977), vervets *Cercopithecus aethiops*, (Horrocks & Hunte, 1983; Seyfarth & Cheney, 1984), and numerous species of macaque (Bernstein & Ehardt, 1985; Chapais, Girard, & Primi, 1991; Cords, 1988; Kaplan, 1978; Kurland, 1977; Massey, 1977; Silk, 1982)].

Indeed, the exchange of grooming for coalitionary support has been set forward as one of the main organising principles of primate social groups. In 1977, Robert Seyfarth proposed that highest-ranking primates are the most desirable coalition partners because they are more successful at winning conflicts. As a result, Seyfarth proposed that individuals groom their higher-ranking groupmates in exchange for coalitionary support (Seyfarth, 1977). Individuals closest in rank to one another would be most successful at competing for grooming access compared to females with greater distance between their ranks, leading to a pattern whereby animals of similar rank groom and support one another most often (Seyfarth, 1977). This model of organization in social primates, termed “the standard model”, has been highly influential because it makes specific predictions about social exchanges and their underlying mechanisms. The standard model predicts that low ranking individuals will provide more grooming than high ranking individuals and the grooming will be directed at females of a higher rank. It predicts that in exchange high ranking individuals will provide more coalitionary support than low ranking individuals and will direct that support towards females of lower rank. The standard model predicts that the exchange of grooming for coalitionary support is mediated by direct reciprocity, so females should be more likely to provide support to females that have groomed them.

A number of studies have tested the prediction laid out in the standard model, confirming that lower ranking individuals provide more grooming than high ranking

individuals and direct it up the hierarchy (Schino, 2001; Seyfarth, 1980; Silk, 1982; Tiddi et al., 2012; Wu et al., 2018), and that high-ranking individuals provide coalitionary support more often than low ranking individuals, and do so down the hierarchy (Schino, 2001; Silk, 1992; Silk, Alberts, & Altmann, 2004a). However, of the standard model's main predictions, the one that has been the most difficult to demonstrate is the exchange of grooming for coalitionary support by direct reciprocity.

The most consistent evidence that grooming is exchanged for coalitionary support comes from the correlational studies of long-term interactions. Many studies have found a positive within-dyad correlation between the amount of grooming and coalitionary support exhibited by pairs of individuals, which cannot be explained by covariation with rank or kinship [male bonnet macaques (*Macaca radiata*) (Silk, 1992) female Japanese macaques (Schino et al., 2007); male chimpanzees (Mitani, 2006) female vervet monkeys (Cheney & Seyfarth, 1990)]. In other words, these results show that individuals spend the most time grooming the individuals to which they provide coalitionary support and provide coalitionary support most often to those individuals with whom they groom. However, researchers have failed to find associations between grooming and coalitionary support in other studies [female bonnet macaques (Silk, 1982); female rhesus macaques (de Waal & Luttrell, 1986) female baboons (Silk et al., 2004a)]. A 2007 meta-analysis compiled the data of 25 grooming-for-support studies from 14 species and found weak evidence of a correlation between grooming and coalitionary support ($r = 0.166$) (Schino, 2007). When the analysis was limited to 9 studies that accounted for maternal relatedness between partners, either statistically or by excluding maternally related dyads, researchers still found evidence of a correlation ($r = 0.157$) between grooming and

coalitionary support (Schino, 2007). None of the studies included in the meta-analysis accounted for paternal relatedness between partners. Despite the empirical weight of this result, correlational studies cannot infer causal relationships. This study indicates that a relationship exists between grooming and coalitionary support, but it does not indicate whether reciprocity, by-product mutualism, or kin-selection through paternal relatedness is responsible for the relationship.

In contrast to the many observational studies of grooming and coalitionary support, only three experiments have investigated the influence of an individual receiving grooming on the likelihood that they provide coalitionary support. These three experiments represent the best evidence to date that the relationship between grooming and coalitionary support is based on direct reciprocity (Cheney et al., 2010; Hemelrijk, 1994; Seyfarth & Cheney, 1984). The first of these experiments is the classic playback study conducted by Seyfarth & Cheney (1984). In this study, conflicts between pairs of adult female vervets were simulated using previously recorded vervet monkey “chutters”, a call used by individuals to recruit coalitionary supporters during conflicts. The study measured females’ responses to recruitment calls played from a concealed speaker in one of two conditions. In the first condition, females were groomed shortly before hearing the recruitment call belonging to their most recent grooming partner. In the second condition, females had no prior interaction with the female whose call they were played. The amount of time females looked in the direction of the speaker was used as an indication of their willingness to provide coalitionary support to the caller. The results of this experiment showed that female vervet monkeys looked longer towards the recruitment call of a female to which they were maternally unrelated if that female had groomed them shortly before hearing the call, compared to the call of a female that had not recently groomed

them (Seyfarth & Cheney, 1984). This result led the study's authors to conclude that females were more willing to provide support to unrelated females that had recently groomed them (i.e., that direct reciprocity was the mechanism underpinning the exchange of grooming for coalitionary support).

A second study artificially induced grooming between unrelated adult female long-tailed macaques housed in groups of three, by smearing a sticky mixture of seeds and syrup on the back of one of the females. After recording which of the other two females groomed the syrup covered female, investigators induced a conflict by providing the females with small pieces of food and documented the formation of coalitions. The results of this study are in line with those of Seyfarth & Cheney (1984); females were significantly more likely to join coalition on the side of the female that had recently groomed them (Hemelrijk, 1994). This study has the advantage of measuring relationship between grooming and actual likelihood of support, as opposed to stand in measures like looking time, however, the conditions under which the animals provided support are far from their natural group-living setting where they have the option of multiple cooperative partners.

The third and most recent experimental study of grooming and coalitionary support was a replication of the 1984 playback experiment, this time with baboons (Cheney et al., 2010). This study also included an additional condition to control for the possibility that any prior interaction with a caller might affect a female's response to a subsequent recruitment call. In this experiment researchers played recruitment calls to a maternally unrelated female baboon shortly after either 1) no prior interaction with the caller, 2) a neutral interaction with the caller, or 3) receiving grooming from the caller. They also used whether or not females' first move was in the direct of the playback speaker as a measure of willingness to provide support,

instead of looking time. The results of this study confirmed the previous results in vervets, that females were more likely to approach the calls of recent unrelated grooming partners. The result indicates that not just any prior interaction with a caller primes females to respond more strongly to recruitment calls, but that grooming in particular caused the change in response (Cheney et al., 2010).

Together, these three experiments contribute substantial evidence that grooming is exchanged for coalitionary support through reciprocity. However, the results of these studies, and their implications, are not without limitations. Although these experiments demonstrate that reciprocity is the most likely mechanism underpinning the exchange of grooming for coalitionary support, they do not isolate the form of reciprocity is responsible. All three studies state the underlying mechanism to be direct reciprocity. However, generalized reciprocity can also explain instances of direct reciprocation (see section 1.4.2.3) and none of the three experiments rule out the possibility that females are simply providing coalitionary support to any groupmate after receiving grooming (Pfeiffer et al., 2005).

Additionally, in all three studies only maternal and not paternal relatedness of experimental partners was known. Paternal relatedness can drive kin selection in female old world monkeys (Widdig et al., 2001; Widdig, Nürnberg, Krawczak, & Streich, 2002). It is therefore possible that some experimental pairs in these studies were paternal relatives and their increased willingness to provide support could be based on kin selection rather than reciprocity.

Lastly, these experiments only investigate how female's willingness to provide support is affected by their most recent grooming interactions. It seems unlikely that a single instance of grooming would provide a sufficient benefit to warrant an exchange for coalitionary support. Instead repeated instances of grooming are likely

needed for a reciprocal exchange of the two behaviours. To better align with correlational studies that use longer-term data to investigate the relationship between grooming and coalitionary support, experimental studies should examine how repeated grooming interactions with a partner over time could affect a female's willingness to provide coalitionary support.

A true test of these experimental findings and Seyfarth 1977's proposed model of grooming-for-support would test both direct and generalized reciprocity as possible mechanisms in a study system with known paternal and maternal relatedness. Such a study would also investigate how receiving grooming affects female's willingness to provide support in the short-term as well as how repeated instances of grooming overtime affect willingness to provide support to a single grooming partner or members of a group as a whole.

1.6 Study System: Rhesus macaques

Rhesus macaques have been used in numerous past studies of reciprocity (de Waal & Luttrell, 1988; Kaplan, 1978; Kapsalis & Berman, 1996b). They possess many of the life-history characteristics that make cercopithecines ideal for studying cooperation. Rhesus macaques are female philopatric, live in large stable social groups with a female dominance hierarchy, and preform a range of cooperative social behaviours including grooming and coalitionary support (Campbell, 2011). They are also largely terrestrial, meaning their interactions are easily observable (Thierry, Singh, & Kaumanns, 2004).

Unlike many other old world monkeys, rhesus macaques possess an especially steep dominance hierarchy and are characterized by a despotic social structure in which rank plays an exaggerated role in individual's access to resources like mates and food (Flack & de Waal, 2004). In rhesus macaques holding a high

ranking in the dominance hierarchy is associated with a number of fitness benefits such as higher reproductive output, earlier maturation of offspring, increased infant survival, and a shorter interbirth periods (Blomquist, Sade, & Berard, 2011; Brent, Heilbronner, et al., 2013; Flack & de Waal, 2004; Silk, 1987). The exaggerated differences in rank related resources make rhesus macaques ideal for the testing the mechanisms that govern behavioural exchanges between individuals with unequal social capital, like the exchange of grooming for coalitionary support described in Seyfarth 1977's model.

1.7 Study Goals

Extensive research has been conducted into cooperation between non-relatives. The mechanism most widely posited to explain cooperation between non-relatives is reciprocity. But within reciprocity, research has been disproportionately focused on only one of the three possible forms, direct reciprocity, despite evidence that generalized and indirect reciprocity are evolutionarily viable (Nowak & Sigmund, 1998; Pfeiffer et al., 2005). Studies of reciprocity have also tended to focus on either long- or short-term patterns of cooperative exchange, rarely taking both patterns into consideration within a single study system. Lastly, studies of reciprocity have failed to sufficiently rule out the role of kin selection because few studies have information on full degree of relatedness between study subjects (Clutton-Brock, 2009; Stuart A. West et al., 2007; Widdig et al., 2001).

The aim of this study is to modify the classic Seyfarth & Cheney 1984 playback experiment to test for the presence of both direct and generalized reciprocity in the exchange of grooming for coalitionary support in the rhesus macaques living on Cayo Santiago island. Our experiment will test the impact of

recent grooming, as well as the effect of grooming interactions over extended periods, on adult females' willingness to provide support to unrelated adult females.

We take advantage of the Cayo Santiago long-term pedigree, which provides full genetic relatedness of all dyads in the population stretching back to 1992 based on 29 micro-satellite DNA markers from blood samples (Widdig et al., 2016). Our experimental dyads can thus be restricted to maternally and paternally unrelated animals. This study will also provide the first experimental test of generalized reciprocity outside of a laboratory setting.

Chapter 2: Direct and generalized reciprocity in the cooperative exchanges of *Rhesus macaques*

2.1. Introduction

Cooperative behaviours, that is behaviours that evolved as a consequence of the benefits they provide to the recipient of the behaviour, are widespread among animals (Stuart A. West et al., 2007). Cooperative behaviours between relatives can be explained by kin selection (W. D. Hamilton, 1964), but cooperation between non-relatives is a long standing evolutionary mystery (West et al., 2007). One of the main explanations proposed for the evolution of cooperation between non-relatives is direct reciprocity, where individuals cooperate with those partners that have cooperated with them in the past (Axelrod & Hamilton, 1981; Trivers, 1971). By taking turns performing and receiving the cooperative behaviours, both partners receive the benefits of the cooperation, thus re-cooping the costs of their initial investments (Axelrod & Hamilton, 1981; Trivers, 1971). Yet, despite 40 years of research, relatively few examples of direct reciprocity have been documented. Moreover, many of the previously proposed cases have been contested (Hart & Hart, 1992; Krams, Krama, & Igaune, 2008; Milinski, 1987; Packer, 1977; Wilkinson, 1984). As an example, some cooperative behaviours initially described as direct reciprocity have since been shown to provide benefits, rather than costs, to the actor, giving rise to the possibility that other mechanisms might be responsible for their maintenance, such as by-product mutualism or low-cost altruism in “service economies” (Bercovitch, 1988; Clutton-Brock, 2009; Connor, 1995b; Noë & Hammerstein, 1994). Concerns have also been raised about the cognitive capacities required to perform direct reciprocity, with doubts as to whether animals are capable of performing the mental bookkeeping required to cooperate only with past

cooperators (Stevens & Hauser, 2004). In response to these doubts, some researchers suggest that animals could use simpler cognitive mechanisms (e.g., ‘emotional bookkeeping’) to perform direct reciprocity (Aureli & Schaffner, 2002). The absence of direct reciprocity could also suggest that the mechanism is simply rare or non-existent. In this case, alternative mechanisms to explain the maintenance of observed cooperative behaviours is required. Other such mechanisms have been proposed. However, few studies have examined these alternatives.

One simpler alternative to direct reciprocity is generalised reciprocity. Generalised reciprocity occurs when individuals cooperate with anyone if they have previously received cooperation from anyone; operating on the simple rule “help if you are helped” (Pfeiffer et al., 2005). To engage in generalised reciprocity, animals need only to recall the outcome of their most recent interaction, making it cognitively simpler than direct reciprocity (Rankin & Taborsky, 2009). Generalised reciprocity is an evolutionarily stable strategy (Pfeiffer et al., 2005) that has been shown to play a role in helping behaviours in lab-based experiments using rats (*Rattus norvegicus*), dogs (*Canis familiaris*) and humans (*Homo sapien*) (Emmons & McCullough, 2004; Gfrerer & Taborsky, 2018; Monica Y. & David, 2006; Rutte & Taborsky, 2007). In addition to its relative cognitive simplicity, generalised reciprocity has appealingly broad explanatory power – an individual cooperating on the basis of generalised reciprocity can direct their cooperation to any other individual, including the individual that originally provided the cooperation being reciprocated. In this way, generalised reciprocity can account for the same patterns of cooperation proposed by direct reciprocity. However, despite addressing doubts of cognitive requirements and its ability to account for patterns that have been previously attributed to direct reciprocity, generalised reciprocity has rarely been experimentally tested outside of a

laboratory setting. Few natural systems possess the circumstances needed to test generalised reciprocity: group-living animals that can cooperate with partners of known relatedness, such that the influence of kin selection can be ruled out.

One clade of animals where individuals have access and opportunity to cooperate with numerous partners are non-human primates. Many primates are gregarious, group-living animals that cooperate repeatedly, making them appropriate candidates for studying reciprocity. Primates, particularly Old World monkeys, spend large portions of their daily activity budget picking through the fur of groupmates, removing dirt and parasites in a behaviour called allogrooming (hereafter called grooming) (Hutchins & Barash, 1976). In many primate species, individuals intervene in agonistic encounters, forming an alliance with one combatant against the other, in a behaviour referred to as coalitionary support (Bernstein & Ehardt, 1985). Grooming and coalitionary support are each examples of cooperative behaviours and have been central to cooperative research in primates (Silk, 2005). Both behaviours are most commonly directed at relatives, suggesting that kin selection partly explains the evolution of these behaviours (Schino & Aureli, 2010b). Conversely, exchanges of grooming and coalitionary support are also common between non-relatives, raising the possibility that reciprocity may also maintain these interactions in primate populations (Chapais, 1995; Silk, 2002).

Indeed, the exchange of grooming for coalitionary support through direct reciprocity has been proposed as a central organizing principle in primate social groups. After observing that grooming between many female primates is directed towards a group's high-ranking females, Seyfarth (1977) proposed that females groom up the dominance hierarchy in exchange for benefits that high-ranking females could best provide. High-ranking females make the best coalition partners

because they are more successful in winning conflicts (Kaplan, 1978; Massey, 1977; Silk, 1992). Evidence from subsequent studies of social exchanges in primate groups support two central claims of Seyfarth's "grooming-for-support" model – confirming that females' grooming is directed up the hierarchy (Schino, 2001), and that low-ranking females provide more grooming than those of higher ranks (Chapais, 1983; Chapais et al., 1991). However, Seyfarth's third prediction – that grooming is reciprocally exchanged for coalitionary support – has proven more difficult to demonstrate. Several observational studies have explored the relationship between grooming and coalitionary support in a number of primate species, with mixed results (Kaplan, 1978; Matheson & Bernstein, 2000; Silk, 1992; Silk, Alberts, & Altmann, 2004b). A meta-analysis of 36 grooming-for-support studies found a significant positive relationship between grooming and coalitionary support that could not be explained by kinship in 14 primates species (Schino, 2007). These results suggest that pairs of individuals that frequently exchange grooming also frequently exchange coalitionary support. While robust, the result of this meta-analysis is only correlational in nature, and thus does not causally link grooming and coalitionary support. Experimental manipulation of one or both behaviours are thus necessary to determine if grooming does, in fact, gives rise to coalitionary support in female primates.

To date, two playback experiments have tested the relationship between grooming and coalitionary support. In the first of these experiments, researchers played previously recorded "chutter" calls, used to solicit support in conflicts, to wild female vervet monkeys (*Chlorocebus pygerythrus*) in one of two conditions: 1) when the subject hearing the call had recently been groomed by the call's owner or 2) after a period where the subject had received no grooming (Seyfarth & Cheney, 1984).

This study found that when the caller was unrelated, subjects looked in the direction of the playback speaker for a longer period of time if the caller had recently groomed them (Seyfarth & Cheney, 1984). This was not observed when subject and caller were maternally related – subjects looked for the same amount of time under both conditions (Seyfarth & Cheney, 1984). From these results, Seyfarth & Cheney (1984) concluded that being groomed by an unrelated female increases the willingness of the groomed female to provide support in the groomer's next conflict. A replication of this experiment in wild baboons (*Papio hamadryas ursinus*) found the same result: females were more likely to approach the source of a call soliciting aid if they had recently been groomed by an unrelated caller (Cheney et al., 2010). In this iteration of the experiment a third condition was added, in which the subject was aggressed by the caller prior to hearing their call. Individuals were not more likely to approach the call's source in this condition, leading researchers to the conclusion that grooming in particular, and not simply any prior interaction between callers and subjects, increased an individual's willingness to provide coalitionary support (Cheney et al., 2010).

Together, the above experiments in Vervet monkeys and baboons provide evidence supporting a causal link between receiving grooming and providing coalitionary support in female Old-World monkeys. However, as is the case for all correlational studies of grooming-for-support, only the maternal relatedness of experimental dyads was known in these experiments. Paternal relatedness can also drive kin-selection: it has been shown that female cercopithecines are more likely to engage in affiliative behaviour with paternal relatives than non-kin (Widdig et al., 2001). To fully remove the possibility that the observed relationship between

grooming and coalitionary support is not being driven by kin selection, a system where both maternal and paternal relatedness can be accounted for is required.

In addition to possessing incomplete knowledge of dyad relatedness, previous studies investigating the relationship between grooming and coalitionary support tend to only examine direct reciprocity, despite the possibility that generalised reciprocity can account for the same patterns of interaction (Pfeiffer et al., 2005). Experimental tests of the relationship between grooming and coalitionary support have also only considered the exchange of cooperative behaviours on a short-term interaction-to-interaction basis, not taking into account how relationships based on past interactions might affect an individual's willingness to provide coalitionary support. However, long-term relationships might be instrumental in understanding reciprocal exchanges. There is limited evidence that individuals exchange benefits equally between individual interactions. In contrast studies have shown that over the course of repeated interactions, the exchange of benefits between cooperative partners are more balanced (Gomes et al., 2009; Schino & Pellegrini, 2009; Silk & Frank, 2009). Some researchers propose this is because the likelihood of two individuals cooperating is influenced by the partners' history of interactions, which cannot be outweighed by a single interaction (Schino & Aureli, 2010a; Schino & Pellegrini, 2009). Long-term patterns of interaction can also be applied to cooperation by generalised reciprocity, where an individual's likelihood of cooperating is influenced by the amount of cooperation they have received from their group as a whole. In this case, the long-term accumulation of interactions is with the entire group, not an individual, and single recent interactions can affect, but not necessarily outweigh, the grooming received over time from the group. What is needed to better understand the relationship between grooming and coalitionary

support is an experimental study that can account for the effects of both maternal and paternal relatedness, and that examines the exchange of grooming for coalitionary support for evidence of both direct and generalised reciprocity.

In the current study, we investigate the exchange of grooming for coalitionary support between females in a population of free-ranging rhesus macaques. In this population, an in-depth genetic pedigree yields information on both maternal and paternal relatedness for all animals, allowing any effects of kin selection to be accounted for. We modify the playback experiments conducted by Seyfarth & Cheney (1984 and 2010) to examine both direct and generalised reciprocity as potential mechanisms for the maintenance of cooperative exchanges, and we explore the influence of both short-term and long-term (accumulative) grooming interactions on individual's willingness to support others. We ask four research questions: 1) Are female rhesus macaques more willing to provide coalitionary support after being groomed? (i.e., short-term generalised reciprocity); 2) Are female rhesus macaques more willing to provide coalitionary support to a recent grooming partner? (i.e., short-term direct reciprocity); 3) Are female rhesus macaques more willing to provide coalitionary support to past grooming partners? (i.e., long-term direct reciprocity); 4) Are female rhesus macaques more willing to provide coalitionary support if they receive more grooming from their group as a whole? (i.e., long-term generalised reciprocity).

2.2 Methods

2.2.1 Study Site and Subjects

We conducted this research at the Cayo Santiago Field Station, a 35-acre island off the southeast coast of Puerto Rico. The site's monkey colony has been

studied since it was established in 1938 with a founding population of 400 Indian-origin rhesus macaques (*Macaca mulatta*) (Kessler & Rawlins, 1986). At the time of this study, there were approximately 1600 individuals living on the island in six distinct social groups. Each monkey is identifiable from a unique set of ear notches and an assigned three-character letter number combination, which is tattooed on their chest and inner left thigh. The ear notches and tattoos are administered at the age of 1 year by the trained staff of the Caribbean Primate Research Centre (CPRC). The island's monkeys are habituated to humans and have participated in numerous past experiments, including playback experiments (S. Gouzoules, Gouzoules, & Marler, 1984; Hauser, 1998; D. Rendall, Rodman, & Emond, 1996; Rosati, Arre, Platt, & Santos, 2016)

Our study focused on adult females (> 6 years of age: Brent, Heilbronner, et al., 2013) from a single social group: Group "F". We used adult female as subjects because coalitionary support occurs most frequently between the females of this species (Kaplan, 1978). At the time of this study, Group F was the largest social group on the island, comprised of 250 individuals with 81 adult females.

We conducted this study in two phases. First, we recorded vocalizations during the mating season (January - May 2017) when female-female conflicts and their associated calls are mostly likely to occur (Gouzoules, Gouzoules, & Marler, 1984; Le Prell et al., 2002; Rendall, Rodman, & Emond, 1996). Second, we conducted the playback experiment between May and September 2017, coinciding with the annual birthing season, when females give birth to and care for dependent offspring (Brent, MacLarnon, Platt, & Semple, 2013).

2.2.2 Determining Relatedness Between Subjects

Long-term data on relatedness were available for all study subjects from the Caribbean Primate Research Center (CPRC). These data include a maternal pedigree based on observed births that stretches back to the founding members of the population and genetic data collected since 1992, which includes known dam and sire for all study subjects using 29 microsatellite markers derived from DNA extracted from blood samples (Widdig et al., 2016). Pairs of animals included in this study were unrelated along both maternal and paternal lines. In keeping with prior playback studies on cercopithecines, we considered females to be unrelated if their coefficient of relatedness (r) was < 0.125 (Seyfarth & Cheney, 1984; Silk et al., 2010; Silk, Altmann, & Alberts, 2006). This cut-off is also in agreement with what is known of rhesus macaque's capacity to differentiate between degrees of maternal relatedness: a study of patterns of affiliation on Cayo Santiago found that females behaved as though they could differentiate between degrees of closely related kin, but treated distant kin ($r < 0.125$) the same as non-kin (Kapsalis & Berman, 1996a). The mean relatedness between pairs in our experiment was $r = 0.025 \pm 0.04$. We aimed only to test experimental dyads that were less than $r = 0.125$ related to one another, but two more closely related pairs were tested in error ($r = 0.254$ and 0.187 , trials 15 and 18). These both occurred as part of our social control condition and were within one standard deviation of the mean latency to look and duration of looking values for trials of that control type (mean latency = 47.41 ± 39.7 frames; mean duration = 100.77 ± 92.48 frames; Trial 15: Latency = 15 frames, Duration = 90 frames; Trial 18: Latency = 17 frames, Duration = 123 frames). Moreover, removing these data points did not alter our results so we retained them in the final analysis.

2.2.3 Long-Term Behavioural Data

We used long-term behavioural data to establish the strengths of grooming relationships between female dyads and to determine individual dominance ranks. Behavioural data were collected as part of a large on-going effort to investigate social processes in the Cayo Santiago rhesus macaques, led by Lauren Brent. Data were collected using 10-minute continuous focal animal samples (Altmann, 1974) using Psion handheld computer in conjunction with Noldus Observer Software. During each focal animal sample, all affiliative and agonistic interactions involving the focal individual were recorded, as well as the identity of any social partners. A total of 300 hours of focal animal samples were conducted on Group F females in 2017 by a team of dedicated field assistants. This information was used to establish the strengths of grooming relationships between female dyads and to determine individual dominance ranks.

2.2.3.1 Determining Dominance Rank

Rhesus macaque dominance hierarchies are linear and transitive, meaning if animal A outranks animal B, and animal B outranks animal C, then animal A also outranks animal C. Males and females have separate hierarchies within a group, with all males are dominant to all females (Strier, 2011). Females are the philopatric sex and their ranks are maternally inherited. That is, a female acquires the rank just below her mother. Subsequent sisters will acquire the rank just below their mother so younger siblings outrank their older sisters (Strier, 2011). Closely related females therefore tend to occupy similar ranks. As a result of maternal rank inheritance,

female ranks are relatively stable over the course of a female's lifetime (Silk et al., 2010).

To determine dominance ranks of our study subjects, we used two types of data: ad libitum observations collected opportunistically, and continuous data collected during focal animal samples. We used aggressive and submissive interactions between pairs of females with clear winners and losers as indicators of their dominance relationships. For example, 64P submitting to 0G5 would indicate that 0G5 is dominant to 64P.

2.2.3.2 Grooming Relationships

To determine which dyads exchanged grooming in the year we conducted our experiment, we calculated a dyadic sociality index (DSI) for every adult female dyad in group F in 2017 using the following formula from Silk et al., 2006:

Equation EQ1.
$$G_{ij}/G_{fy}$$

Where G_{ij} is the frequency of grooming (seconds per hour observed) between dyad i and j , divided by the mean adjusted frequency of grooming for all dyads of group f in year y . The DSI is an indicator of the relative amount of grooming exchanged by a given dyad, where high values indicated dyads that performed more grooming than the average dyad in the group and low values represented dyads that performed less grooming than average. We used grooming data collected during continuous focal animal samples. The same number of focal animal samples are collected for each female in group F, so the observation effort is uniform, and individuals have equal opportunity to be observed grooming.

Pairs of individuals with a DSI value of zero were used as subjects and callers in our null control condition, which stipulated that the caller, the individual whose call is played as a stimulus, cannot have groomed the subject, the individual that hears the stimulus, within the last year. Dyads with a DSI greater than zero were used as subject and caller pairs in our “long-term direct reciprocity condition”, which required the caller to have groomed the subject in the past year. In 10 out of our 11 long-term direct reciprocity condition trials the subject-caller pair had DSI values in the upper 50% of all dyads.

2.2.4 Call Collection

Vocalizations were collected opportunistically throughout the day to maximize the diversity of female callers and the number of calls collected. All vocalizations were recorded on a Marantz PMD661MKII Portable Digital Solid-State Sound Recorder using a Sennheiser directional microphone (MKH 416-P48U3 with a windscreen). The distance between the caller and the microphone was an average of $9.2 \text{ m} \pm 4.8$. We used a handheld sound pressure level meter (Peak Meter MS6708 Digital SLM) to record the intensity of vocalizations. After recording each vocalization, we recorded observational commentary using an Olympus WS-852 digital voice recorder including: the identity of the caller; the identity or age/sex class of the participant(s) in the event precipitating the vocalization; the behaviour of participant(s) in the event; the intensity of the vocalization; and the distance from the microphone to the caller.

2.2.4.1 Stimuli Selection

All vocalizations were transferred to a Mac Book Pro for stimulus selection. Vocalizations used in our playback experiment were recruitment calls, which rhesus macaques use to recruit support from groupmates in conflicts against conspecifics (Gouzoules & Gouzoules, 2000; Gouzoules, Gouzoules, & Tomaszycki, 1998; Gouzoules et al., 1984). Past research has identified five types of recruitment calls used by rhesus macaques, used in different circumstances based on the relative rank of the opposing combatant, relatedness between combatants, and the severity of the conflict (physical or non-physical) (Gouzoules et al., 1984) (Figure 2.1). For our playback experiment, we used only “noisy screams”, which are typically used in physical conflicts with higher ranking, unrelated, groupmates (Gouzoules et al., 1984). Noisy screams are the most commonly used recruitment call in rhesus macaques, comprising 42% of vocalizations in conflicts (Gouzoules et al., 1984). They also represent the most serious form of agonistic threat to individuals and often elicit the quickest and longest reaction from conspecifics (Gouzoules et al., 1984). Past research on the patterns of coalitionary support in Cayo Santiago rhesus macaques also found that individuals intervened in conflicts on the side of “victims” most often when the conflict was serious and involved biting (Kaplan, 1978). Noisy screams thus give the best chance of individuals responding to our playback stimuli.

Prospective vocalizations were visualized as spectrograms in PRAAT 6.0.2. Spectrograms were visually assessed for the acoustic features of noisy screams, which are characteristically atonal with a wide bandwidth, often containing a region of dense energy between 2500 and 3000hz. Noisy screams can vary between 0.5 and 1.5 seconds per scream and come in highly varied bouts of one to thirty

screams (S. Gouzoules et al., 1984). Vocalizations identified as noisy screams were cut from our recordings to be processed into playback stimuli.

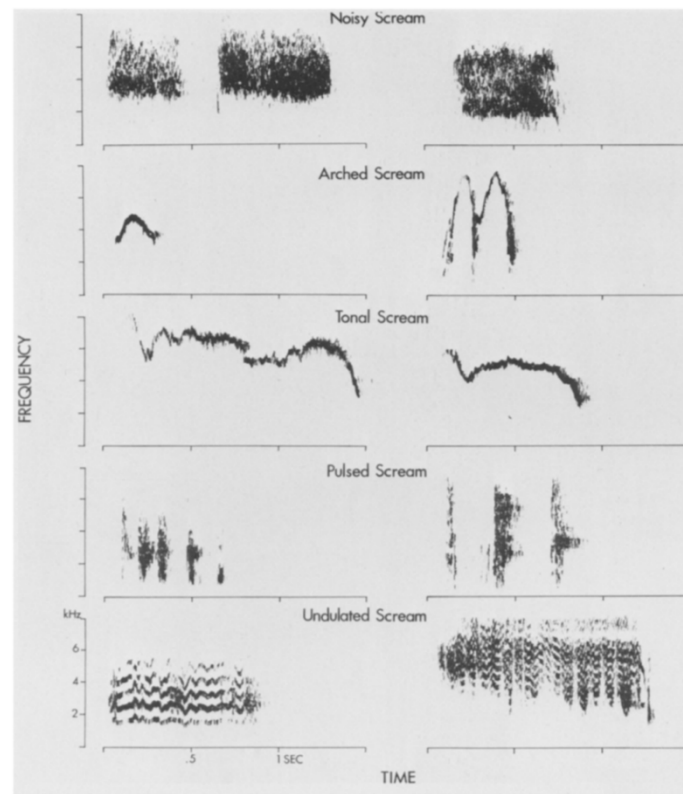


Figure 2.1. *Examples of the five recruitment call or scream classes identified by Gouzoules, Gouzoules, & Marler in 1984: noisy, arched, tonal pulsed, undulated. Screams are shown as spectrograms with each tick representing 1000 Hz. Image was taken from (Gouzoules, Gouzoules, & Marler, 1984).*

2.2.4.2 Call Editing

We used the audio editing program Audacity 2.1.0 to prepare our recruitment call stimulus. Environmental noises that did not overlap with the noisy scream recruitment calls were removed, along with any artificial sounds at onset and offset of the recording. This process generated stimuli that had a high signal-to-noise ratio. Calls were also digitally normalized to a standard intensity to ensure each stimulus was the same volume when played through a speaker. Previous playback experiments have found that recruitment calls containing more than ten scream bouts provoke rhesus macaques to charge in the direction of the playback setup,

resulting in subjects discovering the playback speaker and invalidating the trial (Gouzoules et al., 1984). Other studies have found that macaques can distinguish caller identity from short bouts containing only three screams (Fugate, Gouzoules, & Nygaard, 2008), and there is substantial evidence to suggest that rhesus macaques can identify individuals from their screams alone (Fugate et al., 2008; Gouzoules et al., 1998; Owren & Rendall, 2003; Rendall et al., 1996; Rendall, Owren, & Rodman, 1998). Based on these results, we selected a standard stimulus length of 5-8 scream bouts per recruitment call (mean of 6.47 ± 1.35 scream bouts) resulting in a mean stimulus length of $4.95 \text{ s} \pm 1.69$ seconds. We cut the full-length screams to the above sizes and added 1 second of silence before and 10s of silence after the recruitment call. These intervals of silence enabled us to avoid playing the wrong scream or to accidentally play a second scream immediately following the first.

2.2.5 Experimental Procedure

We conducted all playback experiments using an iPhone 6 connected with a 20m cable to a Mipro MA-707 portable speaker. All stimuli were played such that a subject sitting 10 meters from the speaker would hear them at the same ideal call intensity, which was set as the mean intensity of all calls collected at 10m: 70 dB (± 3.2). Speaker volume was adjusted to maintain the ideal call intensity based on three conditions: 1) the micro-habitat type of the trial area, 2) the amount of wind noise at the time, 3) the distance from the speaker to the subject. The volume settings for each combination of conditions were previously determined using a portable sound level meter to test the intensity of recruitment calls at standard distances (5m, 10m, 15m) in each of the island's microhabitat types (mangroves, open grasslands, open

forest, dense forest, open hillside), and in varying degrees of wind noise (estimated in knots).

The speaker was concealed as close to 90° to the side of the study subject as the environment would allow, with a mean distance of 10m (\pm 2.2) from the subject. One experimenter concealed the speaker and positioned themselves at least 10m from the speaker in a location out of the subjects line of sight to avoid the monkeys associating them with the speaker or its location. A second experimenter used a video camera placed directly in front of the subject at an average distance of 8m (\pm 0.82) to record the subject's response. Trials were conducted when the monkey whose call was to be played was more than 50m away or out of sight. The playback subject also had to be settled; not engaging in potentially distracting activities like feeding or sleeping. The stimulus was played when the subject was looking away from the speaker's location. This was done to make the subject's orientation toward the speaker when the call was played more obvious to experimenters. We recorded the subject's behaviour for 20 seconds before and one minute after the stimulus was played. After the trial was completed, we recorded the date, time, location on the island, microhabitat type, amount of wind, number and identity of individuals within 10m of the subject and the subject's behaviour before and after the trial. We also drew a map including the location, orientation, and identity of the subject, as well as the location and distance to the speaker, camera, and any vegetation.

The following precautions were taken to minimize habituation to the playback procedure: (1) no more than 2 trials we conducted per day; (2) a stimulus, once played, was not replayed for a month; (3) a single stimulus was not played more than three times total over the course of the experiment; (4) we conducted three "mock trials" for every experimental trial, in which observers and equipment were put in

place but no stimulus was played; (5) individual were never used as a subject more than once for any given experimental condition or control; and (6) combinations of subject and caller were never used more than once.

2.2.5.1 Measuring Responses to Playbacks

Video recordings were analysed frame by frame with a 30 frames per second (fps) frame rate, using the behaviour coding software BORIS 6.3.. In order to avoid ambiguity in scoring responses, we defined “looking in the direction of the speaker” as a subject facing within 10° of the speaker’s location. The angle of the speaker’s location relative to the camera accompanied each video file as well as any notes pertaining to the height of the speaker’s location relative to the subject, i.e., 5° above line of sight. We assembled a database of 72 photos of a monkey facing towards each 5° interval of 360° to reference for facial orientation while scoring videos. A video coder blind to the condition type watched each video and assessed the angle at which the subject was looking in each frame. If the scorer determined that the subject was looking within 10° of the speaker’s location, they would score the frame as “looking” and note the angle of the subject’s gaze.

To assess interobserver reliability, a second observer, also blind to experimental condition, scored each frame of a randomly selected subset (20%) of all videos. Interobserver reliability was calculated using Cohen’s *K*. The value of *K* was 0.67, which corresponds to 90% agreement (McHugh, 2012).

We used the data collected in video coding to create two measures of subjects’ responses to stimuli. We had two independent response variables: latency to look and duration of looking. Latency to look was measured as the number of frames between the onset of the stimulus (the call from the speaker) and the

subject's orientation to the direction of the speaker. Duration of looking was measured as the number of frames spent looking in the direction of the speaker in the 20 seconds following the onset of the stimulus minus the number of frames spent looking in the direction of the speaker in the 20 seconds preceding the onset of the stimulus. This adjustment was made to account for the baseline amount of time subjects spent looking in the direction of the speaker. No subjects were observed approaching the speaker during or after a trial.

We used latency to look and duration of looking because they are the most commonly used measures of response strength in the primate playback literature. Duration of looking, often called looking time or response duration, is used as the primary measure of attention to a stimulus in many primate playback studies (Cheney & Seyfarth, 1980, 1982; Cheney, Seyfarth, & Silk, 1995; Fischer, 2004; Fischer, Metz, Cheney, & Seyfarth, 2001; Gouzoules et al., 1984; Hauser, 1998; Lemasson, Palombit, & Jubin, 2008; Palombit, Seyfarth, & Cheney, 1997; Rendall et al., 1996; Seyfarth & Cheney, 1984; Slocombe, Townsend, & Zuberbühler, 2009). There are principally two drivers of duration of looking: the importance of a given stimulus, and its novelty, which, in some cases, may work in opposing directions (Fischer, Noser, & Hammerschmidt, 2013). Animals are expected to look longer at a stimulus of greater social import, such as looking longer in the direction of a vocalization made by a relative compared to that of a non-relative (Pfefferle, Ruiz-lambides, & Widdig, 2014). Animals are similarly expected to look longer at novel or unexpected stimuli compared with routine stimuli (Cheney et al., 1995; Onishi and Baillargeon, 2005; Slocombe et al., 2009). The dual nature of duration of looking means that interpretation is potentially troublesome if both novelty and social importance are both present in a single experimental design.

Latency to look is widely used as a measure of response, often in conjunction with duration of looking (Cheney & Seyfarth, 1980, 1982; Fischer, 2004; Fischer et al., 2001; Gouzoules et al., 1984; Lemasson et al., 2008; Rendall et al., 1996; Slocombe et al., 2009). Latency to look is a measure of a subject's motivation to attend to a stimulus, or an indication of a subject's state of arousal (Palombit et al., 1997). Additionally, latency to look is often more identifiable than the duration of looking because the onset of the response is more clearly identified than the offset (Fischer et al., 2013).

In this study, we evaluate latency to look and duration of looking independently in order to provide more detailed insight into the mechanism driving subjects' responses and attention to vocal stimuli. Some researchers recommend using principle component analysis to generate a composite measure of response from multiple measurements (McGregor, 1992). This can work well for some types of research questions, but it can make biological interpretation of results more difficult because a composite measure does not necessarily have a corollary in the natural world (Fischer et al., 2013). Additionally, composite measures make comparing results between studies more cumbersome if researchers combine different response measures. We use the term "response strength" to refer to both measures. A "strong" response is one with a short latency to look and a long duration of looking, while a "weak" response is one with a long latency to look and a short duration of looking. Following from Seyfarth & Cheney (1984), the strength of a subject's response to the stimulus was interpreted as their willingness to provide coalitionary support to the caller.

2.2.6 Experimental Conditions

Our experimental design consisted of four experimental conditions and two control conditions. In all conditions, the call played to a subject was from an unrelated, lower ranking, adult female of the same group. High ranking members of primate hierarchies participate most often in coalitionary support to non-kin (Silk, 2005). In most cases where coalitionary support is provided to non-kin, the individual being supported is the victim in the conflict and is lower ranking than the supporter (Chapais et al., 1991; Kaplan, 1978; Massey, 1977). To ensure that rank relationships were held constant across trials, and to ensure the greatest probability of response to our playback experiment, subjects were always higher ranking than the female whose call they were played.

For conditions in which the subject needed to interact with another monkey prior to hearing a vocal stimulus, calls were played at least 10 minutes after the subject and social partner had ceased interacting, but no longer than 60 minutes after their interaction (Cheney et al., 2010). If a subject received grooming or was submitted to at any point after their initial interaction, (by any other animal, including males, juveniles, other group members) the trial was aborted. The 10-minute delay was to ensure that subject and social partner's interactions were terminated and to give sufficient time for the subject to move out of sight of the social partner. We chose a 10-minute delay period following Cheney et al. (2010), rather than the 30-minute delay period of Seyfarth & Cheney (1984) to reduce the likelihood that subjects would receive grooming or submissions in the delay period. We capped the time in which a trial could be conducted at 60 minutes, consistent with past studies of grooming reciprocity that use the same time frame (Fruteau, Voelkl, van Damme, & Noe, 2009; Jaeggi, De Groot, Stevens, & Van Schaik, 2013; Majolo, Schino, &

Aureli, 2012; Molesti & Majolo, 2017) or shorter (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Manson, Navarrete, Silk, & Perry, 2004).

For conditions in which subjects needed to be groomed immediately prior to hearing a vocal stimulus, Test subject and caller pairs were selected *ad libitum* when an experimenter observed a female grooming an unrelated higher-ranking female whose recruitment call stimuli was available and that adhered to the limitations stated above. A grooming event was defined as continuous grooming lasting greater than 10 seconds (Majolo et al., 2012). Once an appropriate subject-caller pair was identified the experimenter observed and documented the grooming interaction, recording; the identities of the grooming partners, the duration of each grooming exchange, the total time partners spent grooming, and whether both females were groomed. The mean grooming bout length was 8.9 minutes (range: 1 – 26 minutes). There was no evidence that length of grooming bout preceding a playback trial had an effect on response strength.

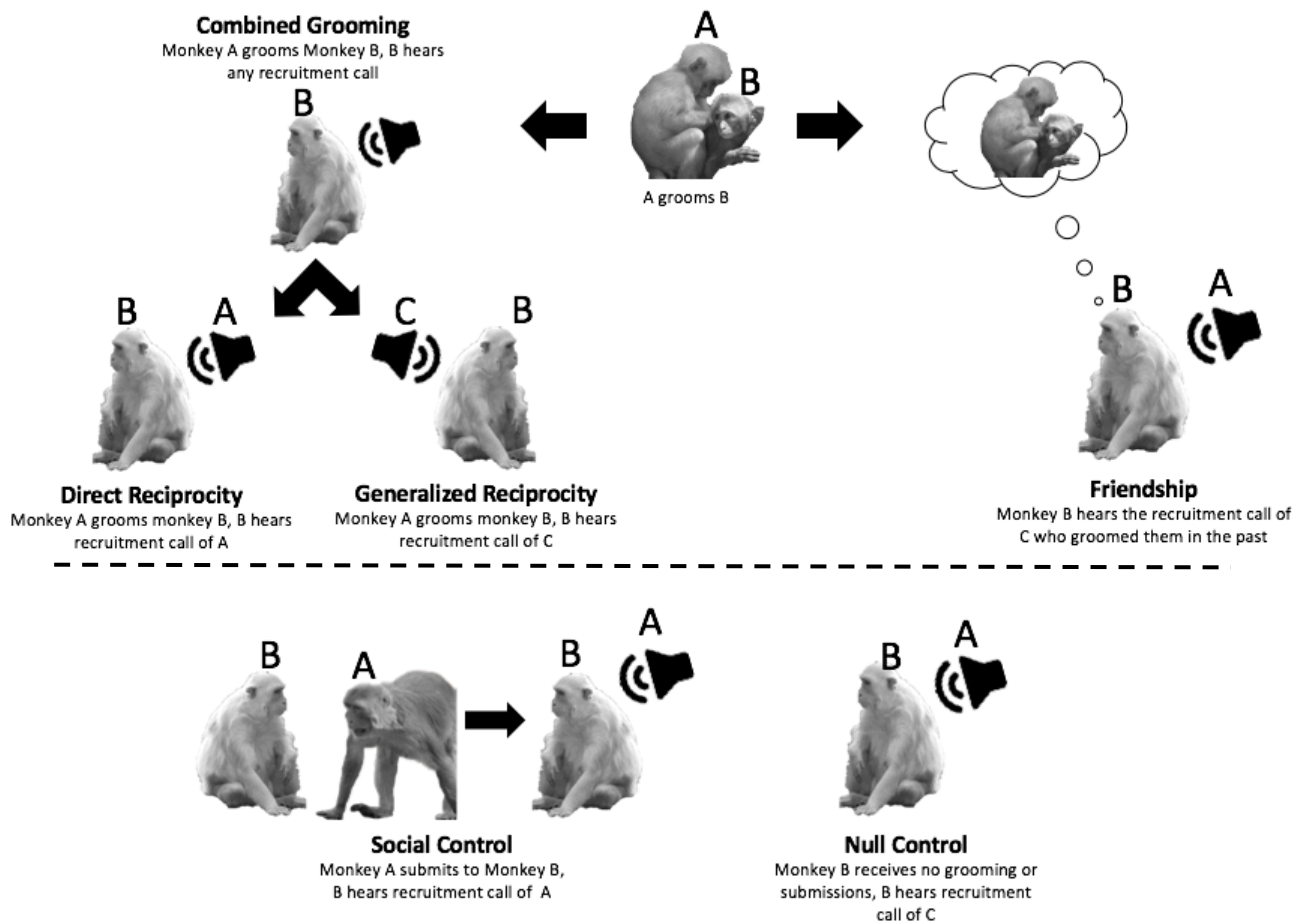


Figure 2.2: Diagram of Condition Types: In all experimental conditions monkey A grooms monkey B. In the **combined grooming condition** monkey B hears a recruitment call shortly after being groomed. The call monkey B hears in the trial determines which of the two sub-conditions that trial belongs to. If monkey B hears the call of their recent grooming partner, monkey A, then it is the **direct reciprocity condition**. If monkey B hears the call of another groupmate, monkey C, then it is the **generalized reciprocity condition**. In the **long-term direct reciprocity condition** monkey B has been groomed by monkey A in the last year, and hears the call of monkey A. In the two control conditions there is no grooming. In the **social control condition** monkey A submits to monkey B, subsequently monkey B hears the call of monkey A. In the **null control condition** monkey B receives no grooming or submission for 90 minutes and then hears the call of monkey A, who has not groomed them in the last year.

The four experimental conditions of our experiment were the combined grooming condition, the direct reciprocity condition, the generalized reciprocity conditions, and the long-term direct reciprocity condition. The combined grooming

condition did not have its own trials; it was formed of the combined trials of the direct and generalized reciprocity condition trials. The two control conditions we used in our experiment were the social control condition, and the null control condition. By comparing females' responses in our experimental conditions to responses in our control conditions we tested our four research questions.

To test our first research question – Are female rhesus macaques more willing to provide coalitionary support after being groomed – we measured female's responses in the **combined grooming condition** (Figure 2.2), in which females received grooming and were subsequently played the recruitment call of a female groupmate. In half of these trials, subjects were played the recruitment call of their most recent grooming partner (**Direct Reciprocity Condition**, Figure 2.2), while in the other half subjects heard the recruitment call of a female groupmate other than their most recent grooming partner (**Generalised Reciprocity Condition**, Figure 2.2).

To test our second research question – Are female rhesus macaques more willing to provide coalitionary support to a recent grooming partner? – we separately measured female responses in the conditions that made up the combined grooming condition; the direct reciprocity condition and the generalized reciprocity conditions.

To test our third research question – Are female rhesus macaques more willing to provide coalitionary support to past grooming partners? – we measured females' responses in the long-term direct reciprocity condition, in which subjects were played the recruitment call of a female with whom she had a past grooming relationship (**Long-term Direct Reciprocity Condition**, Figure 2.2) (see section 2.2.3.2). The strength of the subject-caller pair's grooming relationship was

described by their dyadic sociality index, which in 91% (10/11) of trials were among the highest dyadic sociality index values in the group.

To test our fourth research question – Are female rhesus macaques more willing to provide coalitionary support if they receive more grooming from their group as a whole? – we determined how much grooming each individual female received from other adult females relative to the mean grooming received by all females in the group. The formula we used to calculate the amount of grooming individual females received:

$$\text{Grooming Recieved}_{(i)} = \frac{(G_i/F_i) - \mu}{\sigma} -$$

Equation EQ2

Where G_i is the number of observations in which individual i received grooming from other adult females as a focal individual, F_i is the number of times individual i was a focal individual, μ is the mean of G/F for all females in group F , and σ is the population standard deviation of G/F for all females in group F . This formula produces standardized values, with a mean of zero and a standard deviation of one. Thus, an individual with a positive score received an above average amount of grooming from other adult females and an individual with a negative grooming score received a below average amount of grooming. Like DSI, we used a single year's data to best align females' interactions with their response to the stimulus.

To account for the possibility that any social interaction with a caller prior to hearing the recruitment call primes an individual to attend more to the call, regardless of the interaction's nature (i.e., affiliative or agonistic), we included a **Social Control** condition (Figure 2.2.). In this condition, subjects received a submission from a female and were subsequently played the recruitment call of the same female. Behaviours we considered submissions included: the subject receiving

a fear grimace, displacing another monkey, being avoided by another monkey, or another monkey fleeing from the subject.

To establish the baseline response to a recruitment call of a non-relative, we used a **Null Control** condition (Figure 2.2). In the null control, a subject received no submissions or grooming from groupmates of any sex or age class for a 90-minute period. At the end of the 90-minute period the subject was played a recruitment call of a groupmate with whom the subject had no history of grooming in the past year. We used the period of 90 minutes because it has been used by past playback experiments to establish a behavioural baseline (Cheney et al., 2010) and because it is 30 minutes longer than the length of time after a grooming event in which we conducted playback trials.

2.2.7 Statistical Analyses

2.2.7.1 Comparing experimental conditions

All statistical analyses were conducted using the statistical package R (version 1.1.453, R Core Team, 2017). We analysed duration of looking data using a Generalised Linear Mixed Model (GLMM). GLMMs were fitted using the lmer function from the lme4 R package version 1.1-18 (Bates, Maechler, Bolker, & Walker, 2015). In 16% of our trials (10 of 64 trials) the subject did not respond to the playback stimulus. These “no-look trials” could not be assigned a latency to look value because one cannot have zero time until the onset of an event. Some studies have created ceiling values that have allowed them to include their “no-look” trials (Rendall et al., 1996; Slocombe et al., 2009). In these cases, no-look trials were assigned a latency to look value equal to the maximum time observers recorded behaviour. However, this approach can lead to biased or misleading results because

the ceiling values can artificially inflate the latency values, skewing the overall distribution of data (Jahn-Eimermacher, Lasarzik, & Raber, 2011). Instead, we used a survival model approach that allows for the inclusion of incomplete data points, including no-look trials, as censored observations (Pinheiro & Bates, 2000) to analyse our latency to look data. We used Cox proportional hazard models with mixed effects and a Poisson error to test for differences in latency to look between playback conditions. Survival models were fitted with the `coxme` R package version 2.2-10 (Therneau, 2018).

For each of our two response measures, latency to look and duration of looking, we created three sets of models, each designed to answer one of our four research questions. In each model, the response to the playback was our dependent variable, and playback condition was our main predictor variable, with subject and caller ID included as random effects. Each model additionally contained a set of predictors we identified as potential confounds: the number of individuals within 10 m of the subject during the experiment, difference in rank between subject and caller, number of infants present in a subject's family (described in detail below).

Each model was designed to answer our four research questions. To answer our first research question – are female rhesus macaques more willing to provide coalitionary support after being groomed? – we compared subjects' responses to playback stimuli in the combined grooming condition to their responses in the social control condition and the null control condition. Any difference in subjects' responses between the combined grooming condition and our two controls must come from the nature of subjects' recent interaction – grooming.

To answer our second research question – are female rhesus macaques more willing to provide coalitionary support to a recent grooming partner? – we

compared subjects' responses in the direct reciprocity condition, the generalised reciprocity condition, the social control, and the null control. Any difference between the direct reciprocity condition and the generalised reciprocity condition and social control condition must come from the combined identity of the caller as a recent social partner, and nature of the recent interaction as grooming.

To answer our third research question – Are female rhesus macaques more willing to provide coalitionary support to a past grooming partner? – we compared subjects' responses in the long-term direct reciprocity condition and the null control condition. Any difference in subjects' responses must be due to the history of past grooming exchanges between subject and caller.

To answer our fourth research question – Are female rhesus macaques more willing to provide coalitionary support if they receive more grooming from their group as a whole? – we included the measure “grooming received” as a predictor in each of the above models.

2.2.7.2 Other Predictors

In addition to testing the impact of our experimental conditions on females' responses to solicitations for aid, we included a range of other potentially important predictor variables in our models:

Number of individuals near the subject at the time of the experimental trial

We included the number of individuals within 10 m of the subject as a fixed effect in both models to account for the effect that audience size may have on a subject's willingness to provide coalitionary support to the caller (Table 2.3). There is evidence that social animals modify their scanning behaviour (Di Blanco & Hirsch, 2006; Stojan-Dolar & Heymann, 2010; Treves, 1999) and willingness to respond to

stimuli (McComb, Packer, & Pusey, 1994) based on the number of nearby conspecifics. Rhesus macaques in particular have been shown to modify their responses to conspecific vocalizations based on the presence or absence of other groupmates (Semple, Gerald, & Suggs, 2009). Past playback experiments have used similar terms to account for how audience sizes affect playback responses (Fischer, 2004; McComb et al., 1994).

Rank Distance

We included the term “rank distance” as a binary fixed effect in the models to account for the effect the distance between the subject’s and caller’s dominance ranks might have on the subject’s response (Table 2.3.). Because a significant negative relationship between rank distance and affiliative behaviours, like grooming and coalitionary support, has been documented in several macaque species, We included the term “rank distance” as a binary fixed effect [stumped-tailed macaques (*Macaca arctoides*) (Nieuwenhuijsen, Slob, & van der Werff ten Bosch, 1988; O’Keefe, Lifshitz, & Linn, 1982), rhesus macaques (*Macaca mulatta*) (de Waal, 1991; de Waal & Luttrell, 1986), Japanese macaques (*Macaca fuscata*) (Onishi, Yamada, & Nakamichi, 2013; Yamagiwa, 2010)].

For the purpose of comparing rank relationships between individuals, we divided the dominance hierarchy into three rank categories: high-ranking, medium-ranking, and low-ranking. High-ranking individuals outranked greater than 80% of individuals in their social group, medium-ranking individuals outranked between 80% and 50% of individuals in their social group, and low-ranking individuals outranked fewer than 50% of individuals in their social group (Madlon-Kay et al., 2017). We made rank distance a binary measure with a value of 1 if the subject and caller were in the same rank category and a value of 0 if they were in different rank categories.

We chose a discrete rank scale over a continuous scale because female rhesus macaques of a single matriline occupy adjacent ranks and interact most frequently with members of their own matriline (Kapsalis & Berman, 1996a, 1996b). Most non-kin interactions occur between females belonging to rank adjacent matrilines (Strier, 2011). This has the effect of breaking up interactions along the hierarchy into discrete blocks where females of similar rank interact most with one another – an effect that becomes more pronounced the higher the rank a female holds. Therefore, a binary measure indicates whether or not two individuals are likely to interact more frequently as a result of their ranks.

Infant to Female Ratio

Preliminary exploration of our data revealed a decrease in response strength over the course of our study period. To investigate this pattern in the data, we fit the date of each trial as an independent variable in our models. We found a significant negative relationship between response strength and trial date, with latency to respond increasing and duration of response decreasing as the study period progressed (Figure 2.3.) (Latency: $Z = -2.231$, $P = 0.0293$; Duration: $t = -2.703$, $P = 0.00886$; See Appendix Table 1.).

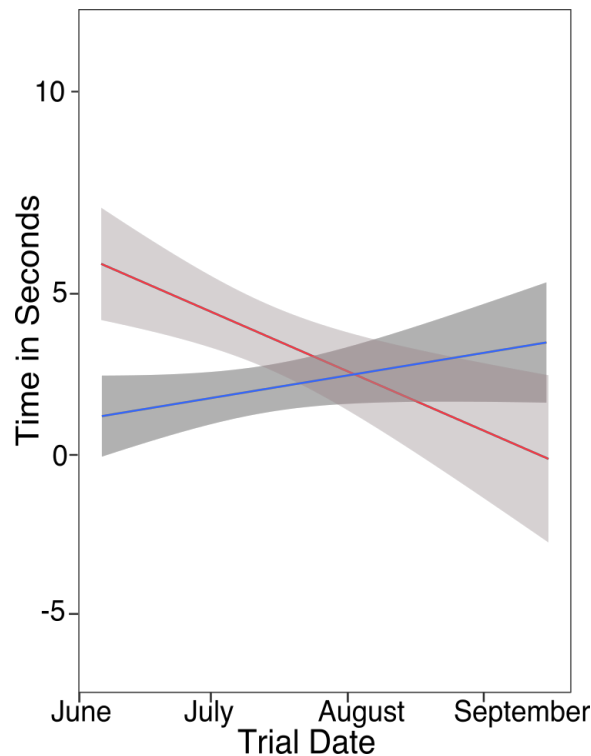


Figure 2.3. Subjects' responses to playback stimulus plotted against the date of the playback trial across the study period. Blue = Latency to Look; Red = Duration of Looking.

A time-related decrease in response strength could be caused by habituation or by seasonal effects. We compiled a list of variables related to these factors for further analysis. We identified two measures of habituation: the number of trials that had preceded each trial, and the number of trials each subject had previously participated in. Measures of seasonal effects were related to the presence of new infants at the field station. Rhesus macaques are seasonal breeders, with a 5-month period of the year in which sexually mature females in the group give birth (Kessler & Rawlins, 1986). Previous studies have shown that patterns of social interaction in the group change during this period (Brent, MacLarnon, et al., 2013; Tilford, 1982). The level of intragroup conflict decreases in relation to the mating season (Berman, 1980; Tilford, 1982), affiliative interactions between matriline decrease, leading to less tightly connected networks of grooming and proximity (Brent, MacLarnon, et al.,

2013), and the size of the group increases as infants are born. The additional attention required for parental care, combined with the changing patterns of interaction, could affect female willingness to provide coalitionary support to non-relatives. Our study period coincided with the annual birthing season on Cayo Santiago (Brent, MacLarnon, et al., 2013) and so we included measures of the birthing season's progress: the number of infants in the group at the time of the trial, whether or not a subject had an infant at the time of the trial, and the ratio of infants to females in a subject's matriline at the time of the trial. The last variable was included to account for the assistance in parental care provided by matriline members (Table 2.3).

All measures of the birthing season's progress were highly correlated because they were different measures of the same process (time). For this reason, we compared each model with each variable using Akaike Information Criterion (AIC; Akaike, 1974; Burnham & Anderson, 2004) values, the most widely used criterion in the model inferencing and averaging literature (Grueber, Nakagawa, Laws, & Jamieson, 2011). Models with >2 AIC (ΔAIC_c) were considered statistically distinct and the model with the lowest AIC for each measure was considered to be the best fitting model (Grueber et al., 2011) (Tables 2.1 & 2.2).

Table 2.1. Candidate models used to explore the relationship between trial date and latency to look. Models are ranked with lowest AIC value at the bottom. The lowest AIC value is highlighted.

Predictor Variable	AIC	ΔAIC	Coef	Exp(Coef)	Se(coef)	Z	P
Trial Date	350.1	0.0	-0.258	0.773	0.183	-2.231	0.029
Trial Number	348.8	-1.3	-0.113	0.988	0.007	-1.56	0.123
Number of Trials Participated	344.5	-5.6	-0.184	0.831	0.204	-0.91	0.362
Number of Infants in the Group	343.6	-6.5	-0.017	0.984	0.008	-1.98	0.048
Focal has Infant	343.0	-7.1	-0.750	0.472	0.374	-2.01	0.045
Infant to Female Ratio	342.8	-7.3	-1.070	0.343	0.564	-1.9	0.050

Table 2.2. Candidate models used to test the relationship of trial date on the duration of looking. Models are ranked with lowest AIC value at the bottom. The lowest AIC value is highlighted.

Predictor Variable	AIC	ΔAIC	Estimate	Std.Error	t value	P
Trial Date	813.9	0.0	1.84	0.64	-2.87	0.005
Number of Infants in the Group	812.6	-1.3	-2.62	0.86	-3.04	0.003
Trial Number	811.6	-2.6	-2.74	0.84	-3.24	0.002
Focal had Infant	810.8	-3.1	-68.50	41.09	-1.67	0.102
Trial Participation	810.4	-3.5	-47.60	23.38	-2.04	0.046
Infant to female ratio	804.2	-9.7	-172.73	58.05	-2.98	0.004

Indicators of seasonality were better fit to the data than indicators of habituation in all cases. Of all the variables examined, “infant to female ratio” had the lowest AIC for duration and was <2 from the lowest AIC for latency to look, meaning it was indistinguishable from the other models. Infant to female ratio also had the largest effect size in both models and was a significant or near significant predictor of both response measures. From these results, we therefore decided to include infant to

female ratio in all models testing to the relationship between responses to stimuli and experimental condition.

Global models were created containing the predictor variables playback condition, grooming received, individuals in 10m, rank distances, and infant to female ratio and the random effects subject ID and caller ID (Table 2.3). Using a likelihood ratio test, global models were compared against simplified models containing only Playback Condition and random effects, as well as null models containing only random effects (Crawley, 2008). In all cases, the global models fit significantly better than either the condition only or null models (See Appendix Table 2 for details). We therefore only present the results of the global models.

Table 2.3: *Description of the predictor variables used to assess responses of female rhesus macaques to playback stimulus.*

Predictor Variable	Description
Playback Condition	The experimental condition of the playback trial (<i>Factor with levels: Direct Reciprocity, Generalised Reciprocity, Social Control Condition, Null Control Condition, Long-Term Direct Reciprocity Condition</i>)
Grooming Received	The amount of grooming a subject received in year prior to the experiment relative to the group average. <i>For calculation see equation EQ2. A positive value indicates that the subject received more grooming in 2017 than the group average.</i>
Individuals within 10m	The number of individuals within 10 meters of the subject at the time of the playback
Rank Distance	Binary: 1 when the subject and caller share the same rank category, 0 when caller and subject are in different rank categories (<i>high-ranking = outrank >80% of social group, medium-ranking = outrank 80%-50% of their social group, low ranking = outrank <50% of their social group</i>)

Infant to female ratio	The ratio of new-born infants to adult females in the subject's matriline, <i>calculated as: infants in matriline /adult females in matriline. (Bounded at 0 and 1)</i>
Subject ID	The identity of the monkey whose response to the recruitment call was being measured.
Caller ID	The identity of the monkey whose recruitment call was played during the playback trial.

2.3 Results

We conducted 64 trials between June 17th and September 16th, 2017. These included: 15 direct reciprocity conditions, 15 generalized reciprocity conditions, 13 social control conditions, 10 null control conditions, and 11 long-term reciprocity conditions. Subjects looked in the direction of the playback speaker in 87.5% of trials ($n = 56$). The average latency to look was 2.02 seconds \pm 2.82 seconds. The average duration of looking was 5.02 seconds \pm 4.13 seconds.

2.3.1 Does recent grooming predict willingness to support?

Female rhesus macaques responded no differently to hearing the recruitment call of an adult female groupmate after recent grooming, after a recent submission, or in the absence of prior interaction. We found no significant difference in subjects' latency to look (Fig. 2.4a) or duration of looking (Fig. 2.4b), for those that were recently groomed or subjects in either the social control condition (Latency: $z = -0.89$, $P = 0.37$; Duration: $t = -0.52$, $P = 0.61$) or the null control condition (Latency: $z = -0.19$, $P = 0.85$; Duration: $t = -0.85$, $P = 0.40$) (Table 2.4).

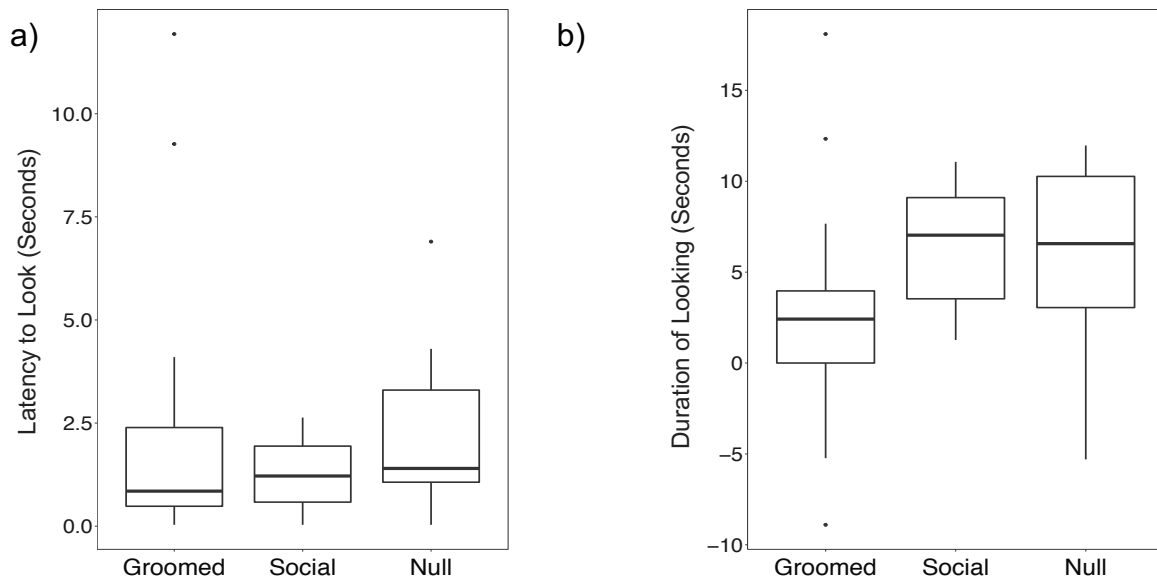


Figure 2.4. Female's mean a) latency to look and b) duration of looking in the direct of the playback stimulus, divided by condition types: Combined Grooming Condition (Groomed), Social Control Condition (Social), and Null Control Condition (Null). Boxplots show the median, inter-quartile range and maximum and minimum values, with outliers represented as dots.

Table 2.4. Does recent grooming predict social response to vocal stimuli?

Terms	Latency to Look				Duration of Looking		
	Coef ± SE	Exp(Coef)	Z	P	Coef ± SE	T	P
Condition							
Combined Grooming -Social	-0.28 ± 0.55	0.75	-0.52	0.61	52.41 ± 58.43	-0.89	0.37
Combined Grooming - Null	-0.48 ± 0.56	0.62	-0.85	0.40	-11.40 ± 59.44	-0.19	0.85
Total Grooming Received	0.26 ± 0.21	1.30	1.25	0.21	-0.74 ± 22.42	-0.03	0.97
Rank Distance	0.93 ± 0.51	2.54	1.81	0.07	16.74 ± 50.52	0.33	0.74
Individuals in 10m	-0.14 ± 0.08	0.87	-1.89	0.06	-8.33 ± 59.44	-1.07	0.29
Infant Female Ratio	-2.63 ± 0.92	0.07	-2.87	0.00	-170.77 ± 79.19	-2.16	0.04

Significant effects are marked in bold.

When subjects' responses in the direct and generalized conditions were compared independently, we found no significant difference in response strength in the direct reciprocity condition compared to the social control condition (Latency: $z = 1.00$, $P = 0.32$, Duration: $t = 0.14$, $P = 0.89$) or the null control condition (Latency: $z = 0.84$, $P = 0.40$, Duration: $t = -0.90$, $P = 0.37$) (Fig. 5) (Table 2.5). Similarly, there were no significant differences in response strength when generalised reciprocity condition

was compared to the social control condition (Latency: $z = -1.08$, $P = 0.28$, Duration: $t = -1.72$, $P = 0.09$) or the null control condition (Latency: $z = 0.-1.24$, $P = 0.22$, Duration: $t = -0.90$, $P = 0.37$) (Fig. 2.5) (Table 2.5).

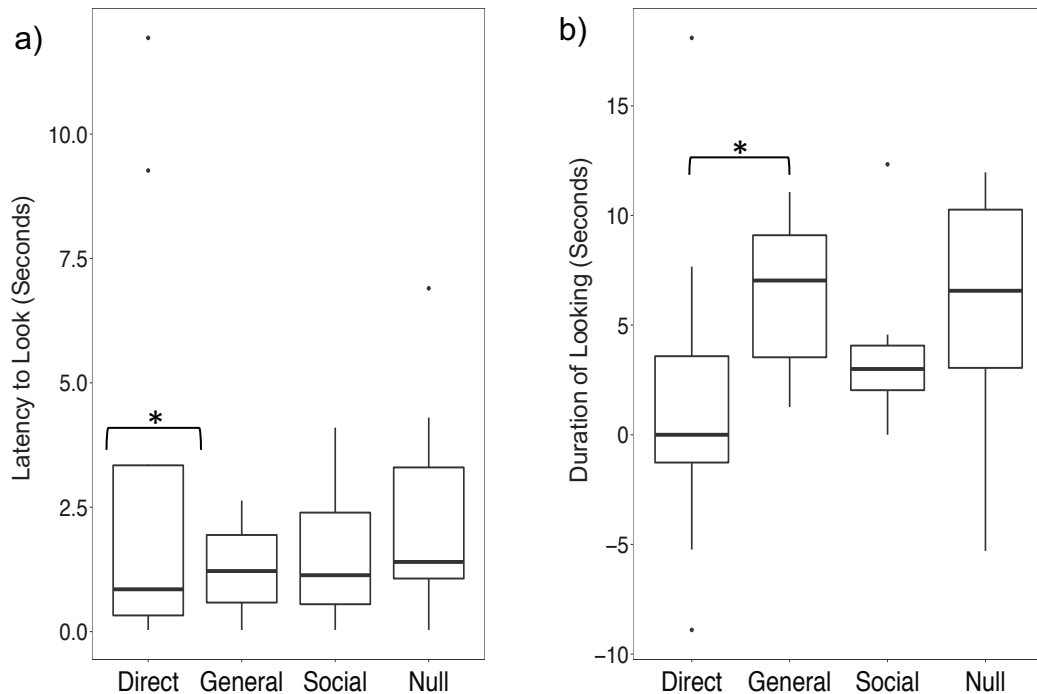


Figure 2.5. Female's mean a) latency to look and b) duration of looking in the direction of the playback stimulus, divided by condition types: Direct Reciprocity Condition (Direct), Generalised Reciprocity Condition (General), Social Control Condition (Social), and Null Control Condition (Null). Significant differences are denoted by a bracket and asterisk.

There was a significant difference in responses between the direct and generalized reciprocity conditions. Subjects in the direct reciprocity condition had significantly shorter latency to look (Fig. 2.5a) and a significantly shorter duration of looking (Fig. 2.5b) than those in the generalized reciprocity condition (Latency: $z = 2.00$, $P = 0.046$; Duration: $t = 2.05$, $P = 0.046$) (Table 2.5). This suggests that females that heard the call of a recent grooming partner looked more quickly towards the speaker but looked for less time than females who were groomed and subsequently heard the call of a female other than recent grooming partner. Interestingly, we also noted that duration of looking in the social control condition was visibly shorter than values

in either the generalized reciprocity condition or the null control condition. This indicates that the two conditions in which the subject interacted with the caller prior to hearing the playback seemed to spend less time looking at the speaker. To explore this further, we created a binary parameter where all trials in which the subject interacted with the caller prior to the playback were scored as 1, and all trials in which the subject had no prior interaction with the caller were scored as 0. We included this binary parameter as an independent variable in two models, with response latency and duration as dependent variables (See appendix Table 3.). We used a loglikelihood test to ensure that both latency and duration models were significantly better than null models (Latency: $\text{Chisq} = 9.52$, $\text{Chi Df} = 3$, $P = 0.02$; Duration: $\text{Chisq} = 8.23$, $\text{Chi Df} = 3$, $P = 0.04$) (See appendix Tables 4. & 5.).

Table 2.5. Does the identity of a recent grooming partner predict response to their vocal stimuli?

Terms	Latency to Look				Duration of Looking		
	Coef \pm SE	Exp(Coef)	Z	P	Coef \pm SE	T	P
Condition							
<i>Direct Rec. - Generalized Rec.</i>	1.27 \pm 0.63	3.54	2.00	0.046	117.15 \pm 57.10	2.05	0.046
<i>Direct Rec. – Social</i>	0.64 \pm 0.64	1.90	1.00	0.32	8.76 \pm 64.18	0.14	0.89
<i>Direct Rec. – Null</i>	0.58 \pm 0.68	1.78	0.84	0.40	61.50 \pm 67.28	0.91	0.37
<i>Generalized Rec. - Social</i>	-0.62 \pm 0.58	0.54	-1.08	0.28	-108.39 \pm 62.88	-1.72	0.09
<i>Generalized Rec. - Null</i>	-0.69 \pm 0.56	0.50	-1.24	0.22	-55.65 \pm 61.016	-0.90	0.37
<i>Social - Null</i>	-0.06 \pm 0.58	0.94	-0.11	0.91	52.74 \pm 68.41	0.77	0.44
Grooming Received	0.25 \pm 0.20	1.28	1.26	0.21	0.86 \pm 21.44	0.04	0.97
Rank Distance	0.75 \pm 0.46	2.12	1.64	0.10	23.87 \pm 48.92	0.49	0.63
Individuals in 10m	-0.10 \pm 0.07	0.90	-1.48	0.14	-7.47 \pm 7.60	-0.98	0.33
Infant Female Ratio	-1.62 \pm 0.83	0.20	-1.95	0.05	-117.24 \pm 80.43	-1.46	0.15

Significant effects are marked in bold.

The analysis showed that subjects that interacted with the caller prior hearing their call had a significantly shorter duration of looking than individuals who had either interacted with another female prior to hearing the call or had no interaction prior to hearing the call (Duration: $t = -2.62$, $P = 0.01$) (See Appendix Table 5.). This

relationship was limited to duration of looking. There was no significant relationship between pre-playback interaction with the caller and latency to look (Latency: $z = -1.43$, $P = 0.150$) (See Appendix Table 4.).

2.3.2 Do past social relationships predict willingness to provide support?

We found that neither of our measures of long-term grooming interactions, either with the caller or with all adult females, were significant predictors of a subject's response to recruitment calls. Subjects responded no differently to the recruitment calls of long-term grooming partners than to the recruitment calls of females who had not groomed them in the last year (Latency: $z = -0.32$, $P = 0.75$, Duration: $t = 0.85$, $P = 0.41$) (Table 2.6) (Fig. 2.6).

Table 2.6. Does grooming history predict social response to a past partner's vocal stimuli?

Terms	Latency to Look				Duration of Looking		
	Coef ± SE	Exp(Coef)	Z	P	Coef ± SE	T	P
Condition							
<i>Long-term Direct Rec. - Null</i>	-0.31 ± 0.99	0.73	-0.32	0.75	48.8 ± 57.18	0.85	0.41
Grooming Received	0.66 ± 0.53	1.93	1.25	0.21	-33.49 ± 35.85	-0.93	0.37
Shared Rank	0.34 ± 1.03	1.41	0.33	0.74	24.49 ± 63.35	0.39	0.70
Individuals in 10m	-0.46 ± 0.25	0.63	-1.88	0.06	10.71 ± 15.96	0.67	0.51
Infant Female Ratio	3.71 ± 1.79	40.91	2.07	0.04	-299.7 ± 112.36	-2.67	0.02

Significant effects are marked in bold. Comparison of latency to look and duration of looking between the long-term reciprocity condition and the null control.

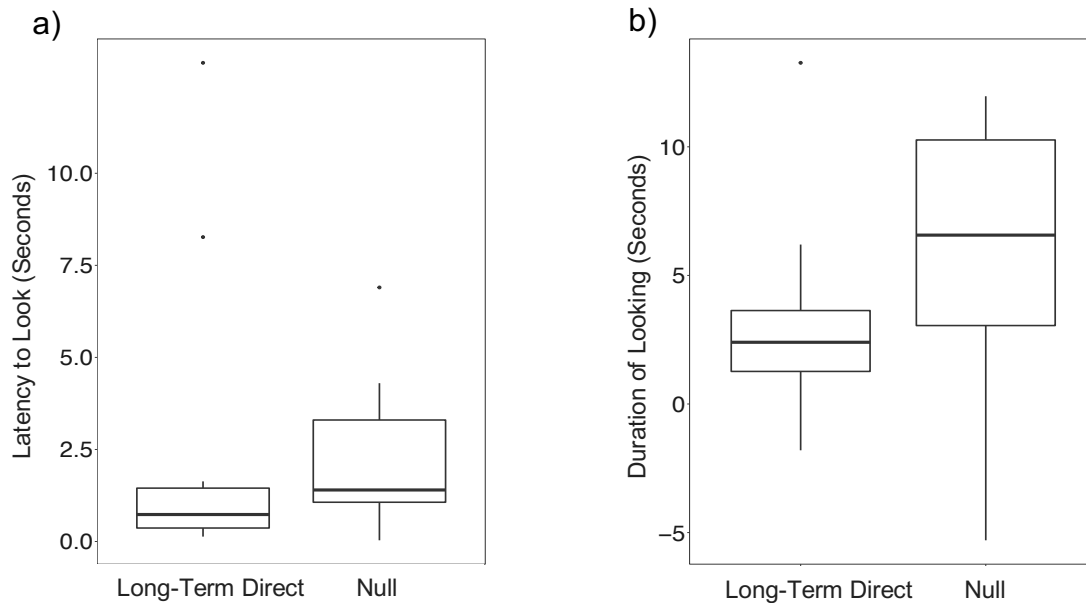


Figure 2.6. Female's mean a) latency to look and b) duration of looking in the direct of the playback stimulus, divided by condition types: Long-Term Direct Reciprocity Condition (Long-Term Direct) and Null Control Condition (Null).

Additionally, we found no evidence for a relationship between the amount of grooming a subject received from all other adult females in her group in the year prior to the experiment and the strength of her responses to recruitment calls. The amount of grooming a subject received was not a significant predictor of either latency to look or duration of looking. This result was the same when the amount of grooming a subject received was the sole fixed effect in a basic model (Latency: $z = 0.29$, $P = 0.77$, Duration: $t = -0.717$, $P = 0.48$) (See appendix Table 5.) and when it was included in the global model with all other fixed effects (Latency: $z = 1.26$, $P = 0.21$, Duration: $t = 0.04$, $P = 0.97$) (Table 2.4.).

Of the fixed effects that were included in the analysis besides our experimental conditions, only the ratio of infants to females in the subject's matriline was a significant predictor of females' responses to recruitment calls. In all but one model the ratio of infants to females in the subject's matriline was negatively correlated with response strength. Relative to the size of their matriline, females with more infants in their matriline were slower to look in the direction of the speaker and

looked for less time compared to females with fewer infants in their matriline (Tables 2.4 and 2.6).

2.4 Discussion

2.4.1 Summary of Findings

Our results show that receiving grooming did not affect female rhesus macaques' willingness to provide coalitionary support to unrelated females. Receiving grooming did not lead to a short-term increase in females' willingness to provide coalitionary support, even to their most recent grooming partners. Nor was a female's willingness to provide support affected by the accumulation of grooming interactions over a longer-term, with either a specific partner or the group as a whole. In other words, we found no evidence that grooming was exchanged for coalitionary support amongst non-relatives by either generalized or direct reciprocity. We propose that the lack of evidence for either type of reciprocity could be due to the despotic nature of the rhesus macaque dominance hierarchy, which strictly defines the costs and benefits of coalitionary support and makes it more likely for females to provide support as a means to gain direct fitness or inclusive fitness benefits. Below I discuss each of these results in turn and in greater detail.

2.4.2 Does recent grooming predict willingness to provide support?

Our results show that receiving grooming has no short-term effect on female's willingness to provide support to others, which suggests that generalized reciprocity does not underpin the exchange of grooming for coalitionary support in unrelated adult female rhesus macaques. Previous studies of generalised reciprocity have explored short-term reciprocity in lab-based experiments using rats, dogs, and humans (Emmons & McCullough, 2004; Gfrerer & Taborsky, 2018; Monica Y. &

David, 2006; Rutte & Taborsky, 2007). After receiving help from an unknown partner in an instrumental cooperative task, rats were 20% more likely to help another unknown partner in subsequent tasks (Rutte & Taborsky, 2007). Similar experimental designs in both dogs and humans also demonstrated an increased willingness to cooperate irrespective of partner identity (Emmons & McCullough, 2004; Gfrerer & Taborsky, 2018; Monica Y. & David, 2006).

Building on that research, our study conducted the first experimental test of generalized reciprocity outside a laboratory setting. The absence of evidence for generalised reciprocity in our study could indicate that there are differences in the way animals cooperate in lab-based tasks compared to how they cooperate in a natural setting. For instance, animals behaving an artificial task may be more forthright with their cooperation because there is little cost to cooperating and a limited number of behavioural responses to the task available.

Indeed, our results more closely echo those found in observational studies of cooperative exchanges in free-ranging and wild primates that show that animals do not indiscriminately cooperate with others after receiving cooperation. Two studies of grooming reciprocity in macaques and two studies of the exchange of grooming for food in chimpanzees all found that the frequency and duration of grooming received did not predict the short-term likelihood that individuals would cooperate with any another groupmate (De Waal, 1997; Majolo et al., 2012; Molesti & Majolo, 2017; Waal & Brosnan, 2006). It could be that individuals do not indiscriminately cooperate with groupmates because there is always a criterion like relatedness, proximity, or previous cooperation that animals can capitalise on to obtain a greater fitness benefit from cooperative acts. This could be particularly true for costly forms of cooperation like coalitionary support and food sharing, where the behaviour's cost incentivizes

individuals to net the greatest benefit from their actions. Indeed, the animals in the above studies preferentially directed cooperation toward those from which they had previously received cooperation in a pattern consistent with direct reciprocity (De Waal, 1997; Majolo et al., 2012; Molesti & Majolo, 2017; Waal & Brosnan, 2006). By contrast, our study found no support for direct reciprocity.

Receiving grooming did not increase females' willingness to support recent grooming partners in our study. Despite a clear difference in our results from the four studies described above, our results do not represent the first time a study has failed to find evidence for the exchange of grooming for coalitionary support via short-term direct reciprocity. In chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), the significant short-term reciprocal effects of grooming on food sharing disappeared when measures of partner's long-term patterns of grooming were taken into account (Jaeggi et al., 2013). The receipt of grooming also did not increase the short-term probability of individuals supporting an unrelated partner in Japanese macaques (*Macaca fuscata*) (Schino, 2007). Lastly, even though unrelated coalition partners groom one another more often than the average unrelated dyad in captive rhesus macaques, there was no evidence that the member of the dyad that provided the most grooming received the most support (Matheson & Bernstein, 2000). In other words, inequalities in the amount of grooming given and received did not translate into coalitionary support in the way predicted by Seyfarth's 1977 standard model. Our finding that receiving grooming did not increase females' willingness to provide coalitionary support in an experimental setting, combined with the results of previously correlational studies suggest that the exchange of grooming for coalitionary support by direct reciprocity over short periods of time may not occur as widely as previously believed.

It must also be noted that our results are in contrast to the findings of previous experimental studies of reciprocal grooming for coalitionary support. In particular, Seyfarth & Cheney (1984) and Cheney et al. (2010) – the playback experiments on which our study is based. These two playback experiments found that female vervet monkeys and baboons responded more strongly to recruitment calls of recent maternally unrelated grooming partners compared to maternally unrelated females that had not groomed them. However, although our study design was largely based on these two experimental outputs, some important differences may have contributed to the differences in our results. The first is the inclusion of a social control condition. In the original 1984 study there was no control condition to account for the possibility that any interaction with a groupmate could influence a subject's subsequent response hearing a recruitment call from that individual – an omission critics have pointed to in the past (de Waal & Luttrell, 1986; Dunbar, 1991; Henzi & Barrett, 1999) and that was dealt with by their follow up study in 2010. In our study, females that interacted with a caller (either via grooming or submission) prior to hearing their call had significantly lower durations of looking – the measure used by Seyfarth & Cheney 1984 – compared to females that had no prior interaction with the caller. Our results therefore suggest that rhesus macaque females were influenced by their previous interactions with the caller, in a manner that was not specific to grooming.

We also conducted our study in a population with a deeply resolved pedigree, where relatedness is known along both maternal and paternal lines. In contrast, the two previous studies had information only on the extent to which their subjects were maternally related (Cheney et al., 2010; Seyfarth & Cheney, 1984). Kin selection can drive cooperation amongst both maternal and paternal relatives (Widdig et al., 2001)

and it is therefore possible that some of the subject-caller pairs in previous playbacks were paternal relatives, which could influence their responses to playback stimuli. However, in order to uncover evidence for direct reciprocity in a spurious manner in these studies, there would need to be a reason to believe that grooming partners were more likely to be paternal kin, and therefore more willing to support each other in conflicts.

But the final and potentially most impactful difference between our experiment and the two previous playback experiments is the study species. An absence of evidence that grooming affects females' willingness to provide support could be a result of the different social structures between rhesus macaques, baboons, and vervets. In rhesus macaque females, the dominance hierarchy is strictly linear, with a higher degree of agonistic asymmetry, meaning high ranking females win virtually all conflicts with lower ranking opponents and there are almost no instances of low ranking individuals retaliating up the hierarchy (Arnold & Auriel, 2011; de Waal & Luttrell, 1988; Flack & de Waal, 2004). Rhesus macaques' conflicts are also more likely to escalate to physical violence, and they possess no reconciliatory behaviours (Flack & de Waal, 2004). In comparison, vervet monkeys and chacma baboons are less despotic, rarely escalate conflicts to physical aggression, and perform a number of post-conflict affiliative behaviours and vocalization that deescalate tensions between combatants (Arnold & Auriel, 2011; Cheney & Seyfarth, 1989; Cheney et al., 1995b). These species-specific differences in agonistic interactions point to important implications for the costs associated with providing coalitionary support, which are likely to be much greater in aggressive despotic species, like the rhesus macaque.

With greater costs associated with coalition formation, female rhesus macaques may only be willing to provide coalitionary support when direct fitness benefits can be gained. In despotic species, direct fitness can be accrued from supporting the status quo with respect to the dominance hierarchy. That is to say females can gain direct fitness benefits by reinforcing their own place in the hierarchy – by winning conflicts against lower ranking females. Females can also accrue direct fitness by reinforcing the ranks of other females – even if they are not related. If a female forms a coalition with the higher ranking of two fighting females, she can increase the likelihood that the higher-ranking females wins the conflict. Should the coalition partners win, both partners gain direct fitness benefits by reinforcing their dominance ranks over the lower ranking opponent. By ensuring the low-ranking female stays low ranking and avoiding a potential rank reversal the coalition partners ensure their continued access to rank related fitness benefits. Forming coalitions to reinforce the hierarchy is also a way of reducing the costs of coalitionary support. A coalition formed of two higher ranking females is likely to win a conflict with a single lower-ranking individual, and to do so with minimal injury. In despotic macaques, patterns of non-kin coalitionary support fit this description. Most non-kin coalitionary support is directed down the hierarchy (Bernstein & Ehardt, 1985; Bernard Chapais et al., 1991; Kaplan, 1978), and is directed to the higher ranking combatant significantly more often than the lower ranking combatant (Berman, 1980; Chapais, 1983, 1992; Chapais et al., 1991; de Waal & Luttrell, 1988). Additionally, females rarely intervene in a conflict between two combatants of higher rank than themselves (Chapais, 1992). The conservative pattern of support described above has been observed in a number of other species with violent

conflicts and despotic hierarchies including chimpanzees (Watts, 2002) and hyenas (Smith et al., 2010).

In theory, if an individual in a despotic species provided a sufficiently large amount of grooming, that individual could expect to be rewarded with coalitionary support. But the benefit would need to exceed the benefits gained by supporting the hierarchy, combined with the cost of potentially losing a conflict. Such a high threshold is not likely to be reached in a single interaction or over a short period of time and could explain why our study, as well as previous observational studies of grooming for support in other despotic macaque species (e.g., Japanese macaques) have failed to find evidence for short-term reciprocity (Schino et al., 2007).

2.4.3 Do social interactions experienced over longer periods of time predict willingness to provide support?

Female rhesus macaques did not respond more strongly to the recruitment calls of their long-time grooming partners compared calls from females that were not their grooming partners. There was also no relationship between the amount of grooming subjects received from other adult females as a whole and the strength of their responses to recruitment calls. These results may imply that even repeated grooming over the period of a year does not provide a sufficiently large benefit to result in coalitionary support amongst unrelated rhesus macaques. This may be especially true during the specific reproductive season in which we conducted our experiment.

We conducted our experiment during the annual birthing season on Cayo Santiago. This 5-month period (May to October) represents the time of year when most infants on the island are born, and coincides with a range of changes in social

interactions for the animals (Kessler & Rawlins, 1986). The level of intragroup conflicts decreases in comparison to the mating season (Brent et al., 2013; Wallen & Tannenbaum, 1997). The density of grooming and proximity networks also decreases as females constrain their social interactions to include mostly maternal relatives (Brent, MacLarnon, et al., 2013). Naturally, one of the biggest changes from the mating to the birthing season is the arrival of infants, and the associated maternal and kin-based care that result from the presence of neonates.

Primate infants require extensive parental investment from their mothers, as well as from their mother's maternal kin (Berman, 1980). Access to resources are determined by dominance rank in female rhesus macaques. A central part of early parental care is therefore assisting new infants to acquire their place in the hierarchy, with maternal kin intervening in conflicts on a related infant's behalf (Berman, 1980). When a female intervenes in the conflict of a maternal infant against a lower ranking female, this benefits the infant because she wins her conflict and reinforces her rank over the lower ranking individual (Chapais, 1995). But this behaviour also benefits the maternal female who intervened. She receives an indirect fitness benefit from helping her infant kin to establish her rank, but she also receives a direct fitness benefit for reinforcing her own rank over the infant's opponent (Chapais, 2001). Lastly, both the female and the infant benefit from supporting the stability of the dominance hierarchy which provides access to resources for them and their matriline (Chapais, 1992, 1995, 2001; Kaplan, 1978). Combined, these results suggest that providing support for new maternal kin is highly beneficial for female rhesus macaques. However, support of female relatives and their new infants may also be time consuming, particularly for matrilines with large numbers of neonates. In matrilines with three females and one infant, the task of infant support can be divided

amongst the three females. But when the ratio of infants to females increases – when there are two or three infants between three adult females – the amount of time and energy a single female must expend in support of maternally related infants is greater. Within the birthing season the benefits of kin-directed support are thus exaggerated, potentially becoming the optimal and most time-consuming behavioural strategy, eclipsing the amount of time available for exchanging grooming for coalitionary support with non-kin. Indeed, a consistent finding in our study was that females with a larger relative number of infants in their matriline responded less to recruitment calls; they were slower to look, and they looked for less time compared to females with relatively fewer infants in their matriline. Females' weakened responses in relation to infant presence could be indicative of the changing costs and benefits associated with supporting non-kin that arise during the birthing season. In contrast, the mating season is characterised by a higher rate of interactions with non-kin and a greater number of conflicts in which to provide support. If we ran this experiment during the mating season, when females are less likely to engage in kin-centric coalitionary support, and thus have more time available, it is possible we would find evidence for the exchange of grooming-for-support amongst non-kin. However, the mating season also introduces female-female competition for high quality mates – another rank-related resource that incentivises females to support the status quo. Future studies should examine the exchange of grooming for coalitionary support in the mating season to determine the extent to which rates of exchange vary across seasons. Studies should also explore how other social exchanges like grooming for tolerance are affected by seasonal shifts in kin-directed behaviours.

The inconsistency of results across studies of the exchange of grooming for coalitionary support in primates suggest we should also examine alternative explanations outside of reciprocal exchange. As previously noted, many studies do not account for kinship, or only account for maternal relatedness. Biases toward interacting with paternal kin (Widdig et al., 2001) and the benefits derived from kin selection could therefore explain some of these results. However, even if these studies were able to fully account for kinship, there are still alternative ways to explain the frequently documented correlation between the amount of grooming and coalitionary support directed within pairs of primates that do not involve the reciprocal exchange of services. For example, cooperation that provides both partners with mutual benefits could produce a pattern of repeated cooperation without reciprocity.

Individuals may form coalitions with unrelated partners to defend shared resources in a mutually beneficial manner as a form of by-product mutualism. That is, coalitions can benefit both partners equally by increasing their ability to defend or access resources. For example, pairs of low-ranking male olive baboons (*Papio anubis*) often form coalitions to overcome high-ranking males guarding oestrous females (Bernstein, 1988; Packer, 1977). These coalitions are mutually beneficial because coalition partners gain equal reproductive benefits from mating with the female (Bernstein, 1988). When this behaviour was first observed it was misidentified as reciprocity because males appeared to take turns supporting and mating with females (Packer, 1977). However, further examination revealed that both males were mating with the oestrous females; netting an equal benefit from their combined efforts (Bernstein, 1988). Coalitions for mutual benefit are also seen in the defence of food patches in chimpanzees (Connor, 2010; Williams, Oehlert, Carlis, &

Pusey, 2004), and hyenas (*Crocuta crocuta*) (Smith et al., 2010). As an example, two unrelated chimpanzees, chimp A and chimp B, are feeding in the same fruit tree. A third individual, chimp C, approaches and attempts to displace chimp A from the tree. If chimp B considers their own access to fruit tree threatened by the newcomer, they may intervene in the conflict, forming a coalition with chimp A, to defend their own access to the fruit tree. Superficially, it could appear as though chimp B provided support in defence of chimp A, but in fact chimp B formed the coalition for their own benefit – to retain access to the fruit tree.

Animals living in dominance hierarchies can form mutually beneficial coalitions in a manner consistent with support of the status quo – only forming coalitions to protect a shared resource threatened by lower-ranking individuals, or to remove lower-ranking individuals from a resource patch (Kaplan, 1978; Massey, 1977; Silk, 1992). If coalition partners repeatedly associate because of shared spatial ranges or social status, a pattern of repeated support would emerge over time, resembling reciprocal exchange. There is evidence that proximity can lead to repeated coalitionary support; a study of captive rhesus and stump-tailed macaques found a positive correlation between a dyad's shared proximity and the frequency with which they formed coalitions; pairs that shared proximity more frequently formed more frequent coalitions (de Waal & Luttrell, 1988).

To test the hypothesis that individuals are providing support for mutual resource defence through by-product mutualism, one could investigate the relationship theoretically, observationally, and experimentally. To test the hypothesis theoretically, an agent-based model simulating repeated interactions between individuals assigned random locations in a two-dimensional space could be generated in order to determine if a pattern of association like that which is observed

in correlational studies of primate reciprocity emerges from shared proximity alone. An observational investigation of the hypothesis could compare the various characteristics of observed coalition partners such as; sex, rank, age, and proportion of time spent in proximity. If there is a correlation showing that coalitionary support is more likely to occur between same-sex partners of adjacent ranks, similar age, and shared proximity, then mutual benefit may be a more parsimonious explanation of the correlation between grooming and coalitionary support than reciprocity. Finally, an experimental test of this hypothesis could be carried out by creating resource patches to artificially manipulate individuals' most common proximity partners. If the partitioning were maintained, and individual's new proximity partners held constant, individuals would be expected to form coalitions more frequently with their new proximity partners.

The same characteristics that provide partners with the opportunity to repeatedly support one another by means other than reciprocity can also lead to repeated grooming interactions. Past research, including two studies of captive rhesus macaques, found that individuals are more likely to groom and form relationships with groupmates they most closely resemble in terms of rank, sex, and age (Sarah F. Brosnan & Waal, 2002; de Waal, 1991; de Waal & Luttrell, 1986). Similar homophilic patterns have been found in associations tendencies of chimpanzees and wild barbary macaques – individuals prefer to associate and cooperate with groupmates more like themselves (Massen & Koski, 2014; Molesti & Majolo, 2016). Therefore, it is possible that females form grooming relationships and coalition partnerships with the same groupmates based on shared proximity and demographic characteristics, creating the correlation between grooming and coalition partners documented in so many studies (Schino, 2007).

Chapter 3: General Conclusion

Cooperation, particularly between non-kin, has been the focus of intense scientific inquiry for the last century. The most widely studied explanation for cooperation between non-kin is reciprocity. Research has focused disproportionately on one of the three main forms of reciprocity, direct reciprocity, despite evidence the other two forms, generalized and indirect reciprocity, are evolutionarily stable and present in nature. The study of reciprocity tends to focus on patterns of reciprocal exchange expressed across either short or long periods of time, but rarely are both temporal possibilities explored in the same study. Lastly, despite the known effects of relatedness as a driver of cooperation, most studies of reciprocity on non-captive subjects only account for maternal relatedness between cooperative partners, failing to rule out the effect of kin selection through paternal relatedness.

This thesis explored direct and generalized reciprocity expressed over both short and long periods of interaction in the exchange of grooming for coalitionary support using adult female rhesus macaques as a study system. Our purpose was to investigate a well-studied cooperative exchange central to primate social organization, and to explore multiple forms of reciprocity in both available time frames without the confounding effects of kin selection.

The results of our experiment show that grooming had no effect on females' willingness to provide coalitionary support. Contrary to prior results, we found no evidence of direct or generalized reciprocity in the exchange of grooming for coalitionary support. There was nothing to suggest that either form of cooperation was present after a single cooperative interaction or after extended periods of repeated cooperation.

Our experiment is the first study of grooming-for-support conducted in which paternal and maternal relatedness was known for all study subjects. Our study is also the first experimental study exploring grooming for coalitionary support in old world monkeys to find no evidence of direct reciprocity. Paternal relatedness could underlie previous positive results of cooperative behaviours that were presumed to occur between non-kin. This has important implications for the design of future research, where relatedness should be accounted for more fully when possible.

Our study also represents the first experimental test of generalized reciprocity outside a laboratory setting. Our null result is in contrast to the results of experiments using lab animals that found animals were more willing to help after receiving help. However, our null result is consistent with the results of correlational studies in wild and free-ranging primates that found individuals were not more likely to cooperate with anyone after receiving cooperation. The differences found between lab-based and wild studies suggest that generalized reciprocity may be a cooperative strategy animal use in laboratory tasks when presented with no other options.

Lastly, ours is the first experimental study to investigate direct reciprocity as an explanation of grooming-for-support using both short- and long-term patterns of cooperative behaviour. Past experiments in vervet monkeys and baboons demonstrated that females are more willing to provide coalitionary support to a grooming partner following a single grooming event. We replicated that study design, but also investigated whether grooming accumulated with a partner in the year prior to our experiment was a better predictor of willingness to provide support to a grooming partner. We found that grooming did not predict females' willingness to provide coalitionary support over the short- or long-term. Below we present three explanations that could explain our null result.

The first explanation is that although our results are contrary to the findings of previous playback studies of grooming for support in baboons and vervet monkey, they are consistent with results from correlational studies in rhesus and Japanese macaques. The agreement of our results with those from other aggressive and despotic species suggest that exchanging grooming for coalitionary support may be a more important source of fitness benefits in some species compared to others. We suggest that in aggressive species with steep dominance hierarchies – where conflicts are costly and dominance rank is closely tied to fitness – the benefits females gain via by-product mutualism by forming coalitions that reinforce their dominance rank are greater than those benefits they could gain by reciprocally exchanging their support for grooming.

The second explanation for our null result is that it could be a symptom of the season in which we conducted our experiment. Females willingness to provide support decreased significantly across our study period, which coincided with the island's yearly birthing season, as the number of infants in the group increased. Females' may have directed the bulk of their coalitionary support to the time-consuming task of supporting maternal infants in conflicts to help female's new kin establish their own ranks within the hierarchy which would give infants access to rank relate benefits. Support directed at maternal infants provides inclusive fitness benefits to the supporting female but is also a time-consuming form of parental care that leaves little time for grooming exchanges with non-kin, particularly in the birthing season when non-kin interactions are rarer to begin with.

The final explanation for our result that receiving grooming does not affect females' willingness to provide coalitionary support is that female rhesus macaques

and other primates may not exchange grooming for support according to direct reciprocity. Instead coalitionary support might be an example of by-product mutualism, wherein individuals form coalitions for mutual benefit through defence of shared resources. The often-observed correlation between grooming and support found in many studies could be a result of individuals homophilic tendencies to interact with individuals like themselves – leading individuals to form mutual coalitions and grooming relationships with the same individuals based on shared proximity and demographic characteristics like age, sex, and rank.

Future research should focus on experimental study designs that are able to infer a causal relationship between cooperation given and received, exploring the effect of individual and accumulated cooperative acts. These studies should take place in species with a diverse range of social structures to explore how the costs of cooperative behaviours may vary between egalitarian and despotic social systems. Researchers should endeavour to acquire complete relatedness information of study subjects, not just maternal relatedness, in order to avoid muddying conclusions with the possibility of kinship biasing results. Previous research on grooming and coalitionary support has focused too heavily on the role of direct reciprocity. Future research should also take a wider view of the possible mechanisms that might underpin these two behaviours, including kin selection, by-product mutualism, and multiple forms of reciprocity. Grooming may be exchanged for support via direct reciprocity, but it is not the only reason individuals provide coalitionary support to one another. A single cooperative behaviour can evolve as a result of multiple cooperative mechanisms. Therefore, to understand a single cooperative behaviour, we must exhaust every cooperative explanation.

References

- Akaike, H. (1974). A New Look at the Statistical Model Identification. *IEEE Transactions on Automatic Control*, 19(6), 717–723. <https://doi.org/10.1093/ietfec/e90-a.12.2762>
- Akçay, Ç., Reed, V. A., Campbell, S. E., Templeton, C. N., & Beecher, M. D. (2010). Indirect reciprocity: Song sparrows distrust aggressive neighbours based on eavesdropping. *Animal Behaviour*, 80(6), 1041–1047. <https://doi.org/10.1016/j.anbehav.2010.09.009>
- Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, 49(3), 227–267. <https://doi.org/10.1080/14794802.2011.585831>
- Arnold, K., & Auriel, F. (2011). Postconflict Reconciliation. In *Primates in perspective* (pp. 608–625). <https://doi.org/10.1111/j.1540-4560.2008.00563.x>
- Aureli, F., & Schaffner, C. M. (2002). Relationship Assessment Through Emotional Mediations. *Behavior*, 139, 393–420.
- Axelrod, R., & Hamilton, W. D. (1981). The Evolution of Cooperation The Evolution of Cooperation. *Evolution*, 211(4489), 1390–1396. <https://doi.org/10.1086/383541>
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 266(1420), 665–670. <https://doi.org/10.1098/rspb.1999.0687>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.1013/s72949250sef3434>
- Bercovitch, F. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behavior*, 36, 1198–1209. [https://doi.org/10.1016/S0003-3472\(88\)80079-4](https://doi.org/10.1016/S0003-3472(88)80079-4)
- Bergmüller, R., Johnstone, R. A., Russell, A. F., & Bshary, R. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, 76(2), 61–72. <https://doi.org/10.1016/j.beproc.2007.07.001>
- Berman, C. M. (1980). Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *International Journal of Primatology*, 1(2), 153–170. <https://doi.org/10.1007/BF02735595>
- Bernstein, I. S. (1988). Kinship and Behavior in Primates. *Behavior Genetics*, 18(4), 511–523. <https://doi.org/10.1007/s10764-005-8862-x>
- Bernstein, I. S., & Ehardt, C. L. (1985). Agonistic aiding: Kinship, rank, age, and sex influences. *American Journal of Primatology*, 8(1), 37–52.

<https://doi.org/10.1002/ajp.1350080105>

- Blomquist, G. E., Sade, D. S., & Berard, J. D. (2011). Rank-Related Fitness Differences and Their Demographic Pathways in Semi-Free-Ranging Rhesus Macaques (*Macaca mulatta*). *International Journal of Primatology*, 32(1), 193–208. <https://doi.org/10.1007/s10764-010-9461-z>
- Borgeaud, C., & Bshary, R. (2015). Wild Vervet Monkeys Trade Tolerance and Specific Coalitionary Support for Grooming in Experimentally Induced Conflicts. *Current Biology*, 3011–3016. <https://doi.org/10.1016/j.cub.2015.10.016>
- Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., ... Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports*, 3(January), 1042. <https://doi.org/10.1038/srep01042>
- Brent, L. J. N., MacLarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque social networks. *Behavioral Ecology and Sociobiology*, 67(3), 349–359. <https://doi.org/10.1007/s00265-012-1455-8>
- Brosnan, S. F., Silk, J. B., Henrich, J., Mareno, M. C., Lambeth, S. P., & Schapiro, S. J. (2009). Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition*, 12(4), 587–597. <https://doi.org/10.1007/s10071-009-0218-z>
- Brosnan, S. F., & Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature*, 13(1), 129–152. <https://doi.org/10.1007/s12110-002-1017-2>
- Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42(4), 551–564. [https://doi.org/10.1016/S0003-3472\(05\)80239-8](https://doi.org/10.1016/S0003-3472(05)80239-8)
- Brown, J. L. (1983). Cooperation: a biologist's dilemma. *Advances in the Study of Behavior*, 13, 1–37. <https://doi.org/10.1034/2324-d242ke34>
- Bshary, R. (2002). Biting cleaner fish use altruism to deceive image-scoring client reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 269(1505), 2087–2093. <https://doi.org/10.1098/rspb.2002.2084>
- Bshary, R., & Bergmüller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology*, 21(2), 405–420. <https://doi.org/10.1111/j.1420-9101.2007.01482.x>
- Bshary, R., & Grutter, A. S. (2006). Image scoring and cooperation in a cleaner fish mutualism. *Nature*, 441(7096), 975–8. <https://doi.org/10.1038/nature04755>
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference. *Sociological Methods & Research*, 33(2), 261–304. <https://doi.org/10.1177/0049124104268644>

- Campbell, C. (2011). *Primates in Perspective*. Oxford University Press.
<https://doi.org/10.1023/375934fj322c2>
- Carter, G. (2014). The reciprocity controversy. *Animal Behavior and Cognition*, 1(3), 368–386. <https://doi.org/10.12966/abc.08.11.2014>
- Carter, G. G., & Wilkinson, G. S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings. Biological Sciences / The Royal Society*, 280(1753), 20122573.
<https://doi.org/10.1098/rspb.2012.2573>
- Chapais, B. (1983). Dominance, relatedness and the structure of female relationships in rhesus monkeys. In *Primate Social Relationships* (pp. 208–217). Blackwell Scientific Publications. [https://doi.org/10.1026/S0003-3472\(05\)83434-](https://doi.org/10.1026/S0003-3472(05)83434-)
- Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In *Coalitions and Alliances in Humans and Other Animals* (pp. 29–59). Oxford Science Publications. <https://doi.org/10.1016/24013-232380851->
- Chapais, B. (1995). Alliances as a means of competition in primates. *American Journal of Physical Anthropology*, 38, 115–136.
- Chapais, B. (2001). Primate Nepotism: What is the explanatory value of Kin, 22(2), 203–229. <https://doi.org/10.1023/A:1005619430744>
- Chapais, B., Girard, M., & Primi, G. (1991). Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*, 41(3), 481–491. [https://doi.org/10.1016/S0003-3472\(05\)80851-6](https://doi.org/10.1016/S0003-3472(05)80851-6)
- Cheney, D. L. (1977). The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behavioral Ecology and Sociobiology*, 2(3), 303–318. <https://doi.org/10.1007/BF00299742>
- Cheney, D. L. (2011). Extent and limits of cooperation in animals. *Proceedings of the National Academy of Sciences*, 108(Supplement 2), 10902–10909.
<https://doi.org/10.1073/pnas.1100291108>
- Cheney, D. L., Moscovice, L. R., Heesen, M., Mundry, R., & Seyfarth, R. M. (2010). Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences of the United States of America*, 107(21), 9562–9566. <https://doi.org/10.1073/pnas.1001862107>
- Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, 28(2), 362–367. [https://doi.org/10.1016/S0003-3472\(80\)80044-3](https://doi.org/10.1016/S0003-3472(80)80044-3)
- Cheney, D. L., & Seyfarth, R. M. (1982). How vervet monkeys perceive their grunts: Field playback experiments. *Animal Behaviour*, 30(3), 739–751.
[https://doi.org/10.1016/S0003-3472\(82\)80146-2](https://doi.org/10.1016/S0003-3472(82)80146-2)

- Cheney, D. L., & Seyfarth, R. M. (1989). Redirected Aggression and Reconciliation Among Vervet Monkeys, *Cercopithecus Aethiops*. *Behaviour*, *110*(1–4), 258–275. <https://doi.org/10.1163/156853989X00501>
- Cheney, D. L., & Seyfarth, R. M. (1990). The representation of social relations by monkeys, *37*, 167–196.
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995a). The responses of female baboons to anomalous social interactions: Evidence for causal reasoning? *Journal of Comparative Psychology*.
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995b). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, *50*(1), 249–257. <https://doi.org/10.1006/anbe.1995.0237>
- Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*(7269), 51–7. <https://doi.org/10.1038/nature08366>
- Connor, R. C. (1986). Pseudo-reciprocity: Investing in mutualism. *Animal Behaviour*, *34*(5), 1562–1566. [https://doi.org/10.1016/S0003-3472\(86\)80225-1](https://doi.org/10.1016/S0003-3472(86)80225-1)
- Connor, R. C. (1995a). Altruism among non-relatives: alternatives to the “Prisoner’s Dilemma.” *Trends in Ecology & Evolution*, *10*(2), 84–86. [https://doi.org/10.1016/S0169-5347\(00\)88988-0](https://doi.org/10.1016/S0169-5347(00)88988-0)
- Connor, R. C. (1995b). The Benefits of Mutualism: A Conceptual Framework. *Biological Reviews*, *70*(3), 427–457. <https://doi.org/10.1111/j.1469-185X.1995.tb01196.x>
- Connor, R. C. (2010). Cooperation beyond the dyad: On simple models and a complex society. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2687–2697. <https://doi.org/10.1098/rstb.2010.0150>
- Cords, M. (1988). Resolution of aggressive conflicts by immature long-tailed macaques *Macaca fascicularis*. *Animal Behaviour*, *36*(4), 1124–1135. [https://doi.org/10.1016/S0003-3472\(88\)80072-1](https://doi.org/10.1016/S0003-3472(88)80072-1)
- Crawley, M. J. (2008). *Statistics: An Introduction Using R*. New York, NY: John Wiley & Sons. <https://doi.org/10.1023/F0003-34780851->
- de Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes*. Harper and Row. <https://doi.org/10.1023/7345f351>
- de Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis FRANS. *Animal Behavior*, *383*–395. <https://doi.org/10.10112/4230003-340851>
- de Waal, F. B. M. (1997). The Chimpanzee’s Service Economy: Food for Grooming. *Evolution and Human Behavior*, *18*, 375–386. <https://doi.org/10.1016/S1090->

- de Waal, F. B. M., & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Primateology*, *46*, 215–234.
- de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanisms of Social Reciprocity in Three Primate Species: Symmetrical Relationship Characteristics or Cognition? *Ethology and Sociobiology*, *18*, 101–118.
- Di Blanco, Y., & Hirsch, B. T. (2006). Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): The importance of within-group spatial position. *Behavioral Ecology and Sociobiology*, *61*(2), 173–182.
<https://doi.org/10.1007/s00265-006-0248-3>
- Dugatkin, L. A. (1977). *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press. <https://doi.org/10.1016/T0003-3472>
- Dunbar, R. (1991). Functional Significance of Social Grooming in Primates, (January 1991). <https://doi.org/10.1159/000156574>
- Edenbrow, M., Bleakley, B. H., Darden, S. K., Tyler, C. R., Ramnarine, I. W., & Croft, D. P. (2017). The Evolution of Cooperation: Interacting Phenotypes among Social Partners. *The American Naturalist*, *189*(6), 000–000.
<https://doi.org/10.1086/691386>
- Emmons, R. A., & McCullough, M. E. (2004). *The Psychology of Gratitude*. Oxford University Press. <https://doi.org/10.104/S0003853430851->
- Fischer, J. (2004). Emergence of individual recognition in young macaques. *Animal Behaviour*, *67*(4), 655–661. <https://doi.org/10.1016/j.anbehav.2003.08.006>
- Fischer, J., Metz, M., Cheney, D. L., & Seyfarth, R. M. (2001). Baboon responses to graded bark variants. *Animal Behaviour*, *61*(5), 925–931.
<https://doi.org/10.1006/anbe.2000.1687>
- Fischer, J., Noser, R., & Hammerschmidt, K. (2013). Bioacoustic field research: A primer to acoustic analyses and playback experiments with primates. *American Journal of Primatology*, *75*(7), 643–663. <https://doi.org/10.1002/ajp.22153>
- Flack, J. C., & de Waal, F. B. M. (2004). Dominance style, social power, and conflict management: a conceptual framework. In *Macaque Societies* (pp. 157–186). Cambridge University Press. <https://doi.org/10.1016/S0003-34720851>
- Fruteau, C., Voelkl, B., van Damme, E., & Noe, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences*, *30*(29), 193–213.
<https://doi.org/10.1073/pnas.0812280106>
- Fugate, J. M. B., Gouzoules, H., & Nygaard, L. C. (2008). Recognition of Rhesus Macaque (*Macaca mulatta*) Noisy Screams : Evidence from Conspecifics and

- Human Listeners, 604(March), 594–604. <https://doi.org/10.1002/ajp.20533>
- Getty, T., Olendorf, R., Getty, T., Scribner, K., & B, P. R. S. L. (2004). Cooperative nest defence in red-winged blackbirds : Reciprocal altruism , Cooperative nest defence in red – winged blackbirds : reciprocal altruism , kinship or by – product mutualism ? References Article cited in :, (February). <https://doi.org/10.1098/rspb.2003.2586>
- Gfrerer, N., & Taborsky, M. (2017). Working dogs cooperate among one another by generalised reciprocity. *Scientific Reports*, 7(October 2016), 43867. <https://doi.org/10.1038/srep43867>
- Gfrerer, N., & Taborsky, M. (2018). Working dogs transfer different tasks in reciprocal cooperation. *Biology Letters*, 14(2), 20170460. <https://doi.org/10.1098/rsbl.2017.0460>
- Gomes, C. M., Mundry, R., Boesch, C., B, P. R. S., Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees Subject collections Email alerting service Long-term reciprocation of grooming in wild West African chimpanzees, 699–706. <https://doi.org/10.1098/rspb.2008.1324>
- Gouzoules, H., & Gouzoules, S. (2000). Agonistic screams differ among four species of macaques : the significance of motivation-structural rules, 501–512. <https://doi.org/10.1006/anbe.1999.1318>
- Gouzoules, H., Gouzoules, S., & Tomaszycki, M. (1998). Agonistic screams and the classification of dominance relationships : are monkeys fuzzy logicians ? *Animal Behavior*, 0, 51–60. <https://doi.org/10.1002/ajp.221>
- Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams : representational signaling in the recruitment of agonistic aid. *Animal Behavior*, 32, 182–193. <https://doi.org/10.1024/j/4f41>
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, 24(4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Hamilton, I., & Taborsky, M. (2005). Contingent movement and cooperation evolve under generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 272(1578), 2259–2267. <https://doi.org/10.1098/rspb.2005.3248>
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7(1), 1–16. [https://doi.org/10.1016/0022-5193\(64\)90038-4](https://doi.org/10.1016/0022-5193(64)90038-4)
- Hammerstein, P. (2003). Why is reciprocity so rare in social animals? In *Genetic and Cultural Evolution of Cooperation* (pp. 98–109). The MIT Press. <https://doi.org/10.7551/mitpress/3232.003.0007>

- Hart, B. L., & Hart, L. A. (1992). Reciprocal allogrooming in impala. *Animal Behavior*, *44*, 1073–1083. <https://doi.org/10.1002/3fe221>
- Hauser, M. D. (1998). Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, *55*(2), 1647–1658. <https://doi.org/10.1006/anbe.1997.0712>
- Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behavior*. <https://doi.org/10.1006/anbe.1994.1264>
- Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, *40*(1), 47–59. <https://doi.org/10.1007/BF02557701>
- Horrocks, J., & Hunte, W. (1983). Maternal rank and offspring rank in vervet monkeys: An appraisal of the mechanisms of rank acquisition. *Animal Behaviour*, *31*(3), 772–782. [https://doi.org/10.1016/S0003-3472\(83\)80234-6](https://doi.org/10.1016/S0003-3472(83)80234-6)
- Hutchins, M., & Barash, D. P. (1976). Grooming in Primates: Implications for its Utilitarian Function. *Primates*, *17*(2), 145–150. <https://doi.org/10.1007/bf02382848>
- Jaeggi, A. V., De Groot, E., Stevens, J. M. G., & Van Schaik, C. P. (2013). Mechanisms of reciprocity in primates: Testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, *34*(2), 69–77. <https://doi.org/10.1016/j.evolhumbehav.2012.09.005>
- Jahn-Eimermacher, A., Lasarzik, I., & Raber, J. (2011). Statistical analysis outcomes in behavioral experiments. *Behavioural Brain Research*, *221*(1), 271–275. <https://doi.org/10.1016/j.bbr.2011.03.007>.Statistical
- Kaplan, J. R. (1978). Fight interference and altruism in rhesus monkeys. *American Journal of Physical Anthropology*, *49*(2), 241–249. <https://doi.org/10.1002/ajpa.1330490212>
- Kapsalis, E., & Berman, C. M. (1996a). Models of Affiliative Relationships among Free-Ranging Rhesus Monkeys (*Macaca mulatta*) I . Criteria for Kinship, *133*(15), 1209–1234. <https://doi.org/10.1163/156853996X00378>
- Kapsalis, E., & Berman, C. M. (1996b). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) .2. Testing predictions for three hypothesized organizing principles. *Behaviour*, *133*(15), 1235–1263. <https://doi.org/10.1163/156853996X00378>
- Kern, J. M., & Radford, A. N. (2018). Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proceedings of the National Academy of Sciences*, *0*, 201801000. <https://doi.org/10.1073/pnas.1801000115>
- Kessler, M. J., & Rawlins, R. G. (1986). *The Cayo Santiago Macaques History Behavior Biology*. State University of New York Press. <https://doi.org/10.1004/3t323221>

- Krams, I., Krama, T., & Igaune, K. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher, 599–605. <https://doi.org/10.1007/s00265-007-0484-1>
- Kristine H. Onishi and Renée Baillargeon. (2005). Do 15-Month-Old Infants Understand False Beliefs? *Science*, 308(5719), 255–258. <https://doi.org/10.1126/science.1107621>.Do
- Kurland, J. A. (1977). Kin Selection in Japanese Macaques. *Contributions of Primatology*, 12, 1–145. <https://doi.org/10.1093/oso/9780198733058.003.0004>
- Le Prell, C. G., Hauser, M. D., & Moody, D. B. (2002). Discrete or graded variation within rhesus monkey screams? Psychophysical experiments on classification. *Animal Behaviour*, 63, 47–62. <https://doi.org/10.1006/anbe.2001.1888>
- Leimar, O., & Hammerstein, P. (2001). Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 268(1468), 745–753. <https://doi.org/10.1098/rspb.2000.1573>
- Leimar, O., & Hammerstein, P. (2010). Cooperation for direct fitness benefits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2619–2626. <https://doi.org/10.1098/rstb.2010.0116>
- Leimgruber, K. L., Ward, A. F., Widness, J., Norton, M. I., Olson, K. R., Gray, K., & Santos, L. R. (2014). Give what you get: Capuchin monkeys (*Cebus apella*) and 4-year-old children pay forward positive and negative outcomes to conspecifics. *PLoS ONE*, 9(1). <https://doi.org/10.1371/journal.pone.0087035>
- Lemasson, A., Palombit, R. A., & Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): Evidence from playback experiments. *Behavioral Ecology and Sociobiology*, 62(6), 1027–1035. <https://doi.org/10.1007/s00265-007-0530-z>
- Liemar, O., & Connor, R. C. (2003). By-product Benefits, Reciprocity, and Pseudoreciprocity in mutualism. In *Genetic and Cultural Evolution of Cooperation* (pp. 203–22). MIT Press. <https://doi.org/10.7551/mitpress/3232.003.0013>
- Madlon-Kay, S., Brent, L. J. N., Montague, M. J., Heller, K. A., & Platt, M. L. (2017). Using machine learning to discover latent social phenotypes in free-ranging macaques. *Brain Sciences*, 7(7), 1–24. <https://doi.org/10.3390/brainsci7070091>
- Majolo, B., Schino, G., & Aureli, F. (2012). The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, 83(3), 763–771. <https://doi.org/10.1016/j.anbehav.2011.12.026>
- Manson, J. H., Navarrete, C. D., Silk, J. B., & Perry, S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, 67(3), 493–500. <https://doi.org/10.1016/j.anbehav.2003.05.009>

- Massen, J. M., & Koski, S. E. (2014). Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35(1), 1–8. <https://doi.org/10.1016/j.evolhumbehav.2013.08.008>
- Massey, A. (1977). Agonistic aids and kinship in a group of pigtail macaques. *Behavioral Ecology and Sociobiology*, 2(1), 31–40. <https://doi.org/10.1007/BF00299286>
- Matheson, M. D., & Bernstein, I. S. (2000). Grooming, social bonding, and agonistic aiding in rhesus monkeys. *American Journal of Primatology*, 51(3), 177–186. [https://doi.org/10.1002/1098-2345\(200007\)51:3<177::AID-AJP2>3.0.CO;2-K](https://doi.org/10.1002/1098-2345(200007)51:3<177::AID-AJP2>3.0.CO;2-K)
- Maynard, S. (1964). Group Selection and Kin Selection. *Nature*, 202, 693–694. <https://doi.org/10.1038/201464a0>
- McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*. <https://doi.org/10.1006/anbe.1994.1052>
- McGregor, P. K. (1992). Quantifying Responses to Playback: One, Many, or Composite Multivariate Measures. In *Playback and the Studies of Animal Communication* (pp. 79–96). Springer, Boston, MA.
- McHugh, M. L. (2012). Interrater reliability: the kappa statistic. *Biochemia Medica*, 276–282. <https://doi.org/10.11613/BM.2012.031>
- Melis, A. P., & Semmann, D. (2010). How is human cooperation different? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2663–2674. <https://doi.org/10.1098/rstb.2010.0157>
- Milinski, M. (1987). TIT FOR TAT in sticklebacks and the evolution of cooperation. *Nature*, 325, 433–435. <https://doi.org/10.1145/3132847.3132886>
- Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. https://doi.org/10.1007/3-540-28277-7_6
- Molesti, S., & Majolo, B. (2016). Cooperation in wild Barbary macaques: factors affecting free partner choice. *Animal Cognition*, 19(1), 133–146. <https://doi.org/10.1007/s10071-015-0919-4>
- Molesti, S., & Majolo, B. (2017). Evidence of direct reciprocity, but not of indirect and generalized reciprocity, in the grooming exchanges of wild Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology*, 79, e22679. <https://doi.org/10.1002/ajp.22679>
- Monica Y., B., & David, D. (2006). Gratitude and Prosocial Behavior: Helping When It Costs You. *Psychological Science*, 17(4), 319–325. <https://doi.org/10.1111/j.1467-9280.2006.01705.x>

- Nieuwenhuijsen, K., Slob, A. K., & Van Der Werff Ten Bosch, J. J. (1988). Gender-related behaviors in group-living stump-tail macaques. *Psychobiology*, *16*(4), 357–371. <https://doi.org/10.3758/BF03327333>
- Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, *71*(1), 1–18. <https://doi.org/10.1016/j.anbehav.2005.03.037>
- Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, *35*(1), 1–11. <https://doi.org/10.1007/BF00167053>
- Nowak, M. A., & Roch, S. (2007). Upstream reciprocity and the evolution of gratitude. *Proceedings of the Royal Society B-Biological Sciences*, *274*(1610), 605–610. <https://doi.org/10.1098/rspb.2006.0125>
- Nowak, M. A., & Sigmund, K. (1998). Evolution of Indirect Reciprocity By Image Scoring. *Nature*, *393*(June), 573–577. <https://doi.org/10.1038/31225>
- Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*(October), 1291–1298. <https://doi.org/10.1038/31225>
- O’Keefe, R. R., Lifshitz, K., & Linn, G. (1982). Relationships among dominance relationships among dominance inter-animal spatial proximity and affiliative social behavior in stump-tail macaques (*Macaca arctoides*). *International Journal of Primatology*, *9*(1), 331–339. [https://doi.org/10.1016/0304-3762\(83\)90012-3](https://doi.org/10.1016/0304-3762(83)90012-3)
- Onishi, K., Yamada, K., & Nakamichi, M. (2013). Grooming-related feeding motivates macaques to groom and affects grooming reciprocity and episode duration in Japanese macaques (*Macaca fuscata*). *Behavioural Processes*, *92*, 125–130. <https://doi.org/10.1016/j.beproc.2012.11.011>
- Owren, M. J., & Rendall, D. (2003). Salience of caller identity in rhesus monkey (*Macaca mulatta*) coos and screams: perceptual experiments with human (*Homo sapiens*) listeners. *Journal of Comparative Psychology*, *117*(4), 380–390. <https://doi.org/10.1037/0735-7036.117.4.380>
- Packer C. (1977). Reciprocal altruism in *Papio anubis*. *Nature*, *265*(1975), 441–443. <https://doi.org/10.1038/265441a0>
- Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of ‘friendships’ to female baboons: experimental and observational evidence. *Animal Behaviour*, *54*(3), 599–614. <https://doi.org/10.1006/anbe.1996.0457>
- Pfefferle, D., Heistermann, M., Hodges, J. K., & Fischer, J. (2008). Male Barbary macaques eavesdrop on mating outcome: a playback study. *Animal Behaviour*, *75*(6), 1885–1891. <https://doi.org/10.1016/j.anbehav.2007.12.003>
- Pfefferle, D., Ruiz-Lambides, A. V., & Widdig, A. (2015). Male rhesus macaques use

- vocalizations to distinguish female maternal, but not paternal, kin from non-kin. *Behavioral Ecology and Sociobiology*, 69(10), 1677–1686.
<https://doi.org/10.1007/s00265-015-1979-9>
- Pfefferle, D., Ruiz-lambides, A. V., & Widdig, A. (2014). Female rhesus macaques discriminate unfamiliar paternal sisters in playback experiments: support for acoustic phenotype matching. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20131628. <https://doi.org/10.1098/rspb.2013.1628>
- Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M., & Bonhoeffer, S. (2005). Evolution of cooperation by generalized reciprocity. *Proceedings. Biological Sciences / The Royal Society*, 272(1568), 1115–1120.
<https://doi.org/10.1098/rspb.2004.2988>
- Pinheiro, J. C. & Bates, D. M. (2000). *Mixed-Effect Models in S and S-Plus*. Springer, New York, NY: Springer Publishing Company. <https://doi.org/10.1111/j.1420-9101.2011.02307.x>
- Raihani, N. J., & Bshary, R. (2011). Resolving the iterated prisoner's dilemma: Theory and reality. *Journal of Evolutionary Biology*, 24(8), 1628–1639.
<https://doi.org/10.13582/j.1420.2011.02307.f>
- Rand, D. G., Ohtsuki, H., & Nowak, M. A. (2009). Direct reciprocity with costly punishment: Generous tit-for-tat prevails. *Journal of Theoretical Biology*, 256(1), 45–57. <https://doi.org/10.1016/j.jtbi.2008.09.015>
- Rankin, D. J., & Taborsky, M. (2009). Assortment and the evolution of generalized reciprocity. *Evolution*, 63(7), 1913–1922. <https://doi.org/10.1111/j.1558-5646.2009.00656.x>
- Rendall, D. J., Owren, M. J., & Rodman, P. S. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *The Journal of the Acoustical Society of America*, 103(1), 602–614.
<https://doi.org/10.1121/1.421104>
- Rendall, D. J., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging Rhesus Monkeys. *Animal Behaviour*, 51, 1007–1015. <https://doi.org/10.1006/anbe.1996.0103>
- Rosati, A. G., Arre, A. M., Platt, M. L., & Santos, L. R. (2016). Rhesus monkeys show human-like changes in gaze following across the lifespan. *Proceedings of the Royal Society B: Biological Sciences*, 283(1830), 20160376.
<https://doi.org/10.1098/rspb.2016.0376>
- Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, 5(7), 1421–1425. <https://doi.org/10.1371/journal.pbio.0050196>
- Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, 62(4), 499–505.
<https://doi.org/10.1007/s00265-007-0474-3>

- Schino, G. (2001). Grooming, competition and social rank among female primates: A meta-analysis. *Animal Behaviour*, 62(2), 265–271.
<https://doi.org/10.1006/anbe.2001.1750>
- Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18(1), 115–120.
<https://doi.org/10.1093/beheco/arl045>
- Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: A meta-analysis. *Biology Letters*, 4(1), 9–11.
<https://doi.org/10.1098/rsbl.2007.0506>
- Schino, G., & Aureli, F. (2009). *Chapter 2 Reciprocal Altruism in Primates. Partner Choice, Cognition, and Emotions. Advances in the Study of Behavior* (1st ed., Vol. 39). Elsevier Inc. [https://doi.org/10.1016/S0065-3454\(09\)39002-6](https://doi.org/10.1016/S0065-3454(09)39002-6)
- Schino, G., & Aureli, F. (2010a). Primate reciprocity and its cognitive requirements. *Evolutionary Anthropology: Issues, News, and Reviews*, 19(4), 130–135.
<https://doi.org/10.1002/evan.20270>
- Schino, G., & Aureli, F. (2010b). The relative roles of kinship and reciprocity in explaining primate altruism. *Ecology Letters*, 13(1), 45–50.
<https://doi.org/10.1111/j.1461-0248.2009.01396.x>
- Schino, G., Di Giuseppe, F., & Visalberghi, E. (2009). The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology*, 115(1), 70–76.
<https://doi.org/10.1111/j.1439-0310.2008.01581.x>
- Schino, G., Di Sorrentino, E. P., & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): Partner choice and the time frame reciprocation. *Journal of Comparative Psychology*, 121(2), 181–188.
<https://doi.org/10.1037/0735-7036.121.2.181>
- Schino, G., & Pellegrini, B. (2009). Grooming in Mandrills and the Time Frame of Reciprocal Partner Choice, 888(March), 884–888.
<https://doi.org/10.1002/ajp.20719>
- Semple, S., Gerald, M. S., & Suggs, D. N. (2009). Bystanders affect the outcome of mother-infant interactions in rhesus macaques. *Proceedings. Biological Sciences / The Royal Society*, 276(1665), 2257–2262.
<https://doi.org/10.1098/rspb.2009.0103>
- Seyfarth, R. M. (1977). A model of social grooming among female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698.
[https://doi.org/http://dx.doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/http://dx.doi.org/10.1016/0022-5193(77)90015-7)
- Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, 28(3), 798–813.

[https://doi.org/10.1016/S0003-3472\(80\)80140-0](https://doi.org/10.1016/S0003-3472(80)80140-0)

- Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541–543. <https://doi.org/10.1038/308541a0>
- Silk, J. B. (1982). Altruism among Female *Macaca radiata* : Explanations and Analysis of Patterns of Grooming and Coalition Formation. *Behavior*, 79(2), 162–188. <https://doi.org/10.1163/156853982x00238>
- Silk, J. B. (1987). Social behavior in evolutionary perspective. In *In Primate Societies* (pp. 318–329). University of Chicago Press. https://doi.org/10.1007/978-1-4612-5202-3_3
- Silk, J. B. (1992). The Patterning of Intervention among Male Bonnet Macaques : Reciprocity , Revenge , and Loyalty, 33(3), 318–325. <https://doi.org/10.1086/204073>
- Silk, J. B. (2002). Kinship in primate groups. *International Journal of Primatology*, 23(4), 849–875. <https://doi.org/10.4324/9781315131207>
- Silk, J. B. (2005). The Evolution of Cooperation in Primate Groups. *Economic Learning and Social Evolution*, xii, 404. <https://doi.org/10.1525/aa.2007.109.2.380>
- Silk, J. B. (2013). Reciprocal altruism. *Current Biology*, 23(18), R827–R828. <https://doi.org/10.1016/j.cub.2013.03.052>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2004a). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, 67(3), 573–582. <https://doi.org/10.1016/j.anbehav.2003.07.001>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2004b). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behavior*, 1–39. <https://doi.org/10.1007/s10071-008-0204-3>
- Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 183–195. <https://doi.org/10.1007/s00265-006-0249-2>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, 64(11), 1733–1747. <https://doi.org/10.1007/s00265-010-0986-0>
- Silk, J. B., & Frank, R. E. (2009). Impatient Traders or Contingent Reciprocators ? Evidence for the Extended Time-Course of Grooming Exchanges in Baboons. *Behavior*, 146(8), 1123–1135. <https://doi.org/10.1163/156853909x406455>
- Slocombe, K. E., Townsend, S. W., & Zuberbühler, K. (2009). Wild chimpanzees

(Pan troglodytes schweinfurthii) distinguish between different scream types: Evidence from a playback study. *Animal Cognition*, 12(3), 441–449.
<https://doi.org/10.1007/s10071-008-0204-x>

Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., & Holekamp, K. E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, 21(2), 284–303. <https://doi.org/10.1093/beheco/arp181>

Sommerfeld, R. D., Krambeck, H.-J., Semmann, D., & Milinski, M. (2007). Gossip as an alternative for direct observation in games of indirect reciprocity. *Proceedings of the National Academy of Sciences*, 104(44), 17435–17440.
<https://doi.org/10.1073/pnas.0704598104>

Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, 8(2), 60–65.
<https://doi.org/10.1016/j.tics.2003.12.003>

Stojan-Dolar, M., & Heymann, E. W. (2010). Vigilance in a cooperatively breeding primate. *International Journal of Primatology*, 31(1), 95–116.
<https://doi.org/10.1007/s10764-009-9385-7>

Strier, K. B. (2011). *Primate Behavioral Ecology* (4th ed.). Upper Saddle River, NJ: Prentice Hall. <https://doi.org/10.4324/9781315663135>

Sylwester, K., & Roberts, G. (2010). Cooperators benefit through reputation-based partner choice in economic games. *Biology Letters*, 6(5), 659–662.
<https://doi.org/10.1098/rsbl.2010.0209>

Therneau, T. M. (2018). *coxme: Mixed Effects Cox Models*.
<https://doi.org/10.4324/978195298425>

Thierry, B., Singh, M., & Kaumanns, W. (2004). Why Macaque Societies. In *Macaque Societies* (pp. 3–11). Cambridge University Press.
<https://doi.org/10.5860/choice.42-5276>

Tiddi, B., Aureli, F., Polizzi Di Sorrentino, E., Janson, C. H., & Schino, G. (2011). Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, 22(3), 663–669.
<https://doi.org/10.1093/beheco/arr028>

Tiddi, B., Aureli, F., & Schino, G. (2012). Grooming up the hierarchy: The exchange of grooming and rank-related benefits in a new world primate. *PLoS ONE*, 7(5), 3–8. <https://doi.org/10.1371/journal.pone.0036641>

Tilford, B. L. (1982). Seasonal rank changes for adolescent and subadult natal males in a free-ranging group of rhesus monkeys. *International Journal of Primatology*, 3(4), 483–490. <https://doi.org/10.1007/BF02693746>

Tim, C. B. (2002). Review : Behavioral Ecology Breeding Together : Kin Selection

and Mutualism in Cooperative. *Science*, 296(5565).
<https://doi.org/10.1457/38359x893>

- Treves, A. (1999). Vigilance and spatial cohesion among blue monkeys. *Folia Primatologica*, 70(5), 291–294. <https://doi.org/10.1159/000021711>
- Trivers, R. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, 46(1), 35–57.
- Voelkl, B., Portugal, S. J., Unsöld, M., Usherwood, J. R., Wilson, A. M., & Fritz, J. (2015). Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. *Proceedings of the National Academy of Sciences of the United States of America*, 112(7), 2115–20. <https://doi.org/10.1073/pnas.1413589112>
- Waal, F. B. M. De, & Brosnan, S. F. (2006). Simple and complex reciprocity in primates. In *Cooperation in primates and humans: Mechanisms and evolution*. (pp. 79–99). New York, NY: Springer. https://doi.org/10.1007/3-540-28277-7_5
- Wallen, K. I. M., & Tannenbaum, P. L. (1997). Hormonal Modulation of Sexual Behavior and Affiliation in Rhesus Monkeys ". *Annual Review of the New York Academy of Sciences*, 807, 185–202. <https://doi.org/10.1111/j.1749-6632.197.tb151920.x>
- Watts, D. P. (2002). Reciprocity and Interchange in the social relationships of wild male chimpanzees. *Behavior*, 139, 343–370. <https://doi.org/10.1163/156853902760102708>
- West-Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *The Quarterly Review of Biology*, 50(1), 1–33. <https://doi.org/10.1253/159573985242708>
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Evolutionary Explanations for Cooperation. *Current Biology*, 17(16), 661–672. <https://doi.org/10.1016/j.cub.2007.06.004>
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2), 415–432. <https://doi.org/10.1111/j.1420-9101.2006.01258.x>
- Widdig, A., Kessler, M. J., Bercovitch, F. B., Berard, J. D., Duggleby, C., Nürnberg, P., ... Schmidtke, J. (2016). Genetic studies on the Cayo Santiago rhesus macaques: A review of 40 years of research. *American Journal of Primatology*, 78(1), 44–62. <https://doi.org/10.1002/ajp.22424>
- Widdig, A., Nürnberg, P., Krawczak, M., Streich, W., & Bercovitch, F. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences*, 98(24), 13769–13773. <https://doi.org/10.1073/pnas.241210198>

- Widdig, A., Nürnberg, P., Krawczak, M., & Streich, W. J. (2002). Affiliation and Aggression among Adult Female Rhesus Macaques : A Genetic Analysis of Paternal Cohorts. *Behavior*, 139(2), 371–391.
<https://doi.org/10.1038/scientificamerican0290-76>
- Wilkinson, G. S. (1984). Reciprocal Food Sharing in Vampire bats. *Nature*, 308, 11–14. <https://doi.org/10.1034/498375937503>
- Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, 68(3), 523–532.
<https://doi.org/10.1016/j.anbehav.2003.09.015>
- Wu, C.-F., Liao, Z.-J., Sueur, C., Sha, J. C. M., Zhang, J., & Zhang, P. (2018). The influence of kinship and dominance hierarchy on grooming partner choice in free-ranging *Macaca mulatta brevicaudus*. *Primates*, 1–8.
<https://doi.org/10.1007/s10329-018-0662-y>
- Nakagawa, N., Nakamichi, M., Sugiura, H. (2010). *The Japanese Macaques*. Springer, Tokyo. 638 <https://doi.org/10.1007/978-4-431-53886-8>

Appendix

Table 1. Results of a Cox proportional hazard model (Latency to Look) and GLMM (Duration of Looking), each with Trial Date as the independent variable.

Predictor Variable	Latency to Look				Duration of Looking		
	Coef ± SE	Exp(Coef)	Z	P	Estimate	T	P
Trial Date	58.24 ± 26.10	2.30	2.23	0.029	-1.74 ± 0.64	-2.70	0.008

Table 2. Likelihood ratio test of global models, condition only models, and null models split by research question and response measure: Latency to Look and Duration of Looking. Global model contains: Condition Type, Grooming Received, Individuals in 10m, Rank Distance, Infant to Female Ratio, and random effects Subject ID and Caller ID. Condition Model contains: Condition Type, and random effects Subject ID Caller ID. Null Model contains only random effects Subject ID Caller ID.

Condition Types Included	Response Measure	Comparative Model Type	AIC	ΔAIC	Loglik	Df	Chisq	Pr(>Chisq)
Combined Grooming vs Social vs Null	Latency to Look	Global Model	272.12		-115.78			
		Condition Only Model	285.43	13.31	131.27	-8.83	30.97	0.00
		Null Model	282.65	10.53	-130.20	-9.14	28.83	0.00
	Duration of Looking	Global Model	635.23		-307.61			
		Condition Only Model	667.36	32.13	-327.68	-4.00	40.13	0.00
		Null Model	683.58	48.35	-337.79	-6.00	60.35	0.00
Direct vs General vs Social vs Null	Latency to Look	Global Model	277.14		-122.69			
		Condition Only Model	281.28	4.14	-132.12	-7.35	18.85	0.01
		Null Model	282.66	5.52	-130.20	-4.74	15.01	0.01
	Duration of Looking	Global Model	623.21		-300.61			
		Condition Only Model	652.48	29.27	-319.24	-4.00	37.27	0.00
		Null Model	683.58	60.37	-337.79	-7.00	74.37	0.00
Long-Term Direct Rec. vs Null	Latency to Look	Global Model	80.12		-25.71			
		Condition Only Model	90.25	10.13	-40.04	-9.26	28.65	0.00
		Null Model	89.94	9.82	-40.86	-10.24	30.29	0.00
	Duration of Looking	Global Model	222.86		-102.43			
		Condition Only Model	260.24	37.38	-125.12	-4.00	45.38	0.00
		Null Model	268.71	45.85	-130.35	-5.00	55.84	0.00

Table 3. Results of cox proportional hazard model (Latency to Look) and GLMM (Duration of Looking) of the effect of a binary measure [(1) interacting with the caller (0) not interacting with the caller] on subjects' response strength to playback stimuli.

Predictor Variable	Latency to Look				Duration of Looking		
	Coef ± SE	Exp(Coef)	Z	P	Estimate	T	P
Interacted with the Caller	-0.51 ± 0.36	0.599	-1.43	0.15	-106.01 ± 40.45	-2.62	0.01*

Significant results are marked with an Asterix.

Table 4. Loglikelihood test of latency to look model testing the effect of interacting with the caller prior to playback and a null model containing only random effects. Significant results are marked with an asterix.

Variable	Df	AIC	logLik	Chisq	Df	Pr(>Chisq)
Null model	8.52	281.28	-138.72			
Response Model	11.13	282.65	-143.48	9.51	3	0.02*

Table 5. Loglikelihood test of duration of looking model testing effect of interacting with the caller prior to playback and a null model containing only random effects. Significant results are marked with an asterix.

Model	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(>Chisq)
Null Model	4	691.57	-341.79	683.57			
Response Model	7	689.34	-337.67	675.34	8.23	3	0.041*