The communicative function of self-directed behaviours in macaques

Jamie Whitehouse

Thesis submitted in partial fulfilment of the requirements for the award of
the degree of Doctor of Philosophy of the University of Portsmouth.

July 2018

Abstract

In humans and non-human animals, stress is often linked to observable behaviours (e.g scratching, self-grooming and other self-directed behaviour). The link between stress and these behaviours is widely accepted, but their adaptive value remains understudied and so, the reasons for their production is unclear. Stress behaviours are often highly visual (e.g. scratching, yawning, self-grooming), and so it has been hypothesised that these behaviours may provide information to others. In this thesis I explored the hypothesis that stress behaviours (e.g. scratching) have communicative function, using a non-human primate model genus, the macaques (*Macaca).*

First, I consider how observers perceive the scratching of others, and more specifically, how they are perceived in comparison to neutral, non-communicative behaviour. Macaques attended to the scratching of others more so than neutral behaviours, with this shift in attention being modulated by the degree to which the subject is bonded with the actor. Second, I measured how the macaques responded to the stress of others, comparing social interactions with and without a preceding scratch. The findings of this study demonstrate that producing stress behaviour significantly impacted the likelihood of aggression from others, and led to more peaceful social interactions. Finally, I considered the function of scratching during two other contexts, preceding behavioural change, and as a signal during grooming interactions, however, I found no evidence for a communicative function of scratching in either of these contexts.

Overall, this thesis supports the idea that stress behaviour is perceived and responded to by others, providing some of the first evidence to suggest that these behaviours may function communicatively. Ultimately, these data adds clarity as to why stress behaviours have evolved, and why they exist in the behaviour repertoire of many social animals (including ourselves).

Contents list

Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

Word count 37,340

Acknowledgements

First and foremost, I would like to thank Prof Bridget Waller and Dr Jerome Micheletta for not only their continuous support and availability throughout my PhD as my supervisors, but for their friendships over the last 4 years. They both have made my time at the University of Portsmouth extremely enjoyable, and I consider any future students of theirs extremely lucky. I would also like to thank my third supervisor, Dr Juliane Kaminski, for her helpful comments and discussion at every stage of my research, and Dr Ed Morrison, Dr Paul Morris, Dr Marina Davilla-Ross, and Dr. Leanne Proops for their comments during annual and major reviews.

I would like to thank the Primate Society of Great Britain, for the financial support from the Captive Care Working Party. I am grateful to Don Walser, Terri May, Lisa Simpkins, and the rest of the keepers and staff at the Monkey Haven for access to their animals and enthusiasm and help throughout. I also thank Sue Wiper and the Trentham Monkey Forest for allowing access to their animals for the collection of stimuli.

I want to thank everyone in Punta Santiago, Puerto Rico, who helped me during my research and made it all possible. More specifically, I would like to thank Angelina Ruiz, Giselle Caraballo, Bianca Giura, Nahiri Rivera, Janet Rivera and the Cayo Santiago boatmen for their help throughout the data collection. I would additionally like to thank Daniel Phillips and Rachel Sweetman for their help during the identification of animals, and Stella Mayerhoff and Louis Thompson for the laughs. The Cayo Santiago population is currently supported by the University of Puerto Rico (UPR) and the Office of Research Infrastructure Programs (ORIP) of the National Institutes of Health (grant number 2P40OD012217).

I want to thank the students who helped me with data collection, video coding, and reliability coding. More specifically, I thank Ariana Weldon, Hoi-lam Jim, and Charlotte Gurney-Read. I would like to thank (and perhaps apologise to) anyone I have shared an office with other the past 4 years; particularly Hannah Cassidy, Eglantine Julle-Danière, Tom Lockhart and Peter Clark – thanks for putting up with me.

Last, but certainty not least, I want to thank my family; my parents for their enthusiasm, interest throughout my PhD (and of course the financial support!). Sasza, I'd like to thank you, I have gained a life-long friend, and Hayley, you have helped turn what should have been one of the most stressful periods of my life, into one of the most enjoyable 6 months I can remember. Thanks all.

Dissemination of research from this thesis

Chapter 2:

- Whitehouse, J., Micheletta, J., Kaminski, J., Waller, B.M., 2016. Macaques attend to scratching in others. Animal Behaviour. 122, 169–175. doi:10.1016/j.anbehav.2016.10.020
- Whitehouse, J., Micheletta, J. & Waller, B. M. 2015 Barbary macaques' responses to conspecifics' self-directed behaviours. Oral Presentation at the Primate Society of Great Britain, Spring Meeting (April 9th & 10th)

Chapter 3:

- Whitehouse, J., Micheletta, J., Waller, B.M., 2017. Stress behaviours buffer macaques from aggression. Scientific Reports. 7:11083. doi:10.1038/s41598-017-10754-8
- Whitehouse, J., Micheletta, J. & Waller, B. M. 2017 Macaques are Less Likely to Attack Others Producing Stress Behaviour. Oral Presentation at EFP meeting (August 22nd - 25 th)
- Whitehouse, J., Micheletta, J. & Waller, B. M. 2017 Stress behaviours reduce likelihood of aggression from others. Oral Presentation at ASAB Spring Meeting (April 5th – 7th)

Chapter 6:

- Part of Chapter 6 appears in: Waller, B.M., Whitehouse, J., Micheletta, J., 2016. Rethinking primate facial expression: A predictive framework. Neuroscience and Biobehavioral Reviews doi:10.1016/j.neubiorev.2016.09.005

List of tables

List of figures

Chapter 1.

General Introduction

1.1 Overview

In humans and non-human animals, stress is often linked to observable behaviours (e.g. scratching, self-grooming and other self-directed behaviour). Although the link between stress and these behaviours is a widely accepted phenomenon, their adaptive value remains understudied and consequently, the reasons for their production in animals are unclear. Research has addressed several proximate explanations for their occurrence. They may for example, attenuate the physiological and cognitive stress response, and by producing stress behaviours, individuals may be able to recover from stress more effectively. However, because of the often overtly visual nature of stress behaviours, it could be possible that they also leak information about an individual’s stressful experience to others. In which case, it could be that these behaviours have been selected for during the evolutionary process to transmit information. Stress behaviours may not, therefore, be just a coping strategy or physiological byproduct, but extend into the communicative repertoire of social species and function as a signal or cue. The aim of this thesis is to explore this overarching hypothesis that stress behaviours can be perceived and responded to by others, and to assess if these behaviours can be considered communication. In this thesis, I investigate this using the non-human primate model genus, *Macaca*, combining observations with experiments to develop an understanding of both the behavioural consequences of stress behaviour, as well as the potential cognitive processes involved in their perception.

There still much debate about how the terms stress and communication are defined and conceptualised. In Chapter 1, I discuss these controversies, beginning with how we currently define and measure stress, as well as the non-verbal behaviours we associate with it. Next, I discuss communication more broadly, considering which criteria should be met for a behaviour to be defined as communicative and more specifically, whether a communicative behaviour should be defined as a signal or a cue. Finally, I propose non-human primates as an ideal model for the study of stress and communication - specifically the macaques.

In Chapter 2, I explore the processes involved in the perception of stress. Using an experimental approach, captive Barbary macaques (*Macaca sylvanus*) were presented with videos of typical stress behaviours (scratching) and videos of neutral behaviours of conspecifics. Firstly, by comparing the type of responses the subjects had to the presentation of these different stimuli types, I was able to assess if stress behaviours are being perceived differently to neutral behaviours – an important criterion for behaviour to function as a signal. Secondly, by presenting our subjects with videos of conspecifics of varying relationship type and quality (e.g. different dominance and friendship relationships), I can begin to broadly understand the adaptive value of these behaviours – for example, a response to the stress of friends, (but not non-friends) could tell us that these behaviours function in a cooperative environment where helping friends may be a good strategy. In this study, the macaques differed in how they attended to the scratching behaviour of others (compared to neutral behaviour), attending to the scratching stimuli for significantly longer. In addition, they attended to familiar (in-group) individuals for significantly longer than non-familiar (out-group) individuals, as well as non-friends, more than friends. This suggests that the macaques perceived the stress and neutral stimuli differently, and that individuals may shift their attention towards stress behaviours in an adaptive way depending on the quality of their relationship with the scratcher. The increased attention towards non-friends may suggest that monitoring stress is more beneficial in a competitive environment. This could link to the fact that stressed animals are more unpredictable and potentially aggressive, and ultimately, that stressed non-friends may represent a bigger threat that needs to be monitored.

In Chapter 3, I look at how individuals displaying stress behaviour (scratching) were responded to socially. If scratching conveys some kind of information, whether emotional or about potential future behaviour, how individuals choose to behave with scratching individuals should be different compared to how they behave with non-scratching individuals. As a test of this theory, I measured the production of, and social responses to scratching in a group of free-ranging rhesus macaques (*Macaca mulatta*). Firstly, the production of stress behaviour was associated with the composition of the social audience, and animals scratched more when in the presence of non-friends and more dominant individuals. These results add to the body of literature confirming that these behaviours are associated with stress. Secondly, I found that the production of scratching significantly reduced the likelihood of receiving aggression from others; and increased the likelihood of affiliation. This study demonstrates that the production of stress behaviours can affect the immediate behaviours of others, in a way that could be considered beneficial and adaptive to the producer. The data presented here, therefore, provides evidence towards a communicative function of stress behaviours.

In Chapter 4, I look at the role of scratching behaviour during behavioural transitions (the changing from one behavioural state to another). In primate species, scratching during behavioural transitions is hypothesised to indicate, or even assist, the changing between contrasting motivational states. However, empirical support for such hypotheses is scant. In this study, I explore the potential functions of scratching around behavioural transitions in a free-ranging group of social primates, rhesus macaques (*Macaca mulatta),* by quantifying the context in which these scratches occur, and how they influence the behaviour of others. Here, we find rates of scratching were heightened preceding behavioural transitions; more specifically during transitions to locomotory behaviour (i.e. before an individual moves off to travel). Although the amount of group mates nearby influenced the production of these behaviours, I found no evidence that neighbours were using these scratching behaviours as information. More specifically, scratching did not affect the likelihood of being followed by others, or, the latency in which an individual was followed. Therefore, my data supports previous findings that scratching is associated with behavioural transitions, but did not find a social function of scratching in this context. Instead, it seems likely that scratching is produced more during transitions as these can be potentially stressful events.

In Chapter 5, I explore the function of scratching and other self-directed behaviours within the context of social grooming. Self-scratching has been argued as a referential signal in both macaques and chimpanzees; indicating a part of the body in which an individual wishes to direct the grooming of others. Other grooming behaviours, such as body-part presentations (i.e. grooming solicitations) have been argued to have similar function. Rates of scratching by the groomee were low, and although grooming solicitation behaviours sometimes elicited responses from others and thus appeared referential (solicitations often led to grooming of the presented location), these behaviours did not meet the other hallmarks of referentiality that were tested (e.g. persistence). A more parsimonious explanation may, therefore be a stimulus enhancement. Grooming solicitations did, however, increase the longevity of grooming bouts and were produced more often towards lower-ranking individuals. These behaviours therefore may function to facilitate more coordinated and elongated grooming interactions.

In the final chapter of this thesis, I will summarise these studies, highlighting the key theoretical and practical implications of the results. Overall, this thesis provides some of the first empirical support that stress behaviours serve an important role in the communicative repertoire in non-human primates.

1.2 Stress in human and animal societies

The concept of stress is still, to this date, subject to debate among the scientific community. The term stress has been used, problematically, to refer to the responses elicited in an individual after being presented with a range of stimulus intensity; from ‘mildly challenging’ to a ‘severely adverse’ stimulus (Koolhaas et al., 2011). The term stress is also used interchangeably to refer to both an animals’ physiological or psychological state. When framing stress in terms of an individual’s physiology, stress is most commonly referred to as stimulus which disrupts an animal’s homeostasis (Chrousos, 2009). This in itself can been argued as a problematic definition, if we consider the range of activities which has the potential to lead to such disruption that are not necessarily stressors (Levin and Ursin, 1991). Thus, such a definition is overly broad and unhelpful. Additionally, within species with higher-order cognitive processing, stress can include the adverse psychological experience accompanying the physiological changes, which, depending on the context, can have both positive and negative effects on cognition (Allen et al., 2014). For example, in immediate threatening situations, the cognitive changes associated with stress are important to appropriately navigate a potentially dangerous environment by increasing immediate awareness (e.g. in a ‘fight or flight’ response), however, chronic and frequent exposure to stressors can eventually be damaging to the health of animals, including humans (McEwen, 2007; Sapolsky, 1996).

During an exposure to a stressor or stressful situation, cortisol is secreted by the adrenal gland in mammals (Allen et al., 2014; Sapolsky, 1996). These changes in glucocorticoids such as cortisol are able to be accurately measured (for example. through faecal metabolites, Young et al., 2014, or blood plasma, Hanson et al., 1976) and thus presence or absence of stress can be accurately quantified in both human and non-human animals. Such tools allow us to compare the experience or susceptibility to stress, with other behavioural or social correlates (Anestis, 2010; Czoty et al., 2009; Hanson et al., 1976; Young et al., 2014) and have been a methodological foundation for what we now understand about the behavioural consequences of stress. Links between the structure of animal societies and stress are well established. We know that stress impacts individuals differently, depending on their social status (Cavigelli and Caruso, 2015), and that responses to stress can further attenuated by maintaining close social relationships with others (Young et al., 2014). We also know that there may be links between stress, and an individuals’ fitness, due to the direct and often negative effects stress has on reproductive systems (Creel et al., 2013). Not only is the social environment in which an individual lives a primary source of psychological and physiological stress (Creel et al., 2013), but also there is evidence that others in your social group may be directly responsive to your stressful experiences

(Buchanan et al., 2012). In humans, watching videos of others experiencing high levels of stress can lead to a stressful physiological response in the observers, specifically, an increase in heart rate (Dimitroff et al., 2017). In non-human primates, apes have been shown to be socially responsive to the stressful experience of others by providing positive support or ‘consolation’ (Clay and de Waal, 2013). However, although the evidence supporting the idea that individuals can process and respond to stress in others grows, the specific behavioural or physiological cues which are being utilised to obtain and process this information remains unknown. Although it is possible that the hormonal responses associated with stress may be detected in secretions (Hanson et al., 1976), the most parsimonious explanation would be that stress is observed via visual (and potentially auditory) cues. Stress in most animal species leads to highly salient changes in behaviour, often accompanied with stereotyped movements (Maestripieri et al., 1992, see Chapter 1.3). In addition, detection of stress has been demonstrated through the presentation of video stimuli alone (Dimitroff et al., 2017). In light on this, a focus on the visual domain assessing how humans and other animals navigate the stress of others in a social environment may provide a practical first step.

1.3 Behavioural markers of stress

1.3.1 Form

Stress is manifest in behaviour. For many animal species, including humans, the physiological (and/or cognitive) experience of stress can directly affect how that individual behaves, often leading to stereotypic and repetitive behaviours. In humans, for example, we can observe an increase in self-directed behaviour such as scratching, yawning, lip-biting, face-touching as an individual experiences stress (Mohiyeddini and Semple, 2013). Stress associated behaviours are rarely unique behavioural movements, and are instead usually derived from behaviours that have evolved to have a different specific function (e.g. scratching serves a hygienic role in removing irritations on the skin, Maestripieri et al., 1992). Such behaviours that are used out of their *'normal'* context, like scratching, were early described as displacement activities (Tinbergen, 1952), and their lack of function relative to their context is often how they are defined (Bradbury and Vehrencamp, 1998). This overlap between stress associated behaviours, and their normal counterparts causes methodological issues, as the true causation of the behaviour becomes difficult to establish. Thus, stress associated behaviours remain an understudied phenomenon (Maestripieri et al., 1992). Nevertheless, there is still a large body of evidence quantifying the link between stress and the production of displacement activities across a range of animal taxa. Key distinctions are made however, between those behaviours associated with normal experiences of stress, and those associated with abnormal experiences of distress. Prolonged exposure to extreme stress can lead to deleterious and self-harming behaviours (e.g. hair pulling and trichotillomania in primates, van Zeeland et al., 2009). Although these behaviours appear to reflect extreme variations of stress behaviour, throughout this thesis I will try not to focus on such extreme behavioural responses, and instead I refer to milder responses associated with natural, and normal stressful experience.

Stress associated behaviours have been described across a range of animal species; for example, yawning in domestic dogs (Tod et al., 2005), chewing in mice (Hennessy and Foy, 1987), preening in birds (Bradbury and Vehrencamp, 1998), suggesting these behaviours are somewhat ancestral, evolutionarily speaking. However, most of what we know about the links between stress and behaviour has been from research into the primates, particularly addressing the link between stress, and scratching. In a macaque species (*Macaca fascicularis)*, Schino et al. (1991) demonstrated that the administration of an stress/anxiety relieving drug (Lorazepam) directly influenced the subjects' rate of scratching. Rates of scratching (and no other behaviours) were specifically reduced during the administration of the drug, suggesting these behaviours may be directly linked with the physiological or psychological experience of stress. In terms of the behavioural evidence, macaques scratch more following intense intragroup aggression (Aureli et al., 1989), when macaque mothers are separated from their offspring (Maestripieri, 2010), and when around strangers where the dominance relationships have yet to be established (Schino et al., 1990). Chimpanzees scratch more when presented with challenging cognitive tasks (Leavens et al., 2001) or when presented with unsolvable problems (Waller et al., 2014). Finally, marmosets respond to the threat of predation with increased rates of scratching (Neal and Caine, 2015). The evidence suggesting a connection between scratching and the experience of stress is therefore plentiful and convincing. However, our understanding of stress associated behaviours beyond quantifying their link to stress remains limited.

1.3.2 Function

The benefits of producing stress associated behaviours are still open for debate. For the most part, researchers focus on the potential proximate explanations for their production, with these behaviours often being described as a by-product of internal regulatory and/or physiological processes (Troisi, 2002). Specifically, it has been argued by some that stress associated behaviour may distract an individual from the stressor, providing a sensory cut-off (Chance, 1962), allowing the negative arousal associated with the stimulus to be reduced (Mohiyeddini and Semple, 2013). Whatever the specific proximate mechanisms at play, evidence suggests that they at least to some degree, assist in regulating the experience of stress, and provide a strategy to help individuals cope with the stress response more effectively (Cheney, 2009). In humans, men who produce more displacement behaviours report lower levels of stress (Mohiyeddini et al., 2013), in bushbabies (*Otolemur garnettii*), increased displacement scent-marking leads to a reduced cortisol response (Watson et al. 1999) and in rats and mice, chewing and gnawing behaviours directly modulate a neural response of stress (Berridge et al., 1999).

In addition to speculating on the proximate causation of stress behaviour, there has been some suggestion that these behaviours may have a communicative role during social interaction (Maestripieri et al., 1992). Whether or not these behaviours do provide a mechanism for coping with stress, or regulating physiological processes, stress associated behaviours are often highly visual and overt. Considering the links between displacement behaviour and stress, there is potential (through either learned, or evolved associations) that these behaviours may be informative to others and allow for the transmission of information about the senders internal state (Bradshaw, 1993). In Japanese and rhesus macaques, there is evidence to suggest that when conspecifics observe the scratching of others, they are then more likely to scratch themselves (Feneran et al., 2013; Nakayama, 2004). This ‘contagious’ phenomena, is interpreted to imply the transmission of psychological states, and that the internal state of the observer can be more easily shared when behavioural patterns are synchronous (e.g. emphany, Nakayama, 2004). Diezinger and Anderson (1986), additionally demonstrate that the social context can affect the likelihood of scratching, and were among the first to suggest that scratching may provide information to others. Finally, it has been observed that some displacement activities are incorporated into signals to increase the salience of the display (e.g. symbolic feeding in Gorillas, Maestripieri et al., 1992; Tinbergen, 1952). However, there has been very little research that directly focuses on how conspecifics perceive the stress behaviours of others, and more importantly, if and how they respond to them.

1.3.3 Applications

Despite a current lack of understanding about the function of these behaviours, quantifying stress behaviours in animals has provided us with a useful tool – both for researchers and non-academics working with managed animals. Collecting accurate measures of stress in animals often requires invasive physiological procedures, such as blood samples or cardiovascular monitors (Hanson et al., 1976), which consequently disrupts animals' natural behaviours and raises ethical concerns. Non-invasive physiological measurements on the other hand, such as hormonal analysis on faecal metabolites (Young et al., 2014), do not allow time-specific collection of samples, rely on opportunistic sampling, and require a large amount of specialised resources and expertise to process the information. Behavioural measures of stress however, although potentially less accurate and less specific, provide a simple and non-invasive way to estimate and measure real-time stress in animals. Researchers can for example, use behavioural markers as a tool to monitor welfare of subjects during experimentation (Ruby and Buchanan-Smith, 2015; Whitehouse et al., 2013), or look at the relationships between stress and other measures such as social rank (Duboscq et al., 2016). Increasing our understanding of stress associated behaviour and their social functions could help provide a more efficient tool to help manage stress in captive animals – whether this means recognising stress earlier and more accurately, or, how to better manage individual or individuals in potentially stressful environments. For example, if stress associated behaviours extend beyond just physiological by-products and are in fact processed and recognised by others, this could influence how animals are housed during stressful procedures, and thus management strategies for captive animal may have to be reconsidered.

1.4 Social communication

1.4.1 The study of communication

The study of communication in non-human animals became a significant topic of research ever since the ideas of comparative signals were laid out in Charles Darwin's (1872) 'The Expressions of the Emotions in Man and Animals' (Laidre and Johnstone, 2013), and the topic remains a fundamental study area. Communication is ubiquitous among all animal species regardless of their degrees of sociality, and describing and quantifying the ways in which animals communicate with conspecifics is one way in which we can define their society (Thierry et al., 2004). Animals use communicative exchanges to alert others about food or predators (Micheletta and Waller, 2012; Slocombe et al., 2010), convey information about reproductive receptivity (Kappeler et al., 2004), communicate expressions of emotion or future intentions (Waller, 2013; Waller et al., 2016a), establish dominance rank (Preuschoft and van Schaik, 2000), and in almost any other type of social interaction (Bradbury and Vehrencamp, 1998). How we choose to define communication however, can vary significantly among researchers and fields (Bradbury and Vehrencamp, 1998; Liebal et al., 2013). For example, to what extent we consider the intentionality of the signaller can change the classification of a behaviour as communicative, significantly (Tomasello, 2008). Or, in behavioural ecology, communication can be conceptualised as a way a sender can manipulate or modify the behaviour of the receivers, without necessarily being accompanied by the transmission of any kind of information (Krebs and Davies, 1993). Here, I will define communication broadly throughout this thesis, as the provision of information by an individual (i.e. the sender) through either signals or cues (see: Section 1.4.3) that can be used by others (ie. receivers) when deciding if and how to respond (Bradbury and Vehrencamp, 1998).

One of the reasons why social communication has been so hard to reduce to a single agreeable definition, is because scientists are often approaching the study of communication at different '*levels*' of explanation (Tinbergen, 1963). To what extent scientists focus on either the causal or adaptive explanations of communicative behaviour, can change the focus on whether we are looking at behaviour at an individual or species level (Liebal et al., 2013). If we are approaching the study of a communicative behaviour with the goal to understand their mechanistic causation (e.g the underlying cognitive or emotional processes), there may be less focus on whomever the communicative behaviour is directed towards and more focus on the individual producing it. Whereas if we are approaching a communicative behaviour to understand functionality (e.g. why were these behaviours selected by evolution), it is important to address how others react, process and respond to the behaviour. By addressing both of these 'how' and 'why' questions (coined as *proximate* and *ultimate* explanations by Tinbergen, 1963) we are able to get a complete understanding of behaviour. They are not, as often confused, competing or contradictory approaches (Liebal et al., 2013) and we should understand that communication operates on multiple, complementary levels. As discussed in Section 1.3, there has currently been overwhelming focus on the proximate explanations of stress associated behaviour. In an attempt to approach these behaviours using a communicative framework, this thesis will focus on the *why* questions, and shift focus from the individual and address why these behaviours may be adaptive for the species.

1.4.2 Signal evolution and emergence

Communication arises from evolved adaptations from the sender and receiver, with each individual incurring a cost to participate. These costs are then ultimately outweighed by the benefits gained from the exchange (Bradbury and Vehrencamp, 1998), and therefore the behaviours can be selected for during the evolutionary process. Such exchanges must however, start with non-communicative precursors; behaviours which function independently of communication, and in a way which could be taken advantage of by receivers through learned or evolved associations between the behaviour and context (Laidre and Johnstone, 2013; Tinbergen, 1952, see Chapter 1.4.3). Such behaviours, for example, may be an inadvertent by-product which is produced in specific contexts (Otte, 1974), or they could be an incomplete action, where a receiver is able to anticipate the end of the behaviour before it is fully completely (i.e. *intention movements,* Bradbury and Vehrencamp, 1998)*.* As an example, animals may open their mouth before biting or attacking. This incomplete action, may be anticipated by others (receivers), and be responded to before the full action is complete (e.g. being bitten, Liebal et al., 2013). The process in which such movements can become simplified and stereotyped into communicative displays is called *ritualization*. A visual representation of the processes involved in signal evolution can be seen in Figure 1.1.

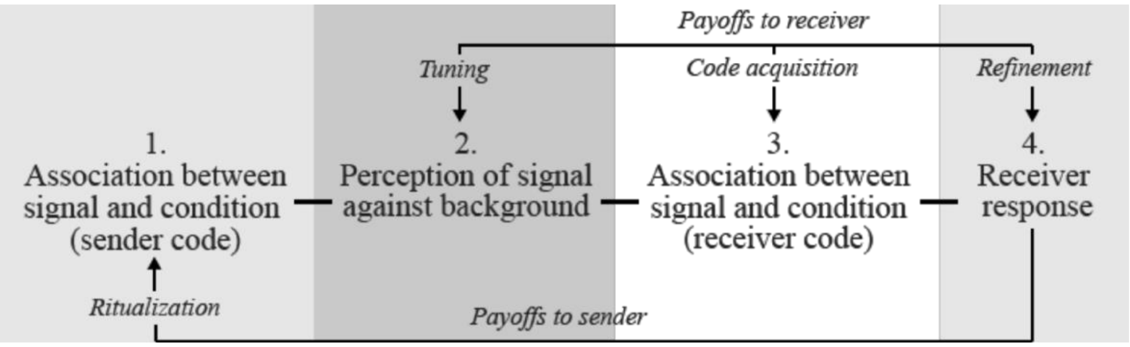

Figure 1.1. Signal Evolution (*modified from Bradbury and Vehrencamp, 1998*). (1) A sender couples a behavioural movement, with a certain condition, which is able to be (2) perceived within the environment by others. (3) This association is evolved or learned in the receiver, which concludes with a (4) decision and response by the receiver. These response then fine-tunes, and *ritualizes* the senders behaviour into a signal movement.

For most communicative signals, this process of ritualization occurs over evolutionary time (Tinbergen, 1952). However, for behaviours that occur using non-specific systems (e.g. bodily movements, and not body shape or colouration), it is also argued that these can develop across development, as opposed to being acquired genetically, a process coined *ontogenetic ritualization* (Tomasello, 2008). Using the same principles described above and in Figure 1.1, communicative behaviours could arise from learned associations (in opposed to evolved associations), and this is a dominant explanation for the emergence of visual gestures (Liebal et al., 2013).

1.4.3 Signals vs. Cues.

Defining communication becomes even more fraught with problems when we consider the fact that communicative exchanges do not *always* need to involve the coevolution of the sender and a receiver’s behaviour. Receivers can process leaked information and respond adaptively, without the selection of the behaviour for it's communicative value (Scott-Phillips et al., 2012). Such an exchange of information is what separates the definition of a *cue* from a *signal,* and can be either beneficial or at a cost to the sender (i.e. eavesdropping, Searcy, 2005). As the positive feedback of the receiver's response to a cue is what ultimately leads to the ritualization of behaviour by the sender, addressing the differences between signals and cues as a dichotomy is somewhat problematic as it can be often difficult to assess to what extent evolution has shaped the senders behaviour. To conceptualise this in the context of this thesis, if stress behaviours are, for example, selected for due to the benefits of coping with stress, but are still responded to by other individuals, such an exchange might be traditionally defined as a cue. However, if stress behaviours are produced because it incurs a selective advantage to look stressed as this may elicit a positive receiver response, then such an exchange might be traditionally defined as a signal. Therefore, whilst it is important to assess the selective pressures on the senders' behaviour, it is not a requirement for communication to exist. Throughout this thesis, I will adopt more focus on the receiver perspective (Guilford and Dawkins, 1991; Rowe, 1999; Semple and Higham, 2013), with less concern about whether behaviours are a signal or a cue, but more on the transmission of information to a receiver.

1.4.4 Comparative approaches to studying communication

Although developing an understanding of the communicative repertoire of individual species is important for us to better understand the biology of that species, conducting research on non-human animals using a comparative approach also provides us with a very powerful tool to look at the emergence and function of communication across evolutionary time. Specifically, the study of communication from a comparative approach has grown in popularity to aid attempts to uncover precursors for evolution of human communication and language (Hobaiter and Byrne, 2014; Tomasello, 2010; Watson et al., 2015). Species that share commonalities in behaviour, including communicative systems, are likely to share a common ancestor, which also had these traits (Tinbergen, 1963). This allows us to pinpoint the emergence of behaviour in evolutionary time and in some cases, allow us to speculate on the pressures that drove their selection by assessing how the behaviours are used in each species. Or, alternatively, comparisons of phylogenetically close species that inhabit different ecological or social environments, will allow us to speculate on how these environmental differences may have shaped the evolution of their behavioural repertoire (Oller and Greibal, 2004).

We know that we share many commonalities with non-human primates in terms of stress associated behaviour. Humans, like non-human primates, produce self-directed behaviour in the form of displacement activities during the experience of stress (Mohiyeddini and Semple, 2013; Mohiyeddini et al., 2015). The most parsimonious explanation for these shared behaviours is that they were also present in our common ancestor, and therefore are likely to share similarities in function. Looking at these behaviours in non-human primates therefore, can inform us about the form and functions of our own behaviours and provide some insight into why they may have evolved, and why they remain conserved in human behaviour.

1.5 The macaques (*Macaca*)

1.5.1 Macaque ecology

Macaques are a genus of old-world monkeys, widespread throughout Asia with a single species inhabiting northern Africa (Thierry, 2007). Up to 23 species make up the genus *Macaca,* many of which have striking differences in their appearance, and ecological preferences (Fooden, 1982; Thierry et al., 2004). They are characterised by their high degrees of sociality and contain species that represent a broad spectrum of social tolerance (from highly cooperative, tolerant species, to highly competitive, intolerant species, Thierry et al., 2004). Such differences attract researchers to this genus, because although this social style can differ drastically between species, many other aspects of their behaviour and ecology are fixed. For example, many communicative signals remain conserved between species (Altmann, 1962; Thierry et al., 2000). Group compositions are similar, with all species forming multi-male, multi-female groups of up to 100 or so individuals. Diets are comparable, with all macaques being mainly frugivorous (Thierry et al., 2004). These key similarities and differences in behaviour, allow researchers to not only assess the evolutionary origins of human behaviour (as a species phyologentically close to apes), but the extent that these differences in cooperative and competitive tendencies provided a selection pressures on other behaviour, during the evolution of each species.

1.5.2 Macaques as a model to study stress and communication.

Within non-human primates, the macaques have been a popular model for behavioural research that examines the visual markers of stress, and much of the physiological research (Maestripieri et al., 1992). Therefore much of our knowledge about stress behaviour is a consequence of research conducted on the macaques. Macaques represent many highly gregarious species, each of which survives in a competitive environment where stress is commonplace (Thierry et al., 2004). This combination of our knowledge of macaque stress and the associated behaviours, and the high frequency of potentially stressful situations that occur naturally, make this genus a particularly appropriate model for research of this focus.

Macaques are highly social, and because of this great social complexity, their behavioural repertoire contains many communicative strategies that allow them to efficiently navigate their social environment (Dobson, 2012; Thierry et al., 2000). Facial expressions (Parr and Heintz, 2009), gestures (Gupta and Sinha, 2016; Maestripieri, 2005), vocalisations (Altmann, 1962) and olfactory signals (Henkel et al., 2015) have all been described in these species, many of which have been selected for their function during conflict management (Maestripieri, 2005). The necessity to reduce the likelihood of escalated conflict provides a strong selective pressure on the evolution of primate behaviour (Aureli and de Waal, 2000), and this is reflected in the communicative repertoire of macaques, in which many signals convey dominance, submission or peaceful intentions in order to reduce social uncertainty (Dobson, 2012).

Given that macaques 1) produce reliable behaviours associated with stress, and 2) have a complex repertoire of already described communicative signals, this genus presents us with an ideal candidate to probe the communicative functions of stress behaviour.

1.5.3 An experimental and observational approach

Although some species within the genus are classified as threatened or endangered (ICUN, 2017), for the most part, macaques are extremely abundant. Many species can be found both throughout world in wild or in captive and/or managed populations. Such abundance means the study of cognition and behaviour in these species is commonplace, often due to easier access to subjects (Cronin et al., 2017). Working with captive macaques for example, allows researchers to manipulate the environment of the animal, or present them with experimental equipment that would be unfeasible in wild conditions. Cognitive research in zoos and laboratory's constitutes most of what we know about memory, problem solving, tool-use and social cognition in animals (Hopper, 2017). More specifically, this ability to manipulate the subjects environment has developed our understanding of the cognitive processes involved during many aspects of macaque communication; e.g. facial expressions (Micheletta et al., 2015; Parr and Heintz, 2009; Waller et al., 2016b), gaze-following (Emery et al., 1997; Micheletta and Waller, 2012), gestures (Maestripieri, 2005), sexual signals (Waitt et al., 2006). Such approaches, such as touchscreen training (Perdue et al., 2012) or video and image presentation (Winters et al., 2015) allow a unique perspective into cognition by allowing researchers to monitor responses to specific controlled stimulus, and therefore extremely helpful in the study of communication.

However, with the convenience and control of a captive environment to study cognition come methodological problems. Social and physical environments differ in captive subjects compared with their wild counterparts (Gazes et al., 2013), which may ultimately elicit differences in cognitive development. Sample sizes of captive groups are invariably smaller than those of wild groups, creating issues if we want to look at social behaviour or cognition, and undermining statistical inference (Field et al., 2012). Pairing experimental approaches with those of field studies on wild or free-ranging animals, in more naturalistic conditions, therefore provides a powerful tool to assess cognitive processes of the individual, as well as group level behaviour which is more generalisable to natural populations. I will, therefore, in this thesis, employ a mixed-design approach, combining experiments on captive animals and observations on animals in more naturalistic social and environmental conditions.

Chapter 2

Macaques attend to scratching in others.

2.1 Overview

Self-directed behaviours in primates as a response to increasing psychological or physiological stress are a well-studied phenomenon. There is some evidence that these behaviours can be contagious when observed by conspecifics, but the adaptive function of this process is unclear. The ability to perceive stress in others and respond to it could be an important part of sustaining cohesiveness in social primates, but spontaneously acquiring stress behaviours (and potentially emotional states) from all group mates via contagion could be maladaptive. To investigate this, a group of captive Barbary macaques, *Macaca sylvanus*, were presented with videos of conspecifics engaging in self-directed behaviour (scratching) and neutral behaviour. Behavioural responses as a result of exposure to the stimuli were compared (1) between familiar and unfamiliar individuals, and (2) within familiar individuals to consider the modulating effects of social relationships. Our results did not show contagious scratching in this species. However, there were differences in how individuals attended to the scratching stimuli. Subjects were more attentive to scratching videos than to neutral videos and familiar than unfamiliar individuals. Within the familiar individuals, subjects were more attentive to those to whom they were weakly bonded. We suggest that increased attention to scratching behaviours may be adaptive in order to monitor and avoid stressed group mates, whose subsequent behaviour may be unpredictable and aggressive. Monitoring group mates who are not allies may also be adaptive as they may pose the biggest risk. These findings will help increase our understanding of subtle cues that can be communicative in primates, and also the evolutionary steps towards understanding others.

2.2 Introduction

In a wide range of animal taxa, humans included, individuals produce self-directed behaviours that often appear irrelevant to current activities (Tinbergen, 1952). Although a social function of these behaviours is yet to recognized, these behaviours, which, for example, include scratching, face touching, self-grooming and yawning in primates (Mohiyeddini et al., 2013; Pavani et al., 1991; Schino et al., 1991; Troisi, 1999), have been shown to reliably indicate the presence of both psychological and physiological stress (Maestripieri et al., 1992; Troisi, 2002). Mice, *Mus musculus*, presented with a novel environment increase chewing behaviours irrelevant to that of feeding or escape in response to stress (Hennessy and Foy, 1987). Many bird species increase rates of preening in stressful situations, for example when disturbed while resting (Delius, 1988). High rates of scratching follow intense intragroup aggression in macaques, particularly in the victims (Aureli et al., 1989) and chimpanzees, *Pan troglodytes*, scratch more frequently when the difficulty of cognitive tasks increases (Leavens et al., 2001) or when frustration is induced through an unsolvable task (Waller, Misch, Whitehouse, & Herrmann, 2014).

Thus, in some contexts, there is a demonstrable relationship between stress and self-directed behaviour in animals.

Unhelpfully, the term stress is used variably throughout the literature, to describe situations from mild stimulation to extreme adverse conditions (Koolhaas et al. 2011). Here, we define stress as a biological response elicited to cope with disruptions to an animal's homeostasis (Moberg 1999), and a natural and common response to challenges animals face in their environment. We separate stress from distress, which can be observed after prolonged periods of extreme stress, and leading to often unnatural, exaggerated and stereotyped behaviours (e.g. feather plucking in parrots and trichotillomania in humans, van Zeeland et al. 2009). The behaviours associated with stress, however, are usually variants of normal functional behaviours (e.g. self-grooming, which also serves a hygienic function, (Maestripieri et al. 1992)

Our current understanding of the adaptive value of these behaviours is that they function to reduce the physiological stress response, playing an important role in how animals cope with stress (Koolhaas et al., 1999). For example, increasing chewing and gnawing behaviours attenuates physiological stress responses of rodents, including a reduced activation of stress associated neural systems (Berridge et al., 1999) and endocrinological responses (Hennessy and Foy, 1987). In bushbabies, *Otolemur garnettii*, individuals that perform increased scent marking in response to stress exhibit a lower cortisol response, and therefore appear to cope with stress more effectively (Watson, Ward, Davis, & Stavisky, 1999), and in human males, those who engage in increased self-directed behaviours during stressful events report lower experienced stress afterwards (Mohiyeddini et al. 2013). The evidence for self-directed behaviours as a coping mechanism is convincing; what we do not know, however, is whether or not these behaviours are socially relevant.

When scientists focus on behaviours that are associated with underlying emotional states there is a tendency to focus on the feelings of the actor and subsequently ignore the potential responses these behaviours may elicit in the receiver (Waller & Micheletta, 2013). Historically, this has been particularly true for the study of facial expression (Darwin, 1872; Fridlund, 1994), and may also be the case for the study of self-directed behaviour. To understand the evolution of stress behaviours, it is imperative to fully explore their functional value and not only their causal value (Tinbergen, 1952). One proposal is that these behaviours could also have a social function by providing information to a social audience about internal states (Bradshaw, 1993). If so, self-directed behaviours may not just function as a coping mechanism, but could be an important aspect of the social repertoire of some gregarious animals. Specifically within the primates, a communicative function of stress behaviours has been proposed (Bradshaw, 1993; Maestripieri et al., 1992; Nakayama, 2004; Waller et al., 2014), but empirical evidence remains elusive.

Although a social function of self-directed behaviours remains undocumented in any species, we do know that these behaviours can, in some cases, be contagious when observed by others. A contagious response has been reported following the observation of both yawning (dogs, *Canis familiaris*, Joly-Mascheroni et al. 2008; budgerigars, *Melopsittacus undulatus*, Gallup et al. 2015; chimpanzees, Anderson et al. 2004; gelada baboons, *Theropithecus gelada*, Palagi et al. 2009) and scratching (rhesus macaque, *Macaca mulatta*, Nakayama 2004; Japanese macaque, *Macaca fuscata*, Feneran et al. 2013). In a handful of these examples, the contagious response has been sensitive enough to be triggered experimentally through the presentation of videos (Feneran et al., 2013; Paukner and Anderson, 2006) and, particularly for the primates, have been discussed mostly alongside the subject's (and species') capacity for empathic behaviours (Lehmann, 1979). However, spontaneous acquisition of stress behaviours (and therefore potentially the acquisition of stress itself) may lack adaptive value. Cognitive function and decision making are significantly impaired in stressed individuals (McEwen and Sapolsky, 1995) and prolonged stress has many recognized negative effects on health (Sapolsky, 1996). If cognitive function and decision making are impaired in the individuals surrounding a stressed animal, this may not produce an optimal social environment that allows for the mitigation of stress or may not allow for a response to stressed group mates in a way that would be the most advantageous. Responding to the stress of others spontaneously through emotional contagion, therefore, has the potential to be a maladaptive strategy. Instead, a more adaptive strategy could be to monitor these behaviours in others and respond to them in a facultative way that is functional (such as a positive or negative social interaction) and provides an advantage for one or all individuals.

If responses to stress behaviours go beyond contagious affect and, instead, elicit functional responses in others, we could expect both the production of a signal and the response to it to be influenced by the sender–receiver relationship (Guilford and Dawkins, 1991; Micheletta et al., 2012). Signals often occur more frequently if the audience contains key social partners (Slocombe et al., 2010), and the response to signals can become stronger as social relationships become more important (Micheletta and Waller, 2012). By addressing how social relationships affect the production and response to communicative behaviours, we can, as a first step, begin to understand their function. A stronger response by friends or kin could suggest a function to facilitate cooperative efforts (Micheletta et al., 2012; Slocombe et al., 2010), whereas a stronger response by competitors could suggest that a signal functions to facilitate competition (Muroyama and Thierry, 1998). In the context of stress, by attending and responding to the stress behaviours of friends and kin, individuals could capitalize on important opportunities to manage social relationships and maintain a cohesive social group (Clay and de Waal, 2013). Conversely, monitoring the potential stress in competitors could provide opportunities to maximize competitive efforts by being able to taking advantage of another’s weakness (Byrne and Whiten, 1989).

Assessing when and how animals respond to the negative emotions of conspecifics could significantly contribute to our understanding of sociality, and has the potential to inform us regarding the evolutionary steps that may have led to the ability to understand others. In the following experiment, we aimed to assess whether behaviours directly related to stress are socially functional, and whether or not these lead to responses in observers. As a species characterized as highly gregarious and cooperative (Thierry et al., 2004) the Barbary macaque, *Macaca sylvanus*, provides an excellent model for the study of social behaviour in animals. We predicted that the macaques would respond to the stress behaviours of others, particularly those with whom they had close social bonds, and in a way that may provide further opportunities for cooperation.

2.3 Methods

2.3.1 Subjects and housing

This study was conducted between February and December 2015. We tested six, unrelated adult Barbary macaques (two males, four females) currently living in a social group at the Monkey Haven, Isle of Wight, U.K. Subjects had free access to a naturalistic, grassy outdoor area (20 x 12 m and 4 m high), filled with trees, logs, ropes, swings and a waterfall. New novel enrichment devices were provided to the animals weekly. Animals also had free access to a smaller outdoor area (5 x 5 m and 4 m high), and a heated indoor area (5 x 3 m and 3 m high). Subjects could be separated into each of the areas as needed; however, the smaller outdoor area was used for all experiments. Prior to this study, all subjects had been exposed to cognitive testing and were habituated to the presence of the experimenter. Macaques were fed daily with assorted fruits and vegetables, nuts, cereals, seeds and commercial monkey pellets. Water was available ad libitum. Our experiments never impacted on the normal dietary and husbandry routines of the animals.

2.3.2 Stimuli and apparatus

For each animal, we prepared 20 experimental videos: 10 scratching videos and 10 neutral videos. Half featured a familiar individual (another Monkey Haven group mate) and half featured an unfamiliar individual (a Barbary macaque from an unknown group). Animals were not exposed to any videos of themselves throughout the experiment. Each video was 3 min long, and was composed of five unique occurrences of scratching (or other neutral behaviour, see below) from a single individual, presented randomly and repeated four times within a video; each scratching occurrence was separated by a blank screen. Scratching was defined as the raking or dragging of fingers or toes over the skin in a repetitive motion, whereas neutral behaviour was defined as a lack of explicit social behaviour or extreme physical movement other than vigilance. Scratching that occurred directly after a conflict or disturbance in the group was favoured in the selection process in case there were any hitherto undocumented differences between stress-induced scratching and hygienic scratching. Neutral stimuli with qualitatively similar movement (i.e. brief limb movements) were favoured wherever possible in an attempt to match the scratching videos and control for simple differences in stimuli salience (to reduce the likelihood of any response resulting from movement alone). Neutral clips were chosen from the same videos as the scratching stimuli to minimize the effects of background information.

The videos of the unfamiliar Barbary macaques were collected at the Trentham Monkey Forest (Trentham, U.K.); individuals at the Monkey Haven had no previous exposure to these animals. The unknown individuals were five randomly chosen adults. All videos (both for the stimuli and for the experiments) were collected with a Panasonic HDC-SD700 video camera and were presented on a 19” Elo Monitor (refresh rate, 75 hz; videos presented at 24 fps). Stimuli were cropped around the animal to reduce excess background information and muted using Adobe Premier Pro CC 2014.

2.3.3 Experimental Procedure

Here, we modified an experimental procedure commonly used to test for yawn contagion (Anderson et al., 2004). A monitor was positioned outside the enclosure with a video camera above it; this provided an accurate record of both the animal’s behaviours and where it was looking during experimental trials. Animals were free to enter our test area voluntarily and approach the experimenter. Once an animal had arrived at the experimental apparatus, the door to the test area was closed and other individuals in the group were locked out. Subjects could leave the test area voluntarily at any point during the experiment, but other individuals could not enter. If any animal chose to leave, the session was aborted and repeated on a different day. After a short delay, allowing the animal to settle in the new area, the experiment would begin. Data were collected opportunistically, and were dependent on the motivation of the animals on a test day. Two videos were presented in each experimental session, one scratching video (SC) and one neutral video (N), of which one was of a familiar individual (F) and one was of an unfamiliar individual (UF) allowing four possible video combinations in each session: FSC & UFN, UFN & FSC, UFSC & FN and FN & UFSC. The video combination presented to the animals in a session was selected at random, to nullify any effects of presentation order. The identity of the individual in the videos was also randomized, until subjects had been tested with all individuals on each video type at least once (or more, depending on the motivation of the subject).

All sessions were videotaped, and followed this procedure: (1) presentation of first video, (2) 3 min observation period, (3) presentation of second video, (4) 3 min observation period. During the observation periods the screen was switched off, and the picture remained blank. After the second observation period, subjects were encouraged to leave the test area and were not tested again for at least 2 h. To increase motivation in the experiment, and to keep subjects seated next to the screen, animals were rewarded with a piece of cereal after the presentation of every stimulus. Rewards were given during the blank screen between stimuli, and reward rate remained uniform across videos (20 rewards per video). Other individuals could not see the videos during testing, but could remain in visual and auditory contact with the subject through mesh. Only a single experimenter was present at any time, and remained as neutral as possible throughout testing. The animals were never rewarded for a particular response, and the experimenter was careful not to act in a way that could influence the behaviour or attention of the subject. The experimenter did not make eye contact with the animals, remained silent at all times and maintained a neutral expression. A video example of the procedure can be found in the online supplementary material of the article (https://doi.org/10.1016/j.anbehav.2016.10.020)

2.3.4 Video coding

All videos were coded using BORIS (Behavioral Observation Research Interactive Software, Friard & Gamba 2016). From the videos, we calculated the rate of scratching, the subject's attention to the video and the subject's orientation towards the rest of their group. Attention to the video was defined as the duration of gazing at the screen by the subject (Figure 2.1). Orientation towards the group was defined as the duration of gazing by the subject towards the rest of its group mates. Owing to lack of motivation (i.e. the animal would not enter the test area), one subject was dropped from the analysis, and analyses were conducted on the remaining five individuals only. A naïve observer coded 10% of the videos to assess interobserver reliability using the intraclass correlation coefficient. We found significant agreement on both the rate (ICC = 0.871, $N = 41$, $P < 0.001$) and duration (ICC = 0.992, $N = 29$, $P < 0.001$) of coded behaviour.

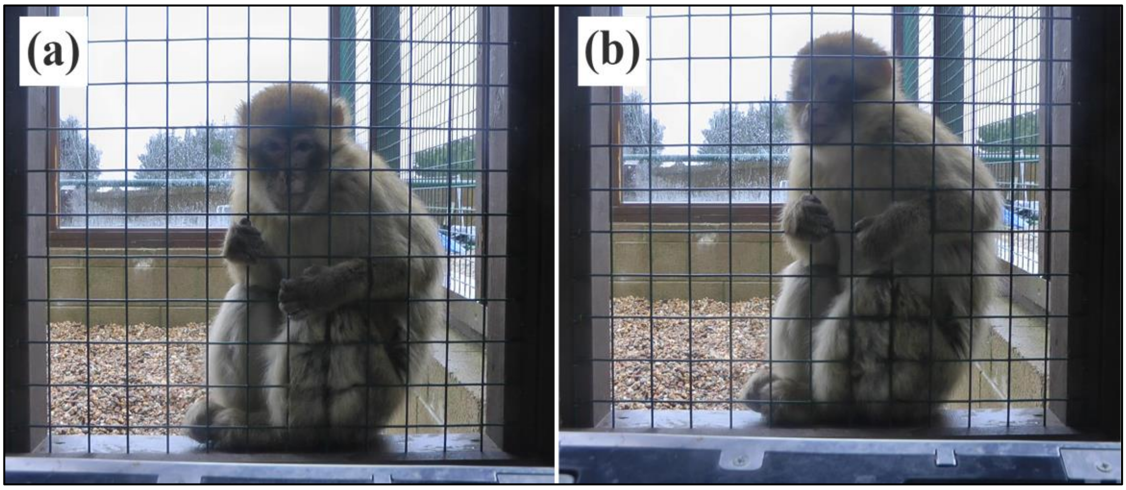

Figure 2.1 Measuring attention. The video camera was placed above the monitor displaying experimental stimuli. Subjects were considered to be attentive to the videos when they directed their gaze at the screen. (a) Attention to the video and (b) no attention to the video.

2.3.5 Measures of relationship quality

To measure social bonds within a dyad, we recorded the frequency of contact sitting and the frequency of grooming interactions between all individuals. Data were collected every 10 min using the instantaneous scan sampling method (Altmann, 1974) resulting in a total of 272 scans over the course of the experiment. Scans were taken during days when experimental trials were not occurring. These data were then used to calculate a composite sociality index (CSI, or friendship index, see Silk et al. 2006); this index provides us with a measure of affiliation between each dyad relative to the rest of the group, and is a commonly used measure of friendship in primates. To calculate the dominance rank, all agonistic interactions with a clear outcome were recorded ad libitum, including conflict and displacement. The outcomes of 64 agonistic interactions were collected during the study. Individuals were then ranked according to their normalized David's score (David, 1987), giving each individual a rank from 1 to 5, where 1 is the highest rank.

2.3.6 Data Analysis

We used a generalized linear mixed-model analysis (GLMMs), applying random intercept/slope models. In our first model, which was applied to the full data set, we included video type (scratching video, neutral video), familiarity (familiar, unfamiliar) and the rank of observer as predictors, including interactions between video type and familiarity. We also included the ID of the subject, and the ID of actor in the video as random factors. In our second model, which was applied to familiar trials only, we included CSI (index of friendship with actor) and rank difference (rank of subject – rank of actor) to the model to assess for the effects of social relationships on behaviour. Again, the ID of the subject and the ID of the actor in the video were included as random factors. Here, the dependent variables were rates of scratching, attention to the video and orientation towards the rest of the group. We fitted GLMMs using the function lmer provided by the package lme4 for RStudio Version 0.99 for R version 3.1.3 (Bates et al. 2014; R Core Team 2014) . We assessed overall fit of the model by comparing our full models to a reduced model including only the intercept and random factors using a likelihood ratio test (LRT, function anova). We considered the significant effects of predictors only if the full model was a significant improvement from the reduced model.

Rates of scratching during the presentation of the video were compared with the rates of scratching during the 3 min during the observation period after the video with a paired t test. As we found no difference in scratching when comparing these first and second observation periods (t test: $t = -1.178$, $p = 0.274$), scratching data from each of these two periods were pooled for subsequent analysis

2.4 Results

2.4.1 Influence on rates of scratching

Our first model, which included video type, familiarity and rank of the observer, was not a significant improvement from the null model (LRT: $X^2 = 1.049$, $p = 0.790$) indicating poor explanatory value of these predictors on the subjects' rates of scratching.

Our second model, which included the CSI and the rank difference between the actor and observer, was also not a significant improvement from the null model (LRT: $X^2 = 1.490$, $p = 0.684$) again indicating poor explanatory value of these predictors on the subjects' rates of scratching.

2.4.2 Influence on attention to the video

Our first model, which included video type, familiarity and rank of the observer, was a significant improvement from the null model (LRT: $X^2 = 28.17$, $p < 0.001$) indicating good explanatory value of the predictors on the subject's attention. Overall, video type was a significant predictor of attention ($t = 2.03$, *p* = 0.046). Subjects attended to scratching videos for longer (mean = 35.38s, SE = 3.89) than neutral videos (mean = 25.78s, SE = 3.14). Familiarity was also a significant predictor of attention (*t* = -4.46, *p* <0.001). Subjects attended to familiar videos (mean = 35.90 s, SE = 4.44) for longer than unfamiliar videos (mean = 29.33 s, SE = 2.54; Figure 2.2). No significant interaction effect between video type and familiarity was found (*t* = -1.77, *p* = 0.08). Finally, the rank of the observer was also a significant predictor of attention (*t* = 5.38, *P* = 0.003), which increased as rank decreased (Figure 2.3).

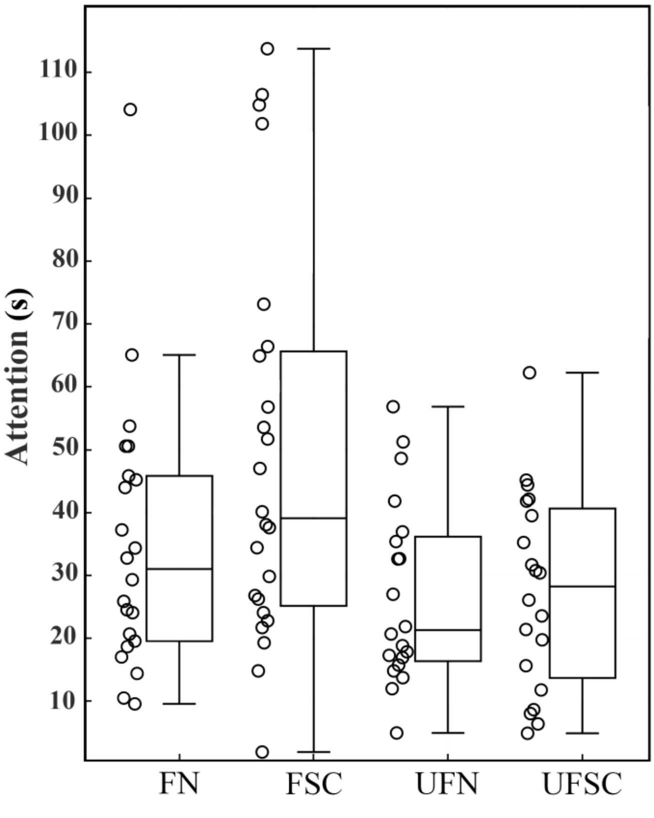

Figure 2.2 Effects of video type and familiarity on attention. Attention of the subjects to familiar neutral videos (FN), familiar scratching videos (FSC), unfamiliar neutral videos (UFN), and unfamiliar scratching videos (UFSC). Boxes represent the interquartile range of the data, lines through the boxes represent the median data point, and the whiskers represent the full range of data. Each circle refers to data points within the analysis

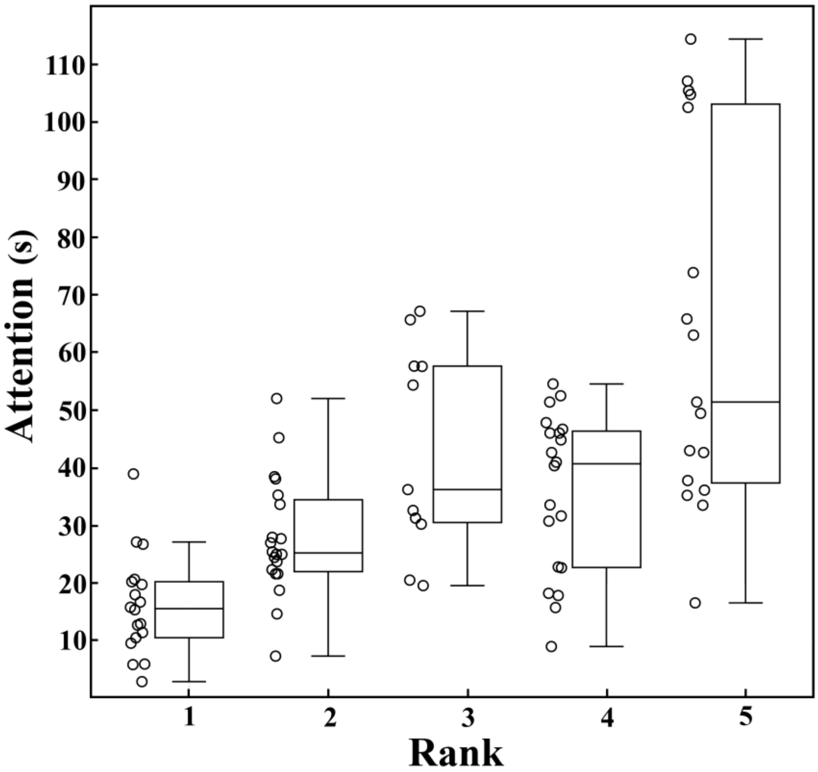

Figure 2.3 Effects of observer rank on attention towards all videos. Attention of the subjects to all videos, compared with their group ranking. 1 represents top ranking, 5 represents lowest ranking. Boxes represent the interquartile range of the data, lines through the boxes represent the median data point, and the whiskers represent the full range of data. Each circle refers to data points within the analysis.

Our second model, which included the CSI and the rank difference between the actor and observer, was a significant improvement from the null model (LRT: $X^2 = 6.61$, $p = 0.037$). CSI was a significant predictor of attention, but only during the presentation of scratching videos ($t = -2.59$, $p = 0.018$), and not neutral videos ($t = 0.413$, $p = 0.685$). Here, subjects increased attention towards weak bonded group mates, as indicated by a lower CSI

(Figure 2.4). Rank difference had no significant influence on attention (*t* = -0.43, *p* = 0.672)

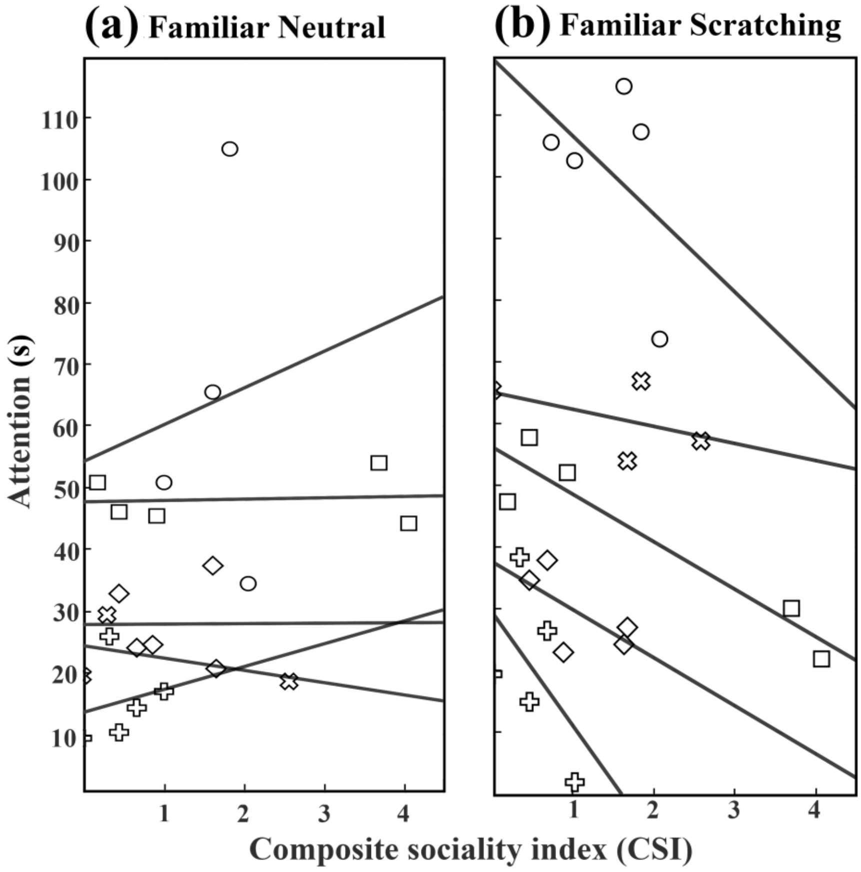

Figure 2.4. Effects of CSI on attention to familiar videos. Attention to (a) familiar neutral and (b) familiar scratching videos in relation to the composite sociality index (CSI) between subject and individual in the video. Shapes represent different subjects, and lines represent the best fit through each subject's data points.

2.4.3 Influence on orientation towards group mates

Our first model, which included video type, familiarity and rank of the observer, was not a significant improvement from the null model (LRT: $X^2 = 3.193$, $p = 0.561$) indicating poor explanatory value of these predictors on the subjects' orientation towards the rest of the group.

Our second model, which included the CSI and the rank difference between the actor and observer, was also not a significant improvement from the null model (LRT: $X^2 = 1.82$, $p = 0.610$) again indicating poor explanatory value of these predictors on the subjects' orientation towards the rest of the group.

2.5 Discussion

When compared with neutral videos, videos of scratching conspecifics elicited a significant behavioural response in the Barbary macaques. This response was not the increase in self-scratching found in some other studies (Feneran et al., 2013; Nakayama, 2004), but instead was increased attention towards the stimuli, with subjects monitoring scratching for longer than neutral controls. The social relationship between the subject and scratcher also affected attention. The macaques were more attentive when they were presented with their group mates scratching, particularly those with whom they were weakly bonded. This increased attention of the observer towards scratching, and these modulating effects of social relationships, suggest that the macaques perceived these behaviours differently from neutral, uninformative postures. Although a social function of stress associated self-directed behaviour has been suggested (Bradshaw, 1993; Maestripieri et al., 1992; Nakayama, 2004; Waller et al., 2014), these data may represent the first empirical evidence to support this idea.

The passive transmission of negative emotional states, through the contagion of associated behaviour such as scratching, has been proposed as an adaptive strategy (Nakayama, 2004). Being able to mirror the negative emotions of others, possibly via an empathetic type of response (Palagi et al. 2009), may enable an increase in awareness of the environment that can enhance an individual's ability to avoid danger (Feneran et al., 2013). In this study, however, we found no contagious effect of scratching. This could be reflective of our small sample size, which reduces statistical power and the likelihood of uncovering significant effects (Field et al., 2012), or alternatively, this response could be weaker or completely lacking in this species. We argue that a facultative response to stress behaviours, depending on both species and context, is a more adaptive strategy. Our subject species (the Barbary macaque), although very closely related, differs greatly in social style to the species previously used in scratch contagion research (rhesus macaque, Feneran et al. 2013; Japanese macaque, Nakayama 2004). The socially tolerant species, such as the Barbary macaque, are characterized by a much greater tendency for cooperation compared with their less tolerant counterparts such as the Japanese and rhesus macaque (Thierry and Aureli, 2006). It could be that instead of a passive transmission of negative emotions seen in the intolerant species, tolerant species may favour an active strategy in which negative emotions, such as stress, are provided as information rather than transferred passively, and where a decision can then be made about how exactly to respond.

Primates acquire and respond to information in ways that match the adaptive value of the information being acquired (Watson, Ghodasra, Furlong, & Platt, 2012). In macaques, we can find both a visual preference (Deaner et al., 2005) and selective attention (Waitt et al., 2006) towards communicative signals, with subjects choosing to view images of signals over nonsignals and directing their gaze towards these for longer periods of time. In our study, subjects systematically attended more towards scratching videos than neutral videos, suggesting the macaques were finding these videos more interesting and potentially more informative than those featuring animals free of any salient behaviour (Waitt et al., 2006; Winters et al., 2015). Although our results cannot inform us exactly why monitoring the scratching of others would be adaptive (at least to the receiver), it could be that the animals are responding to the potential stress of the scratcher (Maestripieri et al., 1992). The ability to assess the emotional state and intentions of other individuals is extremely important for social animals to coordinate future interactions (Parr and Waller, 2006), which could explain why behavioural manifestations of stress are beneficial to produce and were therefore selected. Or, it could also be that these behaviours serve no signalling function at all. As information leaks out through behaviour, as animals attempt to cope with stress (Koolhaas et al., 1999), associations between coping behaviours and behavioural or emotional states could provide an advantage to receivers. This would not necessarily provide a benefit to the stressed individual from a communicative perspective, but instead this information could be exploited and lead to a cost for the producer.

If there is a social function to stress behaviours, we should also expect the relationship between subject and scratcher to play a key role in this shift in attention. Animals select specific opportunities to cooperate with friends and allies, whether that is responding to distress and alarm signals (macaques, Micheletta et al. 2012), cooperative foraging opportunities (ravens, *Corvus corax*, Massen et al. 2015; coral trout, Vail et al. 2014) or reconciling conflict (Aureli et al., 2002). Contrary to our predictions, the macaques, although more attentive to familiar individuals overall, were actually more attentive to their weakly bonded group mates. This suggests that there is another reason to monitor scratching than cooperation and social bonding opportunities. Primates redirect aggression to alleviate stress (Virgin and Sapolsky, 1997), and in some species, aggressors choose the victims of redirection systematically (Aureli et al., 1992). By paying close attention to the stress of weakly bonded group mates, this may provide a strategy to avoid becoming involved in unnecessary conflict by inferring future behaviour (Waller, Whitehouse, & Micheletta, 2016). Additionally, individuals may be looking for key opportunities to increase their competitive success, and by looking for weaknesses in opponents (including weakly bonded individuals), individuals could choose appropriate opportunities for competition (Byrne and Whiten, 1989). If such a shift in attention is competitively driven, it is difficult to interpret these responses as having a signal function. For such a signal to evolve there must be an advantage or benefit for both the sender and receiver; however, these results demonstrate that producing self-directed behaviours may actually provide a disadvantage to the sender. If the animals in this study were responding to stress, it could be that an exploitation of behaviours produced as a product of coping could be a more plausible interpretation here.

Here we found that subjects attended more to familiar individuals than unfamiliar individuals. Although further investigation is necessary, it could just be that subjects were more wary of staring at the unfamiliar individuals, as these could represent a potential threat or danger. Additionally, as rank decreased in our subjects, their attention towards all social stimuli presented increased. This phenomenon was not specific to scratching, however, but instead was found across all conditions. Lower ranking individuals can often be found on the periphery of the social group (Sosa, 2016; Sueur et al., 2011; Whitehouse et al., 2013) and are the most frequent targets of redirected aggression (Aureli et al., 1992). So, perhaps an increased sensitivity to social information, including information about the emotional states of group mates, could allow individuals to both reduce competition from others and capitalize on important social bonding opportunities.

These results not only increase our fundamental understanding of stress behaviours, but also highlight the necessity to address the adaptive function of emotional behaviours in animals through research. Too much focus on the internal state of the sender, and less focus on how this relates to the response of the receiver, restricts our understanding of behaviour and, ultimately, our understanding of why behaviour evolves. By approaching stress behaviours from the point of view of the receiver, this study suggests that they may not only be relevant as coping strategies, but also have the potential to directly impact the future behaviours of others by informing about the actors emotional state. How exactly these behaviours affect social interactions however, calls for further research, in which we should focus on social responses of the receiver as well as on how the composition of the audience affects production of these behaviours.

Chapter 3

Stress behaviours buffer macaques from aggression.

3.1 Overview

Primates (including humans) scratch when stressed. So far, such scratching has been seen as a by-product of physiological processes associated with stress, and attributed proximate, regulatory function. However, it is possible that others could use this relationship between scratching and stress as an indication of the animal's stress state, and thus scratching could potentially have social function. As a test of this theory, we measured the production of, and social responses to scratching in a group of free-ranging rhesus macaques (*Macaca mulatta*). Firstly, we found that the likelihood of scratching was greater around periods of heightened social stress, such as being in proximity to high-ranking individuals, or non-friends. Secondly, when macaques scratched, subsequent interactions were less likely to be aggressive and more likely to be affiliative. Potential attackers may avoid attacking stressed individuals as stressed individuals could behave unpredictably or be weakened by their state of stress (rendering aggression risky and/or unnecessary). Observable stress behaviour could therefore have additional adaptive value by reducing the potential for escalated aggression, benefiting both senders and receivers by facilitating social cohesion. This basic ability to recognise stress in others could also be an important component in the evolution of social cognition such as empathy.

3.2 Introduction

Stress is manifest in the behaviour of animals (Maestripieri et al., 1992; Tinbergen, 1952) Stress is a biological response to the physical and physiological challenges animals face in their environment, and often specifically refers to a disruption of an animal's homeostasis (Cheney, 2009; Moberg, 1999). A stress response can be elicited by many types of physical stressors, and also social factors such as competition for resources or conflict with others (Koolhaas et al., 2011; Maestripieri et al., 1992). There are strong links between the physiological markers of stress (such as raised cortisol level) and behaviour (Schino et al., 1991). One key behavioural correlate of stress, common particularly within the primates, is scratching (i.e the repetitive raking of the skin on face and/or body, with the fingers of the hand or feet, Thierry et al., 2000). For example, scratching is often increased in victims of intense conflict (Aureli et al., 1989), or in mothers who are separated from their newborn offspring (Maestripieri, 2010). In addition, as the difficultly of cognitive tasks presented to chimpanzees increases, so does the rates of self-directed behaviours including scratching (Leavens et al., 2001; Waller et al., 2014). Rates of scratching can be both increased and decreased experimentally in macaques through the administration of anxiogenic and anxiolytic drugs respectively (Maestripieri et al., 1992; Schino et al., 1991). On the whole, therefore, the evidence suggests a link between the experience of stress, the physiology of stress, and scratching.

Scratching is usually interpreted as a by-product of physiological responses (Troisi, 2002), sometimes with proximate value attributed to internal regulatory processes (Gustison et al., 2012; Mohiyeddini et al., 2015; Watson et al., 1999). For example, it has been argued that scratching may distract individuals from the stressful stimulus and/or reduce the negative arousal associated with stressful events (Mohiyeddini et al., 2013). However, given the overt visual nature of scratching, there is also potential for these behaviours to alert others to the state of the scratcher, and therefore have communicative function within a social environment. Scratching could act as a cue (Laidre and Johnstone, 2013) if other individuals take advantage of the association between the scratching behaviour, and other aspects of the scratching individual that could indicate stress. If selection has acted on the scratching behaviour to shape its form and function, scratching could also gain signal function over evolutionary time and be considered an independent signal (Krebs and Dawkins, 1978). Indeed, a number of researchers have proposed that these behaviours could have communicative value (Bradshaw, 1993; Diezinger and Anderson, 1986; Maestripieri et al., 1992; Troisi, 2002). For example, displacement activities have been described in many animals, where a seemingly irrelevant behaviour is incorporated into a display which increases the salience to others (e.g preening as part of the sexual displays of some bird species, Tinbergen, 1952). Through learned or evolved associations between stress and behaviour (Bradbury and Vehrencamp, 1998), an audience could gain valuable and reliable information about the scratching individual. This could in turn motivate observers to direct (or avoid) interactions with the scratching individuals. Such a sensitivity to the internal or motivational states of others, including the experience of stress, would be favoured by natural selection as this would allow individuals to better navigate a social environment by informing their interactions with others (Krebs and Dawkins, 1978). An alternate suggestion is that stress behaviours could be produced to detract attention away from more salient cues about internal state in order to conceal information that could expose weakness (Krebs and Dawkins, 1978; Maestripieri et al., 1992). Evidence to support these claims, however, is lacking and/or anecdotal. In addition, it could be argued that producing behaviours so closely linked to stress could be a maladaptive strategy if it exposes cognitive and physical weakness. An empirical demonstration of how stress behaviours are perceived and responded to by others would therefore be helpful in understanding why behaviours linked to stress have been selected for during evolution.

We know that, at least to some degree, some social animals can be responsive to the emotional experiences of others (Clay and de Waal, 2013) and have even been attributed empathy-like responses (Romero et al., 2010; Sato et al., 2015). We also know that affiliative post-conflict interactions towards victims are common (Aureli and de Waal, 2000), from both the aggressor (Call et al., 1999; de Waal and Yoshihara, 1983) and from bystanders (Call et al., 2002). However, the specific behaviours that elicit these kinds of responses are difficult to identify. Indeed, determining whether the responses are made in reaction to the stressful event itself or to the behaviours or events associated with stress is difficult to determine. For phenomena like *consolation* (de Waal and van Roosmalen, 1979) or *empathy* to develop, however a basic ability to recognise stress and other negative emotional experiences in others through their behaviour could be useful. It could be that these behaviours are used for their predictive value about the scratcher's potential actions (Fridlund, 1994; Waller et al., 2016a). Stress can influence the subsequent decision making and behavioural responses of animals (McEwen and Sapolsky, 1995), for example primates can be more unpredictably aggressive towards others when stressed (Aureli et al., 1992). Considering how stress behaviours can be used by other individuals as potential cues to future behaviour rather than just by-products of an internal state could therefore provide us with a more appropriate framework to begin exploring their adaptive value (Tinbergen, 1963). Such approaches have been fruitful in the study of other communicative behaviours, such as facial expressions (Fridlund, 1994; Waller et al., 2016a).

Here, we examine the social function of stress behaviours in a group of free-ranging rhesus macaques (*Macaca mulatta*), focusing on a stress behaviour commonly documented in macaques and many other social primates; scratching (Maestripieri et al., 1992; Schino et al., 1991). Macaques live in complex societies underpinned by communicative systems that facilitate both cooperative (Micheletta et al., 2013) and competitive (Altmann, 1962; Thierry et al., 2004) efforts between individuals. The extensive communicative repertoire (which include a huge amount of facial expressions, gestures, and vocalisations (Altmann, 1962) in these species therefore makes the macaques a good model for the study of communication. We used a multi-model inference approach, first to explore which social factors, if any, best predict the production of scratching behaviours in the macaques. To do this we looked at the social relationships between the scratcher and their neighbouring individuals, to confirm whether potentially stressful situations are more likely to elicit scratching. Secondly, we explored how the presence of scratching behaviours, among other social factors, modulates future social interaction. If others can use scratching behaviours as cues to potential future behaviour, we expected to see a difference in the type of response we observed after their occurrence. If for example, scratching is less likely to be followed by conflict, this could demonstrate a key adaptive advantage to both producing stress associated behaviours and responding to them.

3.3 Methods

3.3.1 Species and Study Site

We studied a group of free-ranging rhesus macaques (*Macaca mulatta*) in Cayo Santiago (Punta Santiago, Puerto Rico) between June and November 2016. Our subject group (V) consisted of 114–118 individually recognised adult monkeys and approximately 110 unidentifiable juveniles at the time of the study. Data were collected during the birthing season, and therefore the number of infants in the group varied. Animals were provisioned daily with commercial monkey pellets, and natural vegetation and water was available ad libitum.

3.3.2 Data Collection

Monkeys were followed between 7am and 2.30pm, 6 days per week. Data were collected on 45 adult macaques (21 males, 24 females, Appendix 1) using focal animal and instantaneous scan sampling (Altmann, 1974). Identities of animals could be confirmed by tattoos on the chest and thigh, as well as ID ear notches. Focal follows were performed over 30 minute periods in a randomised order and instantaneous scans were performed every 5 minutes within the focal. If an individual went out of view for 10 minutes of the follow, the follow was discarded and the next individual was followed. All behavioural data were recorded on a Samsung Galaxy Tab 4 installed with Prim8 software (McDonald and Johnson, 2014), a free, live behavioural data collection tool for Android based systems which allows a user to record continuous and scan data simultaneously (http://www.prim8software.com, McDonald and Johnson, 2014). We recorded all instances of scratching and all affiliative and aggressive social behaviours (Altmann, 1962), see Table 3.1. For all social behaviours the actor and the receiver were identified. The identities of all nearby individuals to the focal animal (within 0-3m) were recorded in the instantaneous scan samples. Whenever possible, follows on all focal individuals were conducted before any individual was repeated. We conducted 10 follows on each focal individual. Taking into account the time the animals spent out of view of the researcher, this resulted in an average of 280.6 (±16.8 SD) minutes of observation time per animal.

Behaviour	**Definition**
Stress behaviours	
Scratching	The repetitive raking of the skin, with the fingers of the hand or feet (Thierry et al., 2000)
Affiliative Behaviours	
Social-grooming	Grooming/cleaning of the hair on other individual with the hands or mouth (Thierry et al., 2000). Used in hygienic contexts, and during the maintenance of social bonds.
Lip-smacking	Lips are pursed, and lower jaw moved rapidly. Often made up of other visual and auditory components (eg. flattening of ears, head-turns, soft grunting (Micheletta et al., 2013))
Silent-bared-teeth	Both lips retracted to reveal the teeth, often accompanied by a raised scalp and flattened ears. An affiliative signal, but sometimes used as a submissive response to threats (Thierry et al., 2000).
Approaches	An individual moves towards a social partner.
Embrace/contact-sitting	An individual sits in contact with the partner, may include grasping of the hair (Thierry et al., 2000).
Aggressive Behaviours	
Non-contact aggression	Includes aggressive chasing or lunging.
Contact aggression	Includes biting, grabbing, and slapping. Usually following a chase.
Open-mouthed threat	The mouth is half-opened, accompanied by a raised brow and staring. Often includes a rattle vocalisation (Thierry et al., 2000).
Displacement	An individual moves towards another individual, whom then subsequently walks away. A reliable cue of dominance (Thierry et al., 2000).

Table 3.1. An ethogram of stress and social behaviours recorded, and used in this study for analyses along with operational definitions

3.3.3 Measures of relationship quality

To explore the social function of stress behaviours, we needed to take into account the quality of the social relationship during interactions. For each dyad we calculated the strength of the social bond, a difference in competitive success, and a coefficient of relatedness (Appendix 2-4).

To estimate the strength of social bonds between pairs of individuals in the group we calculated a composite sociality index (CSI, Silk et al., 2006), often used as a measure of friendship in animals. This measure is based on two affiliative factors; the frequency of scans where individuals were found in a close proximity, and the frequency of scans where individuals were found engaged in grooming. This is calculated through the following equation:

$$\frac{\left(\frac{Gab}{\mu G} + \frac{Pab}{\mu P}\right)}{2}$$

Where G_{ab}, is the frequency of in which dyad *ab* can be observed grooming, and μG in the mean frequency of grooming for all dyads, and P_{ab} is frequency in which dyad *ab* can be observed within a close proximity (< 3 meters), and μP is the mean frequency of proximity measures for all dyads. This CSI index allows us to characterise the strength of a social bond relative to the rest of the group. As CSI data tends to be positively skewed, this data was log-transformed to an approximate normal distribution before being used in analyses.

To estimate the difference in competitive success, we calculated an ELO-rating for each individual (R package: EloRating, Neumann et al., 2011). In this analysis, all individuals begin with an equal rating, which is then adjusted based on the outcome of an interaction. We looked at outcomes of all observed conflict, and all observed displacement interactions. Winners ratings increase as losers ratings decrease, with the magnitude of change reflecting the expected outcome (e.g. a lower rated individual winning against a high rated individual will result in a higher magnitude of change). The final ELO-rating of adults was converted to an absolute rank (from 1-99, this range is smaller than the total number of adults in the group as some non-focals were never seen engaged in competitive behaviours). The absolute rank of one individual was subtracted from another to provide a difference in competitive success.

Maternal relatedness was known, but paternal relatedness was not. Maternal relatedness was quantified through a *coefficient of relatedness (r)* index that represents the probability that two individuals will have copies of the same gene (Barbara B Smuts et al., 1987). Mother-offspring pairs have an *r* of 0.5*,* grandmother-grandchildren pairs have an *r* of 0.25, siblings have an *r* of 0.25, and unrelated individuals have an *r* of 0.

3.3.3 Statistical Analyses

Two candidate sets of models were produced for analysis, one to assess the factors that affected the production of scratching (Table 3.2), and one to assess which factors (including scratching) affected the likelihood of future aggression (Table 3.3). Data were applied to generalized linear mixed-models with a binomial error structure and logit link function, applying random intercept/slope models. Models were produced using *glmr* function, in the *lmer4* package for R studio (R version 3.3151). For both candidate sets of models, we use multi-model inference approach using Akaike's information criterion to assess the influence of each of the factors. This approach allows for the comparison of multiple potentially competing models simultaneously, providing an approximation that any given model in a set is the best whilst accounting for uncertainty in model selection. Further inferences can be then based on a range of competing models (Symonds and Moussalli, 2011). Such a multi-model inference approach is growing in popularity throughout the study of behaviour and ecology. In this approach, models are judged and ranked based on their AICc value, (Akaike's information criterion corrected for small sample size), where a smaller AICc value signifies a better model fit, and a smaller difference between the AICc of different models signifies when two models are competing, Symonds and Moussalli, 2011). From AICc values, Akaike weights (w) for each model is calculated, a value which represents the probability that the model under consideration is the best approximating model within the set, with strongly fitting models tending towards a w of 1, and weakly fitting models tending towards a w of 0. Model selection, calculation of AICc values, and Akaike weights were all calculated using the function *mod.sel*, in the package *MuMIn* for R. Finally, parameter estimates are averaged across all models (full averaging, Symonds and Moussalli, 2011), to assess the relative contributions of the factors within competing models. Model averaging was calculated using the function *mod.avg* in the package *MuMin*. All full models were tested for multicollinearity (function *vif*, package *car*) and over-dispersion (function *dispersion_glmer*, package *blmeco*). Additionally, residuals were visually inspected for extreme deviation from normality. All models had a low multicollinearity (variance inflation factor <2) and showed no evidence for over-dispersion.

Candidate model	nb of Neighbours	nb Friends	nb of Non friends	nb of Higher ranking	Nb of Lower ranking	nb of relatives
	Factors					
Number of neighbours	1	0	0	0	0	0
Social	0	1	1	1	1	0
High social stress	0	0	1	1	0	0
Low social stress	0	1	0	0	1	1
Dominance	0	0	0	1	1	0
Friendship	0	1	1	0	0	0
Number of friends	0	1	0	0	0	0
Number of non-friends	0	0	1	0	0	0
Number of higher-ranking	0	0	0	1	0	0
Number of lower-ranking	0	0	0	0	1	0
Number of relatives	0	0	0	0	0	1

Table 3.2. Candidate model set 1. Numbers represent inclusion of factor in the model (1) or not (0). Response variable: Occurrence of scratching. Sex of the focal was included in all models. Focal ID and actor ID were included as random factors in all models.

Candidate model	Scratch	CSI	ΔELO	Kin
	Factors			
Full	1	1	1	1
Scratch	1	0	0	0
Social	0	1	1	0
Scratch-social	1	1	1	0
Friendship	0	1	0	0
Scratch-friendship	1	1	0	0
Dominance	0	0	1	0
Scratch-dominance	1	0	1	0
Kinship	0	0	0	1
Scratch-kinship	1	0	0	1

Table 3.3. Candidate model set 2. Numbers represent inclusion of factor in the model (1) or not (0). Response variable: Likelihood of receiving aggression. Sex of the focal was included in all models. Focal ID and actor ID were included as random factors in all models.

For our first analysis, we separated each 30-minute follow into six 5-minute observation periods. For each observation period we measured if scratching was present (did occur (1), or did not occur (0)), how many neighbouring individuals were in proximity to the focal during this period (within 0–3 metres), the number of neighbours that were friends, the number of neighbours which were non-friends, the number of neighbours that were higher-ranking individuals, the number of neighbours that were lower ranking individuals and the number of neighbours which were maternal relatives. We defined friends as dyads with a CSI higher than the 3rd quartile + 1.5 x the interquartile range (i.e the outlier rule; Field at al. 2012), and non-friends as individuals below this. As the number of neighbours was directly associated with other factors (e.g number of friends, number of higher-ranked individuals), these factors were not included together in the same models to maintain low multicollinearity. To control for differences between sexes, the sex of the focal was included as a control in all models. The identification of the focal, and the focal follow that the observation period was extracted from were included as random factors in all models to avoid pseudoreplication (Waller et al. 2013). The candidate models that were built from these factors and applied to the model selection process are found in full in Table 3.2.

For our second analyses, we looked at all received social interactions in our dataset, separating those which were aggressive from those which were affiliative (see Table 3). The likelihood of receiving aggression was set as our binomial response variable (receiving aggression (1) or not (0)). Only social interactions that were isolated from other interactions (ie. no other social behaviour occurred between the actor and receiver within 1 minute prior) were included in the analyses. This was to control for the potential effect of other variables outside of our chosen factors (e.g. other communicative behaviours). We measured whether a scratch occurred within the 30 seconds prior to an interaction (did occur (1), or did not (0)) and included this as a factor in our model selection process. We additionally looked at the effects of friendship (the strength of a social bond; CSI), rank difference (calculated from ELO ratings), and the maternal relatedness of individuals (related (1), or not (0)) on the likelihood of aggression. To control for differences between sexes, the sex of the focal was included as a control in all models. The identification of the focal animal, and the identification of the actor were included as random factors in every model. The candidate models that were built from these factors and applied to the model selection process are found in full in Table 3.3.

3.4 Results

We compared several models that included a range of social variables to assess which social factors best explained the production of scratching behaviours (Tables 3.4 and 3.5, and a full breakdown of these models can be found in the Methods). We considered all models within a ∆AICc of <2 as strongly competing, and those within <4 as weakly competing. Any model with a ∆AICc above this, we considered to be a weaker model fit (Symonds and Moussalli, 2011). All parameter estimates and standard errors have been averaged across all models (full-averaging, Symonds and Moussalli, 2011)

The top ranked model, which included the presence of higher-ranking individuals as a single factor, had the lowest AICc value, and highest Akaike weight of 0.374. In this model, individuals were more likely to scratch when surrounded by higher-ranking individuals (Figure 3.1, $\beta = 0.124$, $SE = 0.069$). A closely competing model included the presence of higher-ranking individuals and non-friends (i.e a high social stress model, $\Delta AICc = 0.97$, $w = 0.231$, $ER = 1.62$). Individuals were also more likely to scratch when surrounded by non-friends (Fig. 1, $\beta = 0.025$, $SE = 0.05$). Each of these models supports the production of scratching as a marker of social stress (Maestripieri et al., 1992). To be cautious, we can also consider a full dominance model containing both the presence of high-ranking individuals, and the presence of low-ranking individuals ($\Delta AICc = 2.01$, $w = 0.137$, $ER = 2.73$). In contrast to the effect of high-ranking individuals on scratching, the presence of lower-ranking individuals reduced the occurrence of scratching behaviours (Fig. 1, $\beta = -0.0002$, $SE = 0.019$). A full social model containing each of the social factors described above, including the presence of friends was weakly competing against these models ($\Delta AICc = 2.43$, $w = 0.111$, $ER = 3.37$), as well as a model containing only the presence of non-friends ($\Delta AICc = 3.68$, $w = 0.059$, $ER = 6.29$). The above models made up 0.912 of the accumulative weight during model selection. Models that included the number of neighbours as a factor did not fit well to the data ($\Delta AICc > 4$); instead it appears quality and type of social relationship with neighbours has a greater influence than quantity of neighbours on the production of scratching. When we directly compare our high social stress and low social stress models, we find that high social stress factors (presence of higher-ranking individuals, non-friends) to be more predictive of scratching behaviour than low social stress factors (presence of lower-ranking individuals, friends, and relatives ∆AICc = 8.96). Overall, males scratched more than females (β = 0.891, SE = 0.172).

Models	**df**	**logLik**	**AICc**	**∆AICc**	***w***	**Acc. *w***	**ER**
Production of scratching							
Number of higher-ranking	5	-1660.06	3330.14	-	0.374	0.374	-
High social stress	6	-1659.54	3331.11	0.97	0.231	0.605	1.62
Dominance	6	-1660.06	3332.15	2.01	0.137	0.742	2.73
Social	7	-1659.26	3332.57	2.43	0.111	0.853	3.37
Number of non-friends	5	-1661.90	3333.82	3.68	0.059	0.912	6.29
Number of neighbours	5	-1662.46	3334.94	4.80	0.034	0.946	11.01
Friendship	6	-1661.65	3335.32	5.19	0.028	0.974	13.37
Kinship	5	-1663.09	3336.20	6.06	0.018	0.993	20.68
Number of friends	5	-1665.00	3340.02	9.89	0.003	0.995	>38
Low social stress	7	-1663.01	3340.07	9.93	0.003	0.998	>38
Number of lower-ranking	5	-1665.22	3340.47	10.334	0.002	1.000	>38
Likelihood of aggression							
Scratch-social	7	-201.45	417.19	0	0.555	0.555	-
Full	8	-200.70	417.77	0.59	0.414	0.969	1.34
Social	6	-205.37	422.96	5.77	0.031	> 0.999	17.91
Scratch-dominance	6	-212.00	436.22	19.03	4.09E-05	> 0.999	> 55
Dominance	5	-216.31	442.78	25.60	1.53E-06	> 0.999	> 55
Scratch-friendship	6	-220.10	452.42	35.23	1.24E-08	> 0.999	> 55
Friendship	5	-224.59	459.33	42.14	3.92E-10	> 0.999	> 55
Scratch-kin	6	-229.57	471.36	54.18	9.54E-13	> 0.999	> 55
Scratch	5	-233.89	477.93	60.74	3.58E-14	> 0.999	> 55
Kinship	5	-235.09	480.34	63.16	1.07E-14	> 0.999	> 55

Table 3.4 Model characteristics. Models are ranked by the AIC value (lowest to highest; best to worse fit). Df = Degrees of freedom, LogLik = Log-likelihood, AICc = Akaikes Information Criterion corrected for small sample sizes, ∆AICc = the difference in AIC between the highest ranked, and target model, *w* = Akaikes weight, Acc. *w* = the cumulative weight between the target model and the highest ranked model, ER = Evidence ratio (the weight of the high-ranked ranked model divided by the target model)

Factors *Production of scratching*	Estimate	SE
(Intercept)	-0.195	0.130
Sex	0.891	0.172
Number of Higher ranking	0.124	0.069
Number of non-friends	0.025	0.050
Number of lower ranking	-0.0002	0.019
Number of friends	-0.005	0.026
Number of neighbours	0.003	0.016
Number of kin	0.008	0.061
Likelihood of aggression		
(Intercept)	-0.132	0.390
Sex	0.851	0.401
Scratch	-1.256	0.534
Friendship (Composite sociality index)	-1.600	0.403
Rank difference (∆ELO)	-0.025	0.005
Kinship	-0.844	1.511

Table 3.5 Model averaged parameters, the parameter estimate, and standard error for each factor in both analyses. Estimates are averaged through *full averaging.*

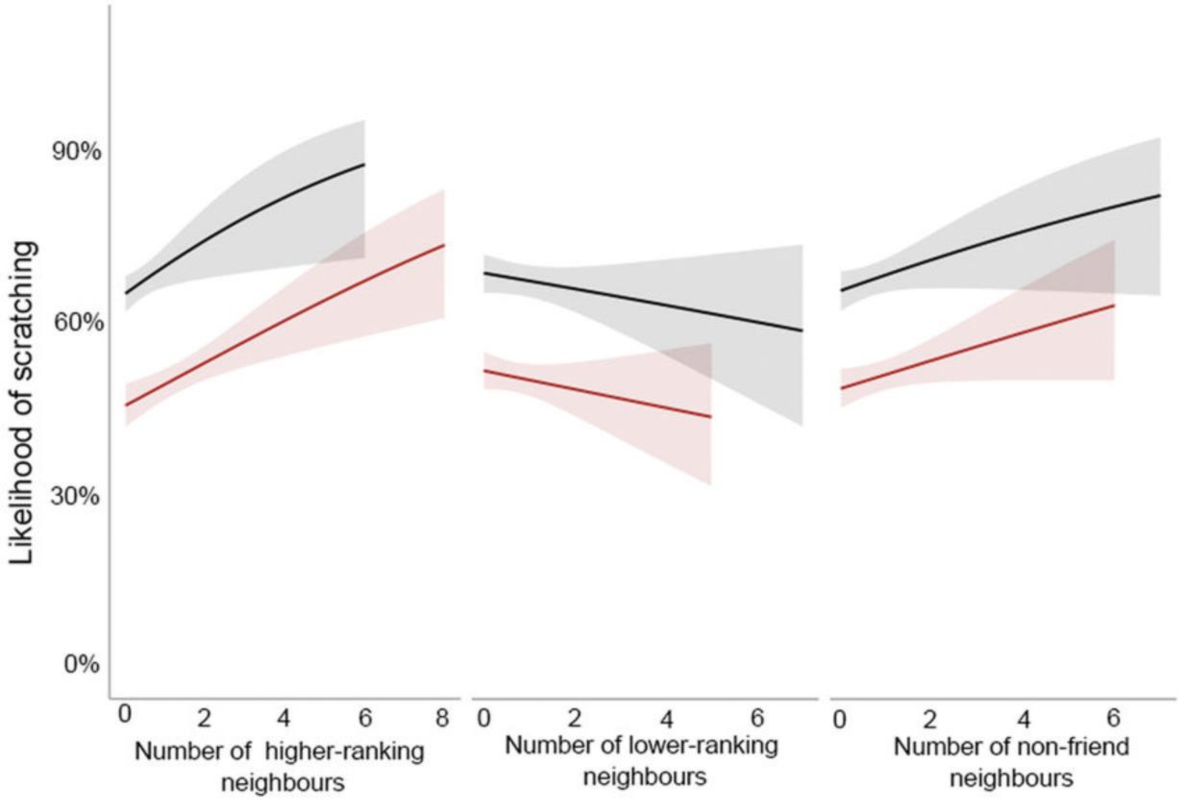

Figure 3.1 Production of scratching. The predicted probability of scratching in the presence of higher-ranking individuals (left), lower-ranking individuals (middle) and non-friends (right). Males in are black, and females are in red. Probabilities extracted from models including only the sex of the focal, the factor in question, and random effects. Shaded areas represent 95% confidence intervals.

To assess how scratching was responded to by others, we looked at all social interactions received by the scratching individual, separating those which were affiliative (0) and those which were aggressive (1). We then compared several models that included scratching and a range of social variables to assess which factors best explained the likelihood of future aggression (Tables 1 and 2, a full breakdown of these models can be found in the Methods). The highest ranked model, the Scratch-social model, which included measures of relationship quality (Friendship; as measured through a composite sociality index (Silk et al., 2006), and rank difference; calculated from ELO ratings (Neumann et al., 2011) as well as the presence of scratching prior to the interaction, had the lowest AICc value, and highest Akaike weight of 0.555. This was followed by a full model, which additionally included measures of kinship (ΔAICc = 0.59, w = 0.141, ER = 1.34); however this model fit was likely inflated by the fact the scratch-social model is nested within the full model, as otherwise, models that included kinship had very poor fit in comparison (ΔAICc > 54). Within the Scratch-social model, friendship and rank difference both affected the likelihood of an interaction being aggressive or not (Fig. 2). The likelihood of aggression increased as friendship decreased ($\beta = -1.596$, SE = 0.403), and the likelihood of aggression increased as rank difference decreased (ie. individuals were more likely to aggress those ranked lowered than them, $\beta = -0.025$, SE = 0.005). Interestingly, this was further modulated by the presence of a scratch; when a scratch occurred prior to the interaction, the likelihood of aggression was lower (Figure 3.2, $\beta = -1.256$, SE = 0.534). The two above models made up 0.969 of the accumulative weight during model selection. When we further compare models within the candidate set, we find the inclusion of scratching with other social factors improved the fit of models in all cases - Scratch-social vs Social model, ΔAICc = 5.77; Scratch-dominance vs Dominance model, ΔAICc = 6.56; Scratch-friendship vs Friendship model, ΔAICc = 6.91; Scratch-kinship vs Kinship model, ΔAICc = 8.98.

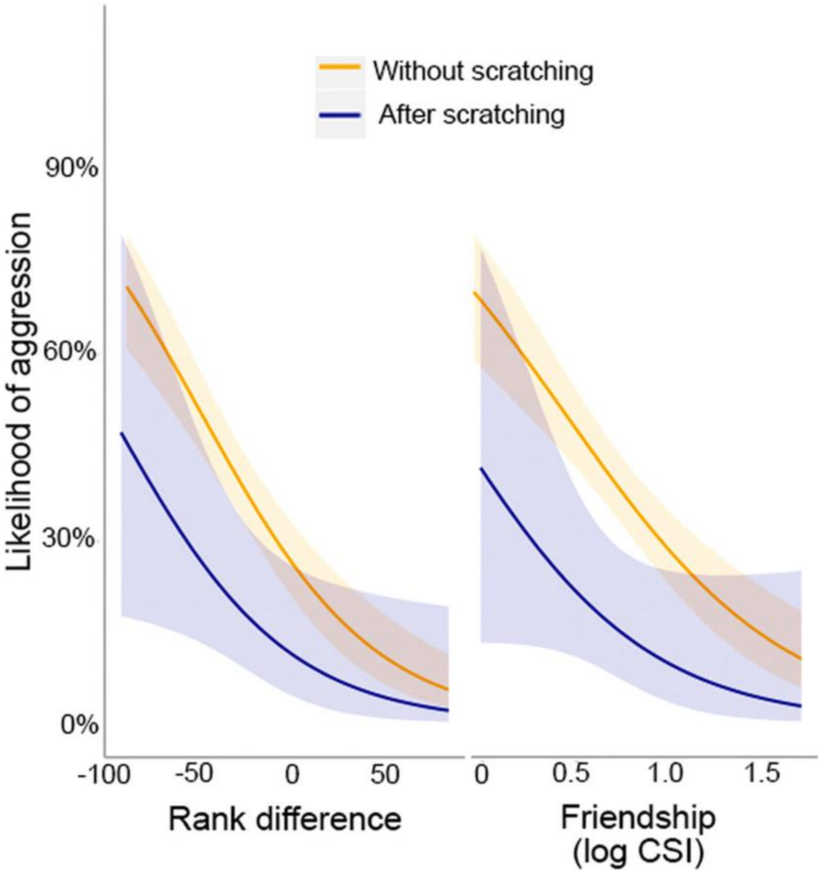

Figure 3.2 Likelihood of received aggression post-scratch. This graph shows the probability of a received interaction being aggressive, depending on if it occurred post-scratch or not. Probabilities extracted from models including only the sex of the focal, the factor in question, and random effects. This is compared against the rank difference on the left, and the friendship (log CSI) on the right. A higher CSI represents a stronger social bond. A positive rank difference implies an individual is ranked higher than the subject, a negative rank difference implies an individual is ranked lower than the subject. Shaded areas represent 95% confidence intervals.

3.5 Discussion

When macaques were in the presence of non-friends or higher-ranking individuals, they scratched more, providing further evidence for the link between social stress and scratching behaviours. Macaques were also less likely to be the target of aggression after they scratched. Scratching, therefore, appeared to elicit an immediate social response from others and seemed to have a broad function of modulating aggression and promoting non-aggressive interaction. This is the first data to suggest that scratching can be detected and responded to socially by others, and provides some evidence towards a communicative function.

We know that macaques appear less stressed (and produce less stress behaviours) after a clear dominance relationship has been established between individuals (Schino et al., 1990). Presumably, after a hierarchy has been established the actions of others become more predictable (Maestripieri et al., 1992). Here, stress behaviours are occurring more frequently around individuals with whom they are less bonded, probably because the likelihood of conflict is higher and/or because the outcomes of any interactions are less predictable, and thus more stressful. Candidate models which included the presence of important social partners such as friends (Silk et al., 2006) and kin were less explanatory of scratching. On the whole, therefore, these data provides little evidence that the production of scratching is directed as a communicative signal, but instead corroborates other data that scratching is a marker of social stress (Maestripieri et al., 1992).

When scratching occurred before social interactions, the likelihood of a subsequent aggressive interaction was reduced. Conflict is extremely costly, in both energy expenditure and risk of injury (Judge, 2005), and behavioural strategies to avoid and reduce physical conflict are common throughout gregarious animals (Aureli et al., 2002; Clutton-brock and Albon, 1979). Recent experimental research has suggested that presence of any emotional facial expressions in primates predicted a reduced likelihood of subsequent aggressive interactions (Waller et al., 2016b). Therefore, it might not be the specific emotional content of facial expressions that is important to others, but more that they indicate something about future behaviours and thus reduce uncertainty in observers. Scratching could be conceptualised similarly, as a reliable cue indicative of potential future behaviour, such as an individual’s potential for unpredictable or aggressive behaviour (Aureli et al., 1992). Recognising stress in others through behaviour such as scratching could function to help anticipate the potential future behaviour of others, allowing for more coordinated interaction and reducing the need for conflict. This could be of great adaptive value in animals with high degrees of sociality such as primates, of which many are dependent on a cohesive social environment.

It is important, however, to be cautious in the interpretation of these data. Although we have attempted to reduce confounding variables by reducing our dataset to social interactions that are isolated from other behaviours, it is extremely difficult to know with absolute certainty that it is the scratch which is being responded to, and that we haven't missed more subtle phenomena affecting the behavioural responses in others. In addition, although the current published evidence connecting scratching to stress is convincing (Maestripieri et al., 1992), self-directed behaviours are extremely complex and have been documented in other behavioural contexts such as behavioural transitions (Buckley and Semple, 2012) and positive emotional arousal (Neal and Caine, 2015). Scratching has also been interpreted as a potential gesture during affiliative interactions in chimpanzees, implying that their production can be intentional (Pika and Mitani, 2006). Further experimental cognitive research, which aims to probe how primates perceive scratching and relate it to context would help better understand primates' perception of these behaviours. For example, we can test whether macaques view scratching as aversive and has to be avoided, or whether they truly understand the association with internal stress.

These findings suggest that stress behaviours are potentially functional, not only for the regulation of internal states, but also in communication with others. This could help stimulate new approaches to stress by situating stress within a social interaction rather than focussing on the individual alone. Such an approach would not only impact our fundamental understanding of stress and the evolution of stress in humans, but also the strategies we employ to manage stress in captive animals. We emphasise the necessity to broaden our study of emotional behaviour to include a more adaptationist framework. We also support the view that behaviours and expressions are not only rooted in the internal state of the senders but can also be conceptualised as indicators of how individuals are likely to behave in the future (Fridlund, 1994; Waller et al., 2016a). By revealing stress, and thus future behaviours and intentions more transparently, animals can ultimately reduce the necessity for conflict and therefore promote a more cohesive social group. Crucially, this basic ability to recognise stress in others could be an important component of social cognition such as emotional perception, and empathy.

Chapter 4

Scratching and behavioural transitions in a social primate

4.1 Overview

Self-scratching in animals (particularly primates) is found to have many behavioural and physiological correlates. Although the links between scratching and specific contexts have been well described, their function is less clear. Within primates, previous research suggests a relationship between scratching and behavioural transitions (the changing from one behavioural state to another). These behaviours are hypothesised to indicate, or even assist, the changing between contrasting internal motivational states, however empirical support for such hypotheses is scant. In addition to these proximate explanations, it could be predicted that scratching that consistently precedes a behavioural change could provide a visual cue to others about future behaviour. Here, we explore the potential functions of scratching around behavioural transitions in a free-ranging group of social primates, rhesus macaques (*Macaca mulatta)*. Our data confirms that scratching rates were heightened preceding behavioural transitions, especially during transitions to moving/locomotory behaviour, but not especially during transitions between contrasting motivational states. We found some effect of the social audience with the likelihood of scratching increasing as the number of neighbours reduced, however there was no evidence that this led to a specific functional response from others. These data provides some support against the idea that these behaviours facilitate changes in motivation, as the biggest shifts in behavioural state were not associated with the most scratching. We find no evidence of a social function of scratching specific to behavioural transitions, and instead, we explore ideas that scratching observed in these contexts may instead be a product of stress.

4.2 Introduction

Displacement activities are described in the literature as patterns of behaviour that occur outside of their normal biological function or to the stimuli which normally elicits them (Armstrong, 1950; Maestripieri et al., 1992). These can come in many different forms, such as sand-digging in sticklebacks during threat displays, excessive preening or grooming in birds (Bradbury and Vehrencamp, 1998; Tinbergen, 1952), scratching in monkeys (Castles et al., 1999; Peignot et al., 2004) or, in humans, behaviours such as yawning or fidgeting (Heery and Kring, 2007). Within the study of human and non-human primate behaviour, the occurrence of displacement activities is described for the most part, in relation to the stressful and/or anxious experience of the individual (Mohiyeddini and Semple, 2013; Schino et al., 1991; Troisi, 2002).

There is, however, evidence to suggest that these behaviours also occur outside of the context of stress, and during other processes such as behavioural transitions (Buckley and Semple, 2012) and even positive emotional experience (Neal and Caine, 2015). The emergence of these behaviours is unclear. It is hypothesised that displacement activities may elicit a sensory cut-off (Chance, 1962) that could distract individuals from a preceding stimulus (that could for example, help with coping with stress, Mohiyeddini et al., 2013), or, allow for a more fluid transition from one motivational state to another (Buckley and Semple, 2012). Whatever the underlying mechanisms driving these behaviours are, it appears that their production is somewhat complex and can occur within many different contexts. Although this strong focus on the study of displacement behaviours as an indicator of stress has been fruitful in advancing our understanding of these behaviours (particular within the primates: Gustison et al., 2012; Leavens et al., 2001; Pavani et al., 1991), consequently our understanding of these behaviours occurring outside of the context of stress has been neglected. Thus, our overall understanding of why these behaviours exist, and how and they provide an adaptive advantage for animals is limited.

It has been reported within the primates that in the seconds preceding a behavioural transition (a change from one behavioural state to another, e.g. from a resting state to a social state), individuals will often scratch or increase the rates in which they scratch. To date, only a handful of studies have quantified this link between behavioural transitions and scratching in primates (Ring-tailed lemurs, *Lemur catta,* Buckley and Semple, 2012; Hamadryas

Baboons, *Papio hamadryas,* Kummer, 1968; rhesus macaques, *Macaca mulatta,* Diezinger and Anderson, 1986), and only one of which had an primary focus to addresses these phenomena explicitly (Buckley and Semple, 2012). Of these, there has been very little to no investigation into what specific contexts these scratches occur in and instead, the transitions from any behaviour, to any behaviour are normally quantified equally. It is important to broaden our approach to quantify which kinds of behavioural transitions elicit scratching, and in what specific behavioural or social contexts they occur, to better understand their underlying mechanisms. Importantly, addressing and comparing scratching in a more context-specific way will allow us to build empirical support for (or against) the current explanations regarding the occurrence of these behaviours outside the context of stress. Assessing whether scratching is more likely around behavioural changes that represent potentially conflicting motivation would allow us to better support or challenge the underlying explanations for displacement behaviour. For example, if scratching is heightened around transitions from affiliative behaviour to aggressive behaviour (Buckley and Semple, 2012), compared with resting and moving behaviours, scratching could likely be linked to the shift in motivation stage.

So far, most attempts to explain the causes of displacement activities has focused more on the proximate level (i.e. what internal states are regulating these behaviours, and what physiological or cognitive processes lead to their production), and less on the adaptive benefits these behaviours may provide (Maestripieri et al., 1992; Whitehouse et al., 2016). Recent studies into the adaptive value of displacement activities however, are beginning to uncover some examples of their potential function within a social environment. For example, sneezing behaviours in African wild dogs (*Lycaon pictus*) can facilitate collective movements by helping recruit group mates (Walker et al., 2017), and stress associated scratching behaviours can modulate the outcomes of social interactions in macaques, potentially by communicating underlying states and/or potential future behaviour (Whitehouse et al., 2017). If others can be sensitive to displacement activities relative to the context in which they are produced, including around behavioural transition, then it is possible that they act as communicative cues regarding future behaviour. The fluid coordination of individuals within social group is important within gregarious animals (Krause and Ruxton, 2002), and this could be improved by being able to better anticipate the immediate future behaviours or intentions of others through communicative cues (Fridlund, 1994; Waller et al., 2016a, 2016b). To see how non-dyadic behaviours such as displacement activities sit within a social framework, it is important to not only consider the actions of the acting individual, but also those around them who could influence, or respond to the behaviour (Semple and Higham, 2013). Considering the social environment when behaviours are produced can allow us to make some broad inferences about their potential communicative value (Slocombe et al., 2010) as behaviours selected for their signalling value are likely produced more so when information transfer is maximised (Bradbury and Vehrencamp, 1998). Additionally, the immediate responses or changes in behaviour of others can allow us not only to make predictions about the signal value of a behaviour, but also to explore what kind of information may be being transferred by looking at the quality and type of response they elicit (Whitehouse et al., 2017).

In this study on free-ranging rhesus macaques (*Macaca mulatta*), we explored the production of scratching around behavioural transitions, the behavioural and social contexts these behaviours are produced in, and their potential social consequences. If these scratches are not only by-products of physiological processes or internal conflict, but extend into the social repertoire as communicative behaviours, then their production should be maximised during socially optimal environments. In addition, if these scratches are in fact linked to specific contexts, the associations between the scratch and behavioural change could provide useful information to others, allowing the anticipation of the future behaviour. We therefore hypothesise that individuals will respond to the behavioural changes of others more effectively when these are preceded by a scratching behaviour (potentially leading to a more frequent and quicker response rate).

4.3 Methods

4.3.1 Subjects and Study Site

Our subjects belonged to a free-ranging group of rhesus macaques (*Macaca mulatta*), inhabiting the island of Cayo Santiago (Punta Santiago, Puerto Rico). The group consisted of approximately 230 individuals, of which 114-118 were individually recognisable adults (>5 years old, identified by facial and body features, chest and thigh tattoos, and unique ear notches). The remaining individuals where unrecognised juveniles and sub-adults. Data were collected between June and November 2016. As this period is the birthing season for this population, the number of infants varied between the beginning and end of data collection. Animals were provisioned daily with commercial monkey pellets, and natural vegetation and water was available ad libitum.

4.3.2 Data collection

Data were collected six days a week, between 7am and 2.30pm. Thirty-minute follows were conducted on 45 adult animals (21 males, 24 females). During the follows, 30-minute continuous focal samples were performed, as well as scan samples at 5-minute intervals (Altmann, 1974). During focal follows, all displacement activities and social behaviour (including identities of the actors and the receivers) were recorded. During scan samples, the identities of all individuals nearby the focal animal (within 3 meters) were recorded. 10 focal follows were conducted on each individual (except two males who only had seven and nine follows before they migrated). This resulted in an average of 280.6 (±16.8 SD) minutes of observation time per animal, after taking into account the time animals were out-of-view from the researcher. If during a follow, any individual went out of view for more than 10 minutes, the follow was discarded and repeated at the next possible occasion. A Galaxy Tab 4, handheld computer, running the software Prime8 (http://www.prim8software.com, McDonald and Johnson, 2014) was used to collect all behavioural data.

4.3.3 Defining behaviour transitions

We monitored 5 behaviourally exclusive states to generate data for behavioural transitions (Table 4.1). We defined any change from one of these states to another, as a behavioural transition. Behaviours that did not have an obvious instantaneous start/end were not included in the analysis (e.g. it is often to pin-point the exact moment foraging starts and stops).

Behavioural State	***Behaviours included***
Rest	Laying or sitting with eyes closed/asleep.
Vigilance	Laying or sitting with eyes open, eyes shifting suggesting monitoring of the environment
Moving	Walking, running or climbing
Aggression (as actor)	Contact, or non-contact aggression, including bites, slaps, chases, lunges, facial threats (as actor only)
Affiliation (as actor)	Grooming, embracing, lipsmacking, contact sitting (as actor only)

Table 4.1 Behavioural states used in analysis. A change of state from one of these, to another, was defined as a behavioural transition

The start of the second behavioural state was considered to be the moment the behavioural transition occurred. Subsequently, for each animal, rates of scratching were calculated 5 seconds before this point (before transition period), 5 second after this point (after transition period), as well as for an overall baseline (the total frequency of scratching, divided by the total observation time, per animal).

4.3.4 Statistical analyses

Firstly, to measure how the rate of scratching changes around transitions, the mean rates of scratching before and after transitions for each individual were compared with a baseline rate of scratching, and with each other (Fig 4.1a). These data did not follow a normal distribution (Kolmogorov-Smirnov test; all $p<0.05$) and therefore non-parametric tests (Wilcoxon signed-ranked test) were used for this part of the analysis. For subsequent analyses, generalised linear mixed models (GLMM's) were used, which allowed us to look at each individual data point whilst controlling for random effects and minimising the effects of pseudoreplication (Waller et al., 2013). Depending on the question, a candidate model with a binomial or continuous outcome variable was produced (using functions *glmer* and *lmer* respectively from the package *lme4* for R version 3.31, Bates et al., 2014; R Core Team, 2014). Candidate models were firstly compared with a null model containing only the intercept and random factors using a likelihood ratio test (function: *anova*). For candidate models that were significantly improved from the null model, we then looked at the individual effect of the predictors within the model. For predictors with multiple levels, we used a tukey multiple comparison test (function: *glht*, package: *multcomp*) to check for significance between all levels.

4.4 Results

4.4.1 Scratching around transitions

Rates of scratching were significantly higher before transitions compared with baseline (Figure 4.1b, Wilcoxon signed-ranked test; n=45, v = 7, *p* = <0.001) and after transitions (Figure 5.1d, n=45, v= 981, *p* = <0.001). There were no differences in scratching after transitions compared with baseline (Figure 4.1c, v = 409, *p* = 0.225). Compared with baseline, 44 out 45 monkeys showed increased scratching before transitions, and compared to after transition periods 40 out of 45 monkeys showed increased scratching before transitions.

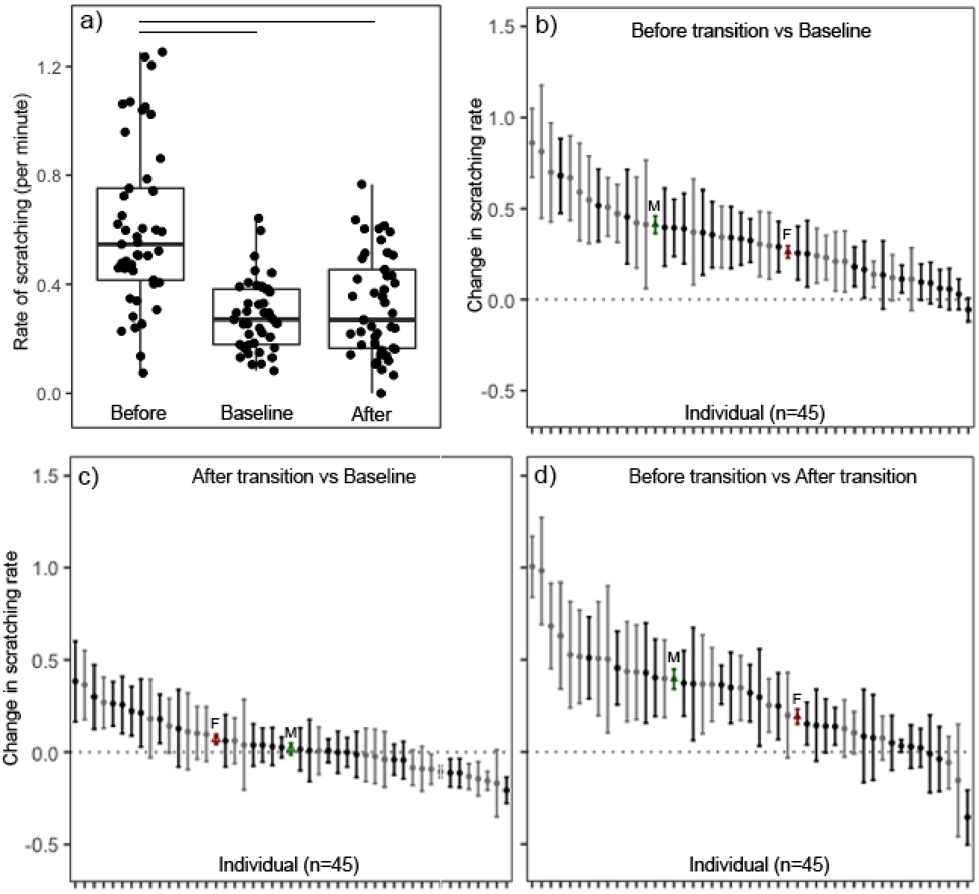

Figure 4.1. Comparison of scratching between before transition periods, after-transitions periods, and baseline.

a) Data used for analyses. ‘Before’ data is calculated from the period 5 seconds before behavioural transitions, ‘Baseline’ data is calculated from the total observation period, and ‘After’ data is calculated from the period 5 seconds after a behavioural transition. Boxes represent the interquartile range, line represents the median data point, whiskeys represent the range of data, and black dots represent each individual. b,c and d) represent the range of data for each individual (n=45) from each follow (n=10) with data presented as a change in scratching rate between each period. In b) positive values represent a higher rate of scratching before transitions compared to baseline, in c) positive values represent a higher rate of scratching after transitions compared to baseline, and in d) positive values represent a higher rate of scratching before transitions compared with after transitions. Grey points are male individuals, black points are female individuals, M= male average, F=Female average. Error bars are ±1SE.

4.4.2 Behavioural contexts eliciting scratching

To further explore the production of scratching before transitions, we looked at which behaviours were being transitioned to and from when scratching is produced. Here, we looked at 8918 transitions between the behavioural states: resting, vigilance, moving, aggression and affiliation. A more complex model containing both predictors (transitioning to, and transitioning from) failed to meet model assumptions when used simultaneously, and thus two simpler models were produced separately instead.

Our first model included the occurrence of a scratch before the transition as a binominal dependent variable (i.e. scratch (1) vs no scratch (0)), the behaviour being transitioned to as a predictor and the ID of the subject as a random factor. This model was significantly improved from a null model containing random factors only (likelihood ratio test: X^2 = 109.14, p = <0.001), therefore multiple comparison tests were conducted to assess for significant differences between factor levels. Multiple comparisons suggested scratching before behavioural transitions were significantly more likely when transitioning to moving/locomotory behaviour (Figure 4.2a). Scratching was more likely when transitioning to moving behaviours, compared with resting (ß = -0.727, SE = 0.238, z = -3.052, p = 0.014), affiliation (ß = 0.947, SE = 0.281, z = -3.364, p = 0.005), vigilance (ß = -0.980, SE = 0.102, z = -9.525, p <0.001) and aggression (ß = 2.078, SE = 0.712, z = 2.919, p = 0.022). All other comparisons were non-significant at p > 0.05.

Our second model included the occurrence of a scratch before the transition as a binominal dependent variable (i.e. scratch (1) vs no scratch (0)), the behaviour being transitioned from as a predictor, and the ID of the subject as a random factor. This model was significantly improved from a null model containing random factors only (likelihood ratio test: $X^2 = 101.81$, $p =$ <0.001), therefore multiple comparison tests were conducted to assess for significant differences between factor levels. Multiple comparisons suggested scratching the likelihood of scratching was lower when transitioning from moving/locomotory behaviours (Figure 4.2b). Scratching was less likely when transitioning from moving behaviours, compared with resting (ß = 0.949, SE = 0.209, z = 4.546, $p < 0.001$), and affiliation (ß = -0.858, SE = 0.226, z = -3.802, $p = 0.001$), vigilance (ß = 1.021, SE = 0.116, z = 8.819, $p < 0.001$) All other comparisons were non-significant at p > 0.05.

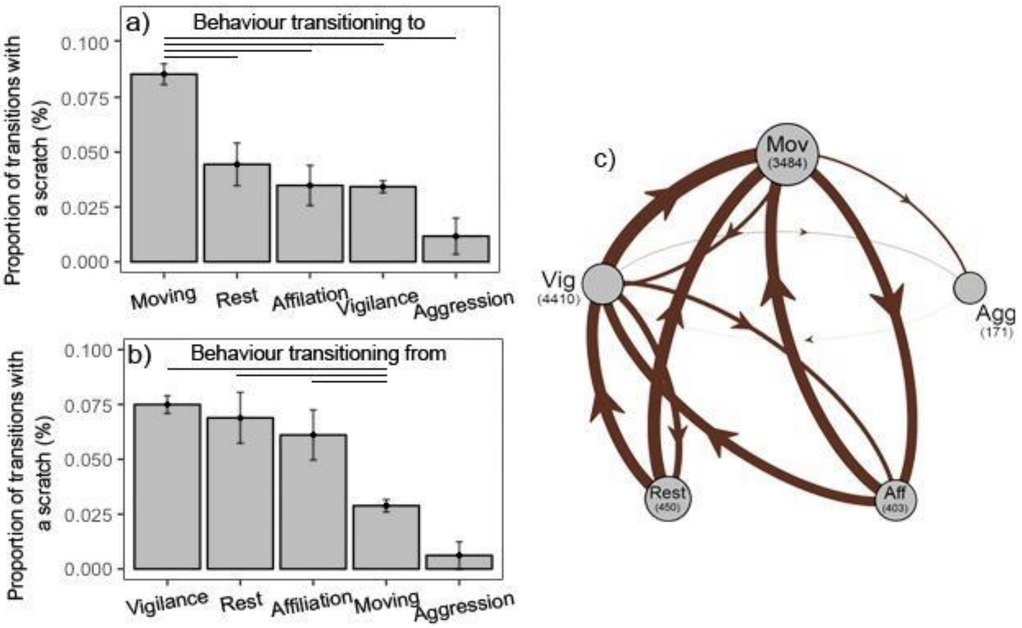

Figure 4.2. Likelihood on scratching depending on context. The proportion of transitions that occurred after a scratch when transitioning to (a) and from (b) each behavioural context. Error bars represent ±1SE, and comparison lines represent significant differences at p<0.05. Then panel on the right (c) represents a sociogram of data. Each node represents a behavioural context, the edge-weight represents the proportion of transitions with a scratch (thicker the line, the higher the proportion, numbers in brackets represent data points of that context) and the size of the node represents the in-degree centrality. In-degree centrality is a measure of incoming links to that node; the more connections leading into the node, the larger the in-degree centrality and the larger the node.

4.4.3 Adaptive value of scratching before moving

Next, we wanted to address whether or not the scratching behaviours before the animals move provide a reliable cue to others about potential future behaviour. Firstly, we looked at their production, and whether scratching around these transitions occur more readily in a social vs. a non-social environment, and if they provided an indicator of the intensity of future behaviour (e.g. if animals moved further distances when scratching before a transition). We looked at data with all behavioural transitions to moving behaviour (n=3484). Our model included the occurrence of a scratch as a dependent variable (scratch (1) vs no scratch (0)), the amount of neighbouring individuals during the transition (<3m proximity) and the duration of the following movement as predictors, and the ID of the subject as a random factor. This model was significantly improved from a null model containing random factors only (likelihood ratio test: $X^2 = 6.611$, p = 0.037) so predictors were further explored for significance. As the number of neighbours increased, the likelihood of a scratch before a behavioural transition decreased (Figure 4.3, ß = -0.107, SE = 0.046, z = -2.324, $p = 0.020$), suggesting the scratching is related to the social context. The amount of time the individuals moved for, did not affect the likelihood of a scratch preceding the behavioural transition (ß = -0.002, SE = 0.002, z = -1.010, $p = 0.312$).

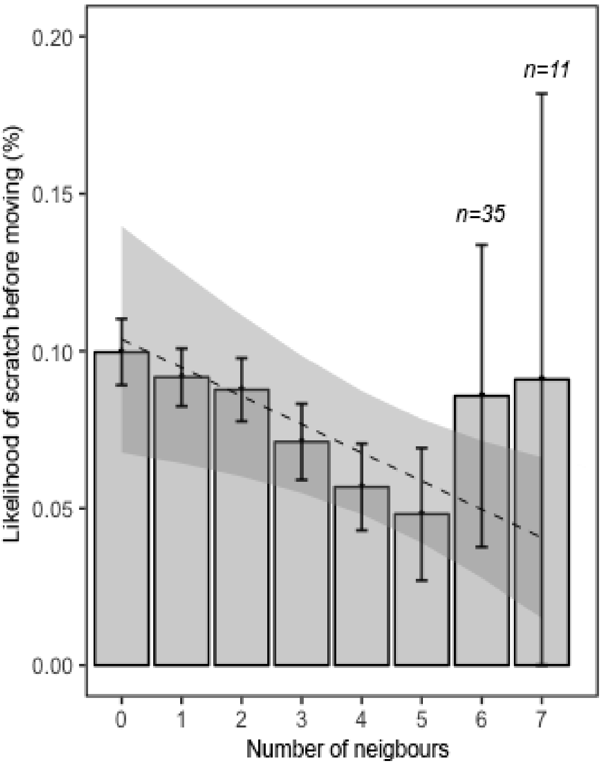

Figure 4.3 Audience effects of scratching when transitioning to a moving context. The proportion of transitions that occurred after a scratch when transitioning to a moving context, relative to the immediate social audience (individuals within 3 meters). Error bars represent ±1SE, for any bars (and error) calculated with less than 100 data points, the *n* is presented above.

To test for a social response to scratching before transitioning to moving behaviours, we tested the hypothesis that these scratches could facilitate collective movements by signalling to an audience that the scratcher is ready to move off. If these behaviours do facilitate collective movements and allow for the anticipation of behaviour, movements following a scratch should be responded to 1) more often, and 2) quicker. In the first case, our data included all transitions to moving behaviour. Our model included whether or not the individual was followed (within 1 minute of movement, 1/0) as a dependent variable, whether a scratch was present preceding the follow as a predictor, and the ID of the subject as a random factor. Although a trend is present in the data (Figure 4.4), this model was not a significant improvement from a null model (likelihood ratio test: $X^2 = 2.829$, $p = 0.091$). Therefore, scratching did not explain the variation in the likelihood of being followed. In the second case, our data included all transitions to movements that resulted in a follow. Our model included the delay between the movement and the follow, whether a scratch was present preceding the follow as a predictor, and the ID of the subject as a random factor. This model was not a significant improvement from a null model; likelihood ratio test: $X^2 = 1.320$, $p = 0.251$), Therefore, scratching did not explain the variation in the response time to be followed.

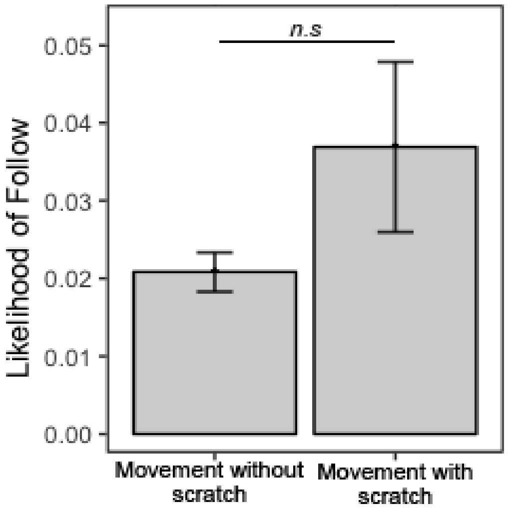

Figure 4.4 Following response to transitions to moving, with or without a scratch The proportion of transitions that occurred after a scratch when transitioning to a moving context that was immediately followed by a follow from another individual. Bars compares are transitions with or without a prior scratch. Error bars are ±1SE.

4.5 Discussion

In this study, we found scratching behaviours were elevated directly before, but not after, the transitioning between behaviours. This corroborates the observations of other studies of the same (Diezinger and Anderson, 1986) and different (Buckley and Semple, 2012) primate species. When further exploring the context of their production, it is apparent that increased scratching is restricted to transitions to a moving/locomotory state from any other behavioural state. Scratching around transitions occurred more when fewer individuals were in proximity, compared to when the animals were in larger subgroups. However, although these behaviours were modulated by the amount of neighbouring individuals (e.g. potential observers), we found no evidence that this relationship results from a communicative exchange, and the presence of a scratch did not affect the response to the changes in behaviour from others.

One of the pioneering and leading hypotheses of the occurrence of scratching (and other displacement activities) around periods of behavioural change was that it assists individuals when adjusting their internal motivational state, by allowing a sensory cut-off between behaviours (Chance, 1962; Wilz, 1970) and subsequently allows for a more fluid transition between potentially conflicting internal states. The current evidence for these ideas are from two main pieces of work, the first of which identified that sticklebacks displace displacement digging when transitioning from courtship behaviours, to aggression territorial behaviours (Wilz, 1970). The second identifies an increase in displacement activities in honeybees, when transitioning between a waggle-dance and foraging behaviours (Root-bernstein, 2010). Although many years have passed since these original ideas, evidence for these hypotheses remains particularly scant, particularly among mammals. If this is a valid explanation, we should expect transitions that represent major motivational shifts to elicit more pre-transition scratching (e.g. transitions to aggressive behaviours, Buckley and Semple, 2012). This is not supported by our data. Instead, scratching was highest when transitioning specifically to locomotory behaviours (irrespective of the preceding behaviour), and transitions leading to other highly valenced behaviours such as affiliation or aggression (where the change in internal motivation is likely to be greatest) did not produce such elevated patterns of scratching. Other research has demonstrated that higher degrees of restlessness in macaques (defined as the rate of behavioural change), are associated with higher rates of scratching (Higham et al., 2011). This increased restlessness is discussed as an additional marker of stress and/or anxiety in the actor. A similar phenomenon that has been described in humans (i.e. fidgeting, Heery and Kring, 2007). This could explain our results. Instead of facilitating a change in motivation, both the scratching and the behavioural changes could be linked to stress (Koolhaas et al., 1999) and thus be found to covary. However, in this case, we may also expect rates of scratching to occur more so not only after behavioural transitions, but before (as general rates of scratching should be increased around behavioural change), which is a pattern not represented in our data. Alternatively, it could be that the behavioural change could be an attempt to avoid or escape a stressor within the environment (e.g. sitting in close proximity to more dominant individuals, or ectoparasites), and this subsequently may lead to this stereotypic scratch-move pattern.

Although it is important to focus on the proximate explanations driving these behaviours, we need to also consider their potential adaptive value and ultimately, why they were selected for during evolutionary processes (Tinbergen, 1952, 1963). Here, we tested a hypothesis that these behaviours may have a functional role within social interaction. Firstly, if these behaviours were selected as reliable cues for others, we would expect their production to vary depending on the audience. Although we found an impact of the social audience on the likelihood of individuals scratching before they move, this relationship was negative - the likelihood of scratching before the transition reduced as the potential audience increased. If these behaviours were providing information to others, we would perhaps expect their production to be maximised when there are more potential observers (Bradbury and Vehrencamp, 1998) as producing communicative behaviours when there are no, or few observers will incur unnecessary costs to the producer. Or, perhaps, these communicative behaviours could be most salient with fewer individuals around if their function is to recruit others, or facilitate a collective movement (Sueur et al., 2011). Such a signal may not be as necessary when individuals are already in larger groups.

We found, however, no relationship between the duration of travel and the likelihood of prior scratching. Scratching in this context therefore, did not seem to provide information about future travel and movements lasting a few seconds were not less likely to have a preceding scratch than those lasting a few minutes. In addition, although visual inspection of the data suggests a trend, individuals who scratched before moving were not more likely to elicit a collective movement from other individuals, nor were the collective movement responses faster when a scratch was present. Although more generally speaking, a social role of scratching may exist (Maestripieri et al., 1992; Whitehouse et al., 2017), this data does not support a social function of scratching in the context specific form of behavioural transitions. If scratching in this context is merely reflective of the stressed state of the animal, it could be that socially isolated individuals (in this case, individuals with less neighbours) are more stressed, thus scratch more, and individuals central to the social network are less stressed and thus scratch less (Young et al., 2014). This could explain the audience effect on these behaviours. Or, animals in larger subgroups could be more likely to be around friends and kin, which could in turn have a modulating positive effect on stress (Whitehouse et al., 2017).

This data confirms a pattern between scratching and subsequent behavioural transitions in rhesus macaques, and adds to the small body of literature currently describing this phenomenon within primates (Buckley and Semple, 2012; Diezinger and Anderson, 1986). Although it remains difficult to explain why these behaviours occur based solely on this data, we provide evidence against the current hypotheses that these behaviours facilitate a change in motivational state of the actor. Ideally, future research should address such research questions alongside physiological correlates of stress (e.g. measurements of glucocorticoids, (Crockford et al., 2008) to address if these stereotyped behavioural patterns are a consequence of stress (Tinbergen, 1952). Lastly, we hope this study will encourage more focus on these behaviours within an adaptationist framework, and more so from the perspective of potential receivers, allowing for a better understanding of these widespread yet poorly understood behaviours in animals.

Chapter 5

Exploring the function of grooming signals in a group of free-ranging macaques.

5.1 Overview

Social grooming is an almost ubiquitous behaviour throughout social mammals and has been long established as an integral part of sociality in non-human primates. It is therefore unsurprising that communicative behaviour to encourage, direct or navigate grooming interactions has evolved alongside grooming. The aim of this research was to further explore the potential referentiality of scratching and body-part presentation behaviours during grooming, whilst considering lower-level explanations for these patterns of behaviour. Behavioural observations were conducted on a group of free-ranging rhesus macaques (*Macaca mulatta*) on the island of Cayo Santiago, Puerto Rico. Our findings suggest that grooming solicitation behaviours appear to lead to functional responses in the receiver: a presentation of a body part often leads to the grooming of that body part. However, these patterns may be more easily explained by mechanisms such as local enhancement rather than referentiality. These signals were more often directed towards lower-ranking individuals, and the production of these behaviours subsequently increased longevity of the grooming bout. We propose that these behaviours additionally function to signal benign intent, and communicate a willingness to groom to social partners, allowing for more coordinated social interactions and reducing the likelihood of a grooming bout being terminated due to social tension.

5.2 Introduction

Social grooming is an almost ubiquitous behaviour throughout social mammals (Grueter et al., 2013) and has been long established as an integral part of sociality in non-human primates (Carne et al., 2011). Although historically, there has been some debate whether or not the adaptive value of grooming stems from a social function, or whether it is more simply due to the hygienic benefits of parasite removal (Dunbar, 1991), there is now a general agreement that these explanations are not mutually exclusive and are both supported (Grueter et al., 2013). Instead, we consider these functions as proximate and ultimate explanations that are complementary to each other, and each important to fully understanding these behaviours (Tinbergen, 1963). Grooming provides opportunities for individuals to develop (Fedurek et al., 2009), and repair (Aureli and de Waal, 2000) social relationships with both kin and non-kin group mates (Ueno and Yamada, 2014). In fact, data regarding the occurrence of social grooming between pairs of individuals is now commonly used when calculating the degree to which individuals are socially bonded with each other (Silk et al., 2006). The establishment of such relationships through grooming leads to indirect fitness benefits for individuals in the future, such as alliance and coalition formation (Dunbar and Sharman, 1980). Social grooming is often reciprocated, with the amount of grooming given reflecting the amount received in the future, and has been shown to exchanged for other non-grooming commodities; such as access to food and resources (commodities which would otherwise be less accessible due to dominance, Carne et al., 2011). Thus, the occurrence of social grooming among primates (and many other mammal species) represents an important and necessary activity to manage a stable, socially bonded and cohesive social group (Lehmann et al., 2007).

As social grooming is an integral part of social behaviour in monkeys and apes, it is unsurprising that communicative behaviour to encourage, direct or navigate grooming interactions have evolved. One recognised group of such behaviours in many non-human primates, are *grooming solicitation* behaviours (Tsukahara, 1990; Ueno and Yamada, 2014); here, one individual presents an outstretched body part to a partner in close proximity, which subsequently induces social grooming from others (Thierry et al., 2000). These behaviours have not only been demonstrated to initiate social interactions, but elicit immediate reciprocity of grooming during the same social interaction (Ueno and Yamada, 2014). Although these behaviours are typically described at the beginning of grooming bouts, they also have been described to readily occur throughout the interaction and after grooming has already begun (Gupta and Sinha, 2016; Whitehouse, personal observation). Therefore, although one function of these behaviours may be to initiate grooming, it is likely that this explanation does not fully explain their occurrence. In fact, how these behaviours function within a grooming bout, or how they modulate or influence an interaction (outside of an initiation) is understudied. To avoid semantic confusion, we refer to presentations that elicit the start of grooming as *initial grooming solicitation* behaviours, and those that occur during grooming as *grooming solicitation* behaviours.

It has been proposed that these communicative signals may function to direct partners to groom specific parts of the body (Gupta and Sinha, 2016). In fact, the cognitive processes involved in these grooming solicitation behaviours have been described within a framework on referentiality (Gupta and Sinha, 2016), i.e. ‘Monkey A’ wants ‘Monkey B’ to groom their arm, and therefore presents this body part to their partner. In addition, a *directed scratching* behaviour in chimpanzees has also been described, used by individuals to direct or redirect grooming interactions referentially i.e. ‘Chimpanzee A’ wants ‘Chimpanzee B’ to groom their arm and therefore scratches this location (Pika and Mitani, 2006). For grooming socilitation behaviours to be assessed as referential, some form of mental state attribution may be necessary, taking into account the knowledge of the receiver by the sender (Pika and Mitani, 2006). To measure and test for referentiality and intentionality within signalling, we adopt a framework where some additional criteria should be met; specifically the presence of persistence and/or elaboration (Leavens and Hopkins, 1998). If an individual is intentionally communicating to achieve a specific goal, we should observe persistent signalling until the goal is met, and potentially, the signal should be elaborated to increase the chances of a response (Leavens and Hopkins, 1998).

Although referentiality may be involved in these communicative grooming behaviours, it could be that less cognitively demanding processes can explain their occurrence. Similar patterns of sender/receiver interactions can be seen throughout the animal kingdom that are free from explanations of referentiality, including in species where cognitive processes such as referentiality cannot be assumed (e.g. specific dancing in honeybees to elicit grooming from others, Land and Seeley, 2004). It therefore could be that more parsimonious explanations are available for grooming solicitation behaviours within the primates, which do not require mental state attribution of the sender. For example, as receiving grooming incurs direct benefits such as reduced stress (Gust et al., 1993) and increased endorphin secretion (Keverne et al., 1989), strategies to simply increase the longevity of grooming bouts may be employed. Grooming solicitation behaviours could be perceived as referential due to the effects of local enhancement, where groomers are attracted to the body parts being presented, due to the increased movement and salience of these body parts during the behaviour, and are not necessarily driven by the desires of their social partner (Hoppitt and Laland, 2013).

The aim of this research is to further explore the potential referentiality of communicative grooming behaviours, whilst considering cognitively less demanding explanations for these patterns of behaviour. We will firstly consider if groom presentation behaviours elicit a functional response; if the presentation of the body part leads to the grooming of this area, as this may suggest the groomer is responding to the desires of the groomee (Gupta and Sinha, 2016). We will also measure the degree of persistence after a failed signal, as this can inform us more about the mental state of the signaller (Leavens et al., 2007), e.g. do the animals repeat their signal if it does not elicit an immediate positive response in the groomer? The repetition of a signal suggests that the signallers goal has not been met, and suggests a specific desire of the individual (Leavens et al., 2007). Additionally, if presentation behaviours are referring the specific body parts, we should find a similar rate of response during the presentation of smaller and larger body part size; otherwise, if bigger body parts are responded to with greater success, this could provide evidence of local enhancement (Hoppitt and Laland, 2013). For example, the presentation of an arm vs. the presentation of the back should be responded to in similar ways, as this would suggest specificity to the presentation behaviour and response (a hallmark of referentiality, Townsend and Manser, 2013).

To test the hypothesis that grooming solicitations may act as benign signal to decrease uncertainty in the receiver (and communicate the willingness to continue the interaction), and to further assess for functional referentiality, we will see how solicitation behaviours affect both the duration of the grooming bout and how the production of the behaviours are modulated by social relationships. The function of many facial displays can be explained as signals of benign intent, with bared-teeth and play-faces communicating affiliative intentions before and during physical interaction (Silk, 2002; Waller and Dunbar, 2005). If grooming solicitation behaviours function similarly, grooming bouts should be longer after solicitations and solicitations should be used more so in social situations where uncertainty may be increased (when engaging with higher ranking, or less socially bonded group mates). To explore this, behavioural observations were conducted on a group of free-ranging rhesus macaques (*Macaca mulatta*) on the island of Cayo Santiago, Puerto Rico. This species ais highly sociable (Thierry et al., 2004) and grooming presentation behaviours have been described anecdotally in rhesus macaques since the first descriptions of their social repertoire (Altmann, 1962). As a species that is communicatively complex (Dobson, 2012) and that engages in frequent grooming behaviour (Thierry et al., 2004), they represent an ideal model for the study of these signals.

5.3 Methods

5.3.2 Subjects and study site

Our subjects were a free-ranging group of approximately 230 rhesus macaques (*Macaca mulatta*), inhabiting the island of Cayo Santiago (Punta Santiago, Puerto Rico). See Section 3.3.1 for further details about the study group site.

5.3.2 Data collection

Data were collected 6 days a week, between 7am and 2.30pm. Thirty-minute focal follows were conducted on 45 animals (21 males, 24 females), using continuous and scan sampling methods (Altmann, 1974). Full details about the data collection methods on this study group can be found in Whitehouse et al. (2017). Each thirty-minute follow was recorded with a HD video camera (Panasonic HDC-SD700, refresh rate, 75hz; videos presented at 24 fps) and a handheld computer was used to collect all grooming behavioural data (Galaxy Tab 4, installed with Prime8 software, McDonald and Johnson, 2014).

5.3.3 Video extraction and coding

Videos of grooming interactions from the focal follows were extracted for subsequent analysis. We included only interactions between recognisable adults in our final dataset. Grooming interactions involving juveniles, interactions that were bidirectional, interactions that were triadic, and footage that was of insufficient quality for detailed analysis were discarded. This resulted in 152 dyadic, unidirectional grooming bouts (350.25 minutes total, mean±SE: 2.27±0.2) for analysis. Grooming here, was defined as *cleaning the skin or fur of a partner, with the hands or mouth* (Thierry et al., 2004). Fifteen seconds before the grooming interaction, and fifteen seconds after the grooming interaction were included in each video clip to address pre- and post-grooming behaviours. A grooming interaction was defined as ended, if 10 seconds elapsed with no physical contact between individuals. If a grooming interaction reversed (i.e. the groomer becomes the groomee and the interaction continues), this was treated as a new grooming bout in our dataset. The occurrences of 4 body movements were coded; *initial grooming solicitation, grooming solicitation, position change* and *scratch* (Table 5.1). We recorded the location being presented or scratched; *head, body (back), body (front)* and *limbs.* We also recorded any immediate response of the grooming recipient (within 10 seconds) of the groomer (Table 5.1). Data were coded using Solomon Coder (version: beta 17.03.22; https://solomoncoder.com, by András Péter). Video coding was conducted by Charlotte Gurney-read. Reliability analyses on a random 5% of the dataset were conducted between Charlotte Gurney-read and Jamie Whitehouse to test for suitability of the coding scheme, and significant agreement was found for behaviours (cohens kappa; k = .871), responses (k = .825), groom locations (k = .771), and groom durations (Intraclass correlation cooefficience: .990); all agreement was significant at $p < 0.05$.

Table 5.1 Coded behaviours during a grooming bout.

Behaviour	*Description*
Initial grooming solicitation (n=81)	An individual presents a body-part to a partner, which subsequently leads to the initiation of a grooming bout.
Grooming solicitation (n=172, Figure 5.1)	An individual presents a body-part to a partner, occurring during a grooming bout.
Position change (n=53)	Change in the orientation of the body whilst being groomed, with no obvious presentation of a body-part (Gupta and Sinha, 2016).
Scratch (n=47)	Recipient of grooming scratches a body part during the grooming interaction.
Response	*Description*
Congruent initiation	Behaviour elicits the start of a grooming bout that matches the location being presented or scratched.
Incongruent initiation	Behaviour elicits the start of a grooming bout in a groom location which does not match the location being presented or scratched
Congruent response (Figure 5.1)	Behaviour elicits a change in groom location that matches the location being presented or scratched.
Incongruent response	Behaviour elicits a change in groom location which does not match the location being presented or scratched.
No change	Behaviour elicits no change in groom location in the groomer

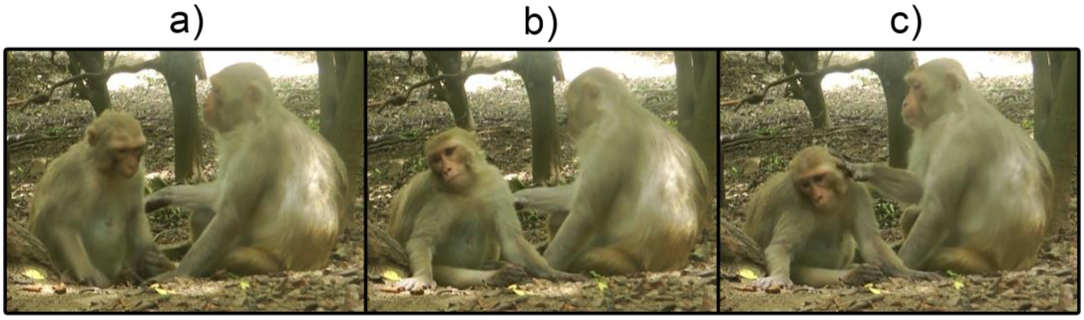

Figure 5.1 Grooming solicitation. (a) During a dyadic grooming bout, (b) one individual presents a body part (head) which leads to a (c) congruent response in their grooming partner, who then grooms the presented location.

5.3.4 Social relationships

To estimate the strength of social relationships in the group we calculated a composite sociality index (CSI, Silk et al., 2006), often used as a measure of friendship in animals, and the ELO-rating, a measure of competitive success (i.e. hierarchical rank). Prior to analysis, the difference in competitive success (the final ELO-rating of the groomee, minus the final ELO-rating the groomer) were converted to a Z scores (Z $= \frac{X - \mu}{\sigma}$). See Section 3.3.3 for more details on how these measures are calculated.

5.3.5 Data analysis

Models

For our analyses, generalised linear mixed models (GLMM's) were produced, GLMM's in this case allowed us to look at each individual data point whilst controlling for random effects and minimising the effects of pseudoreplication (Waller et al., 2013). Depending on the question, a candidate model with a binomial or continuous outcome variable was produced (using functions *glmer* and *lmer* respectively from the package *lme4* for R version 3.31 (Bates et al., 2014; R Core Team, 2014).

Referentiality hypotheses

Firstly, to assess for persistence of signalling, we looked at how a successful or unsuccessful response (binary response variable: whether the groomer groomed the presented location (1) or not (0)), affects the likelihood of the individual presenting the same body part during the remainder of the grooming bout (binary predictor variable: did (1), or did not (0)). We also assessed if a successful or unsuccessful response affected the likelihood of the individual presenting the same *or different* body part during the remainder of the grooming bout (binary predictor variable: did (1), or did not (0)). If the groomed individual has a specific referential goal, we should expect that individuals are more likely to repeat their signal when it was originally unsuccessful. Or, change strategy and produce a different signal type if their original signal was unsuccessful. Thus, we should also expect individuals to stop signalling if their goal was achieved. To assess whether groomers are responding to the specific body part being presented, we looked at if the presentation of the (predictor variables) *head, body (back), body (front)* or *limbs* affected the likelihood of a successful response (binary response variable: whether the groomer groomed the presented location (1) or not (0)). If the recipient is sensitive to the body part being presented, presentation of all body areas should be responded to with comparable success.

Benign signal hypotheses

To see if grooming solicitation behaviours were produced differently depending on the social relationship between the actor and the receiver, we looked at whether CSI and ELO-rating difference (continuous predictor variables) affected the likelihood of soclicitations (binary response variable: soclicitations occured in the grooming bout (1) or soclicitations did not occur (0). Additionally, we looked at whether the total amount of solicitation behaviours (continuous response variables) in the grooming bout was affected by these social relationship measures. Lastly, to assess if grooming solicitation behaviours prolonged a grooming bout, we calculated the duration between the production of soclicitations behaviour and the end of the grooming bout. If there were multiple solicitations per grooming bout, durations were calculated for all instances. If the behaviours increase longevity of a grooming bout, we should expect grooming time after solicitations to be longer, compared with total grooming bouts without these behaviours. Here, we look at remaining grooming time, rather than the duration of the full grooming bout as we could expect there to be more solicitation during longer grooming bouts, simply because there is more time for them to occur. Therefore, looking at remaining grooming-time post-behaviour is a better indication of a behaviour's influence on grooming longevity.

5.4 Results

5.4.1 Descriptive statistics

Ninety-four of the 152 grooming bouts observed were females grooming females, 33 were males grooming males, 18 were males grooming females, and 7 were females grooming males. Seventy-nine of the 152 grooming bouts (52%) were initiated with grooming soliciation behaviours. Females initiated grooming 47% (53/112) of the time, and males initiated grooming 65% (26/40) of the time. Seventy-four of the 152 grooming bouts (48.7%) contained groom solicitations behaviours during the bout, 39 (26.0%) bouts contained a position change and 35 (23.0%) bouts contained a scratch. A breakdown of the responses to these behaviours can be found in Table 5.2.

Table 5.2 *Descriptive statistics of responses*

Behaviour	*Congruent response*[1]	*Incongruent response*[1]	*No change*
Initial grooming solicitation	70 (86.4%)	11 (13.6%)	n/a[2]
Grooming solicitation	92 (53.5%)	11 (6.4%)	69 (40.1%)
Position change	7 (13.2%)	n/a[3]	46 (86.8%)
Scratch	8 (17.0%)	17 (36.2%)	22 (46.8%)

[1] See Table 5.1
[2] If grooming is initiated with this behaviour; this implies a response.
[3] As changes in body orientation are not associated with the presentation of a specific body part, responses cannot be congruent or incongruent, and instead, this data represents a 'change' in groom location.

Data was not sufficient for detailed analysis on scratch behaviours; therefore further analysis was conducted on grooming solicitation behaviours only.

5.4.2 Tests for referentiality

When the groomed individual initiated grooming by indicating a specific body part, or presented a body part during the grooming bout, the groomer responded to this by grooming that part of the body in over half of the occurrences (Table 5.2). Such a response was not seen during changes in body orientation (position change), and for scratching behaviours, suggesting grooming solicitation behaviours may have some referential function.

Unsuccessful responses (incongruent responses, or no groom location change in the receiver) to groom soliciation behaviours did not increase the likelihood of future presentation of the same (Fig 5.2a, *ß* = 0.367, SE = 0.635, *z* = -0.710, *p* = 0.478) or any (Fig 5.2b, *ß* = -0.114, SE = 0.319, *z* = -0.358, *p* = 0.720) body part. These data show that a negative response to the signal had no effect on the likelihood of the individual repeating the signal in the future, compared to a positive response. Thus, we find no evidence for persistence.

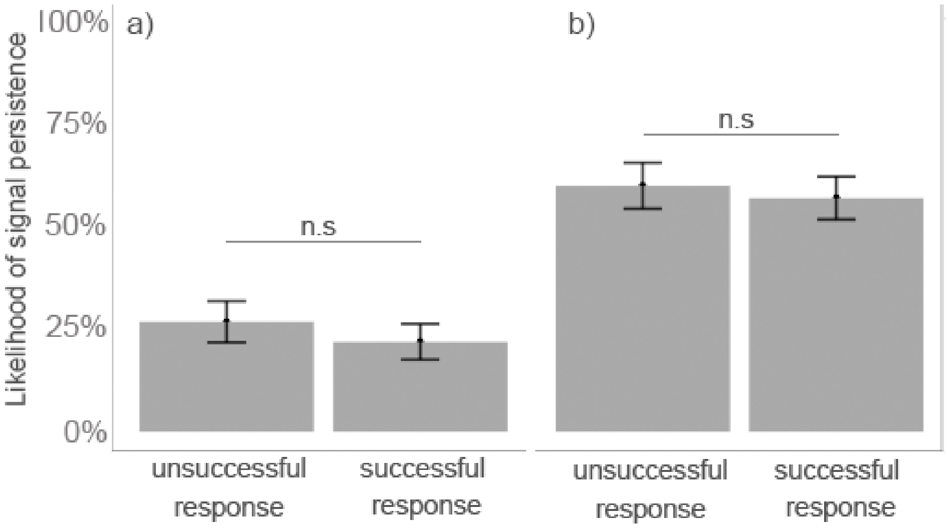

Figure 5.2 Likelihood of persistence. Bars represent the likelihood that an individual will (a) repeat the same solicitation signal (same body part presented) or (b) repeat any solicitation signal (any body part presented) during the remainder of the grooming bout, following an unsuccessful or successful response to the original signal. Errors bars represent ±1SE. Data shows no different in signal repetition following a successful or unsuccessful response.

The likelihood of a groom solicitation behaviour eliciting a successful response in a grooming partner varied depending on the body part being presented. When the grooming partner presented their *back*, this was significantly more likely to elicit grooming a redirection of grooming to this specific area, than when individuals presented their head (Figure 5.3, *ß* = -1.110, SE = 0.377, *z* = -2.945, *p* = 0.003) or front (Figure 5.3, *ß* = -1.527, SE = 0.552, *z* = -2.765, *p* = 0.006). These data suggests that the recipients were not always responsive to the area being presented.

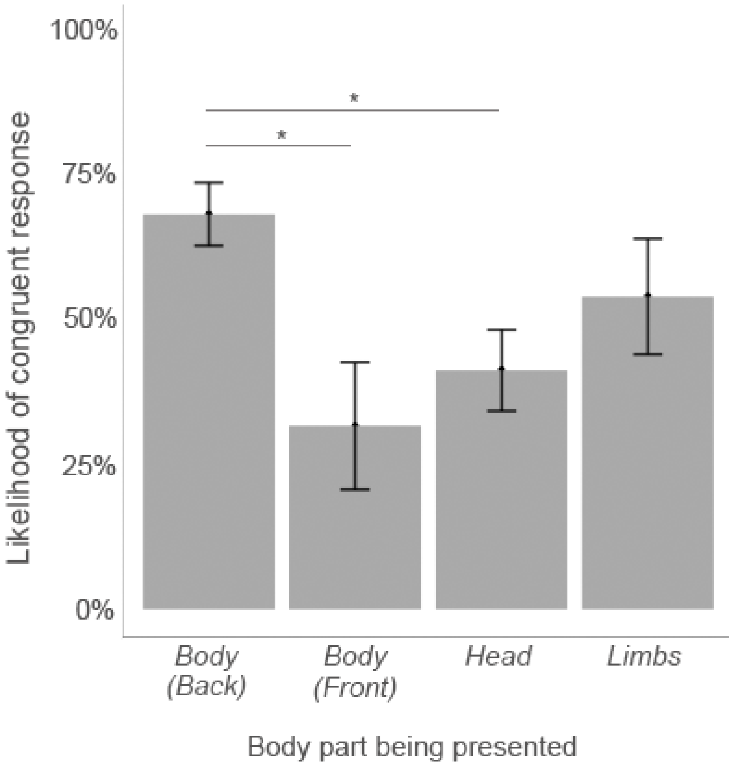

Figure 5.3 Likelihood of a congruent response, depending on signal type. Bars represent the likelihood a grooming solicitation will lead to a congruent response (a change in groom location to that body part), depending on which body part is being presented. Errors bars represent ±1SE. *Significant at $p < 0.05$.

5.4.3 Benign signal hypothesis

Firstly, we looked at the production of groom solicitation behaviours in relation to the social relationship between the actor and receiver. We found that the rank difference between the dyad affected the likelihood that the grooming bout would contain solicitation behaviours; individuals were more likely to present when they ranked higher than their grooming partner (Figure 5.4a, *ß* = 0.397, SE = 0.197, *z* = 2.018, *p* = 0.044). We found no effect of friendship on the production of solicitation behaviours (Figure 5.4b, *ß* = 0.170, SE = 0.635, *z* = 0.267, *p* = 0.789). There was no linear relationship between the strength of social relationships, and the frequency of solicitations; rank difference (*ß* = 0.058, SE = 0.148, *t* = 0.393, *p* = 0.698), friendship (*ß* = -0.300, SE = 0.486, *t* = -0.618, *p* = 0.539). These data suggest rank relationships affect the likelihood of solicitation behaviours occurring during the interaction, however not the overall frequency at which they are produced.

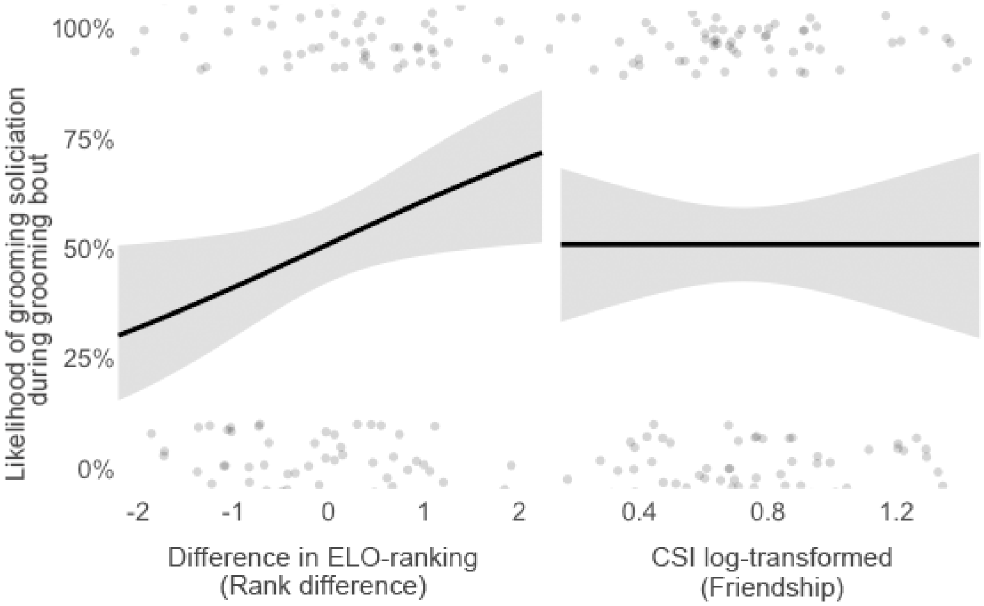

Figure 5.4 Likelihood of grooming soliciation behaviours occurring in a grooming bout in relation to social relationships. Black lines represent the predicted probability from the model, and the grey error bars represent confidence intervals. ELO-ratings were converted to Z scores; a positive value represents a signaller in higher rank to the recipient, a negative value representations a signaller in lower rank to the recipient. CSI scores were log-transformed; a higher value represents a stronger social relationship relative to the group, a lower value represents a weaker social relationship relative to the group. Points represent the data (grooming soliciation occurred (1) or not (0)).

After a grooming solicitation, the average remaining duration of the grooming bout was 144.9 seconds. After an initial grooming solicitation, the average total grooming bout was 143.4 seconds. Grooming bouts that had no solicitation behaviours lasted an average of 62.7 seconds. The remaining bout duration following a grooming solicitation was significantly longer than grooming bouts without soclicitation behaviours Figure 5.5, *ß* = 71.62, SE = 17.39, *t* = 4.119, *p* = <0.001). The duration of grooming bouts that were initiated with grooming solicitation behaviours, were also significantly longer than grooming bouts without solicitation behaviours (Figure 5.5, *ß* = 48.25, SE = 16.56, *t* = 2.914, *p* = 0.004).

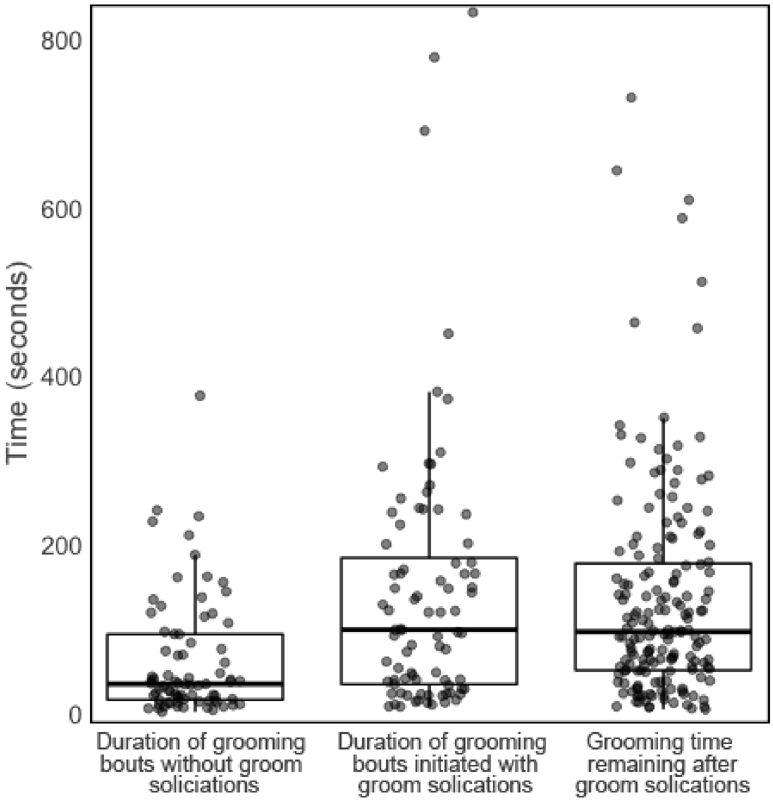

Figure 5.5 Duration of grooming bout in relation to soliciation behaviours. The boxes correspond to the first and third quartiles (the 25th and 75th percentiles), the whiskers correspond to 1.5 x the interquartile range. The horizontal middle line corresponds the median. Points correspond to data points in the analysis.

These data suggests that it is the solicitation behaviours, whether occurring at the beginning or the grooming bout, or during the grooming bout, increase the longevity of the bout and lead to a significantly longer social interaction.

5.5 Discussion

This study assessed the function of a series of potentially communicative behaviour found during social grooming, by quantifying the behavioural responses elicited in their grooming partner. When the monkeys presented a body part, this elicited a positive change in behaviour in the grooming partner, who then often redirected their grooming to the new area. Animals were sensitive to the rank-relationship they have with their partner, which subsequently modulated the production of these behaviours – perhaps to signal to lower-ranking individuals benign intentions. Signalling a willingness to be groomed could allow for more fluid and coordinated interactions, and could explain why in our data we found evidence that grooming longevity was increased by the production of these behaviours. Finally, it is possible that although groomers are responding to the desires of their grooming partners, our data suggest that the positive responses seen by grooming partners could instead be a consequence of stimulus enhancement.

Persistence of signalling is a hallmark of referentiality (Tomasello, 2010), as repeating a failed signal may imply that such a behaviour is goal-orientated, and thus an individual should repeat the behaviour until an appropriate response is given. Our subjects repeatedly presented a body part in about one-quarter of all occurrences, and were found to present the same or different body part in about half of the grooming occurrences, however, these repetitions (or, persistence of signalling) were not related to the partners' response. Although there were occurrences where one individual presented a body part, and re-presented this body part when the social partner did not respond, there were similarly a number of occasions where the body part was re-presented after the partner did show a positive response. In addition, the likelihood of a solicitation behaviour eliciting a positive response in their partner varied depending on the body part being presented.

Presentation of larger body parts (e.g. back), were more successful than others (e.g. head). If receivers were responding to the specific information within the signal, we would expect a similar response to the presentation of all body parts. We believe that congruent responses to soclicitation behaviours, could instead be a product of local enhancement (Hoppitt and Laland, 2013), and the solicitation behaviours more simply increase the salience of a body area, which is consequently more likely to be groomed (Liebal et al., 2013). These two findings suggest that these communicative signals are not necessarily as specific as other signals that are classified as referential (Leavens et al., 2007), and therefore conclusions of referentiality in the production of these signals is unsupported.

Individuals were more likely to produce groom solicitation behaviours during a grooming bout when they were of higher hierarchical rank than their social partner. However, the frequency of solicitations was not predicted by rank, e.g. a greater distance in rank did not lead to more solicitations. There are many examples of communicative behaviours in primates that have been selected for the function of mitigating conflict, and decreasing uncertainty in social interactions (Schino et al., 1990; Waller and Dunbar, 2005). For example, it has been proposed that relaxed open-mouthed ‘play face’ expressions are often used during play interactions as they allow individuals to distinguish between playful and aggressive intent of their partner (Waller and Dunbar, 2005, Pellis and Pellis, 1996). Such social signals of *benign intent* (Silk, 2002) may be more important during interactions where the risks of conflict are higher (e.g. an interaction between a high-ranking and a low-ranking animal, Schino et al., 1990). This could explain the pattern of data we find with grooming solicitations. In this case, higher-ranking individuals may use solicitation behaviours to signal to their lower ranking social partners that they have affiliative intentions, and that a continued interaction will not lead to escalated aggression.

Our data shows that solicitation behaviours increased the longevity of the social interaction. After grooming solicitation behaviour, whether it initiated the bout or occurred during the grooming interaction, the average remaining duration of the social interaction was doubled compared to the length of grooming bouts free of soclicitation behaviour. When looking at how solicitation behaviours affected longevity, we looked at remaining grooming time, rather than the duration of the full grooming bout as we would expect there to be more solicitation during longer grooming bouts (simply because there is more time for them to occur). This way, we could look at how soclicitation behaviours affect the grooming time, rather than how the grooming time affects soclicitation behaviours. The proximate reasons to prolong a grooming bout could be that it provides immediate positive feedback; it may be enjoyable for the groomee to be groomed (previous work has quantified the link between grooming and endorphins, Keverne et al., 1989), or provide immediate hygienic benefits (e.g. parasite removal, Akinyi et al., 2014). Adaptively, longer grooming bouts could allow for increased opportunities for social bonding and relationship development (Fedurek et al., 2009) which ultimately affects an individuals long-term fitness (Silk et al., 2010). Again with support from these data, we propose that communicating benign intent is allowing grooming bout longevity to be increased, and grooming bouts have a decreased likelihood of being disrupted prematurely by social tension after a willingness to groom has been communicated.

The use of scratching behaviours as a referential tool to direct grooming has been more recently described in a macaque species (Gupta and Sinha, 2016), in addition to the first documented cases in chimpanzees (Pika and Mitani, 2006). In our group, scratching whilst being groomed was especially rare compared to other behaviours recorded, and therefore full analysis of persistence of these behaviours was not possible. However, based on response success rates alone, our preliminary data suggests that scratching did not have a referential role in grooming bouts. Of the scratching produced, around half (22/47) led to no change in the receiver's behaviour, and in the cases where the receivers behaviour did change shortly after scratching (25/47), most of these changes in groom location did not match the area being scratched (17/25). This means only a small amount of scratches (8/47) led to a positive response. We therefore cannot conclude from this data alone that scratching is used as a gesture during grooming, however, more research is needed.

This study proposes a function to body part presentation behaviours that occur during grooming in addition to the current literature on referentiality. Although, studying communicative signals within an intentional and/or referential framework is important about advancing our understanding of the evolution of human communication (Liebal and Call, 2012) this study highlights the importance of considering other complimentary (or alternate) functions to signals. It could be that behaviours fit better within frameworks that do not assume the capacity for higher cognitive processing, and that we may be mistakenly labelling signals as more cognitively sophisticated than they in fact are.

Chapter 6

General Discussion

6.1 Overview

The overarching focus of this thesis was to explore the communicative function of the behaviours commonly associated with stress, and provide evidence for their selection within a social environment. First, this thesis provides evidence that in monkeys, stress behaviours are perceived by conspecifics differently to neutral, non-communicative behaviours, thus, demonstrating that these behaviours have the potential to have communicative function. Second, this thesis demonstrates that individuals producing stress behaviours can elicit responses in others that appear to be adaptive and beneficial to both the actor and receiver. In each of these cases, both in terms of the perspective of the sender and the receiver, there is evidence that these behaviours are driven by the quality of social relationship they have with their partner. The communication and response to stress was observed in more risky social situations (e.g. interactions with less bonded, or higher ranking social partners), suggesting that these behaviours could play a key role in the mitigation of social uncertainty, and allow for more fluid interactions with others. The products of this thesis stem from both experimental and observational approaches, live coding and video coding, and encompassing subjects from both captive and free-ranging populations; demonstrating the effectiveness of a mixed-methods approach in the study of communication. The findings of this thesis provide a new framework to examine stress and its associated behaviours, and instead of approaching stress solely in terms of an individual's experience, we should also consider stress to be situated in a social environment. Such a framework could have important welfare implications for the management of captive animals, where a shift in focus may be needed to not only consider the social audience as well as the experience of individuals undergoing stressful procedures.

6.2 Main findings and implications

6.2.1 Stress behaviours as information

Communication involves a provision of information, by one individual to another, and the subsequent use of that information in formulating a decision on how to respond (Bradbury and Vehrencamp, 1998). During the emergence of a communicative system, whether through evolution or development, there are different selective pressures on both the sender and receiver; both of which are trying to maximise the benefits of the communicative exchange (Guilford and Dawkins, 1991; Liebal et al., 2013). First, for a visual signal to emerge, there needs to be a link between a behavioural action, and the information to be transferred. Therefore there should be a pressure on the senders' behaviour to increase the salience of this link, as this will drive signal emergence. We provide additional evidence in this thesis that scratching (a known marker of stress, Maestripieri et al., 1992) is linked with both a social and behavioural context. The likelihood of scratching was much greater around periods of heightened social stress, such as being in proximity to higher-ranking individuals, or non-friends. In addition, the likelihood of scratching was much greater prior to behavioural transitions, a phenomenon that could also be linked to increase stress (i.e. restlessness, Higham et al., 2011). Our data therefore suggests that scratching is associated with contexts outside normal hygienic function, and may have a direct link with the stressful experienced by an individual (which has the potential to act as information for a receiver).

Second, for visual communication to emerge, the information needs to be transmitted through the environment to reach potential receivers. Therefore, there should be a pressure on the receiver to be sensitive to the signals of others to maximise information transfer. Human and non-human animals modulate their attention adaptively towards information (Winters et al., 2015), and by comparing how individuals attend to different kinds of stimuli, we can get a basic understanding of whether they are perceiving them as informative or not (Waitt et al., 2006). In this thesis, I demonstrate that macaques attend more to stress behaviours than neutral behaviours. Although interpretation of looking time data is complicated and imperfect (Winters et al., 2015), these data at the very least, inform us that the animals are seeing neutral body postures and stress behaviours as distinct. Therefore, these findings suggest that the cognitive systems are in place for individuals to send and receive information regarding psychological or physiological stress.

Finally, for a communicative exchange to emerge, feedback from the receiver in the form of a decision and response is needed. On average, this response should incur a positive fitness benefit for both individuals as this provides the most optimal condition for the emergence of communication (Bradbury and Vehrencamp, 1998). The data in this thesis suggests that scratching behaviours directly modulates an individual’s social interaction with others, in a way that could be interpreted as beneficial, and adaptive, for both the sender and receiver. Individuals were less likely to receive aggression from others, and more likely to engage in affiliation interactions after they scratched. Observable stress behaviour could therefore have adaptive value by reducing the probability of escalated aggression, benefiting both senders and receivers by facilitating social cohesion. This could provide a significant selection pressure to communicate stress to others, and represent an adaptive value of scratching (and potentially other self-directed behaviours) outside of coping strategies (Cheney, 2009; Gustison et al., 2012).

6.2.2 Stress behaviours as a signal or cue?

A key distinction between whether communicative behaviour exists as a signal or a cue, is the extent to which the actor and receivers behaviour has been shaped by natural selection (Laidre and Johnstone, 2013). Both signals and cues convey information, but only signals have evolved to do so, whereas information transfer from cues are often inadvertent or a by-product of other behaviour. However, as many signals can be derived from cues (see Chapter 1.4.3, Laidre and Johnstone, 2013), it can be often difficult to assess to what extent evolution has shaped the senders behaviour. Here, both the quantity and quality of the social audience each affected the production of scratching behaviours, and after their production, a positive social response was elicited in the receiver. However, it is difficult to pick apart whether individuals were communicating stress because of the presence of a social audience, or whether, more simply, the presence of a social audience elicited more stress and therefore more associated behaviour. If scratching is produced socially, and receivers respond as a result of an evolved association between scratching and stress – these behaviours could be considered a signal. However, if scratching is produced for other purposes (i.e. coping), and receivers are responding to these as a result of a learned association between scratching and stress – these behaviours could be considered a cue. It is however, very difficult to tell from this data (or perhaps any data) with certainty, to what extent evolution has shaped stress behaviours as a communicative signal, and to define these behaviours in the traditional sense of a signal or cue.

6.2.3 The role of social relationships.

By addressing how social relationships (i.e. rank, kinship and friendship) affect the production and response to communicative behaviours, we can begin to understand their function. If, for example, we observe a stronger response to a signal or cue by friends, this may suggest that the behaviours function in a cooperative environment (Micheletta and Waller, 2012; Slocombe et al., 2010). In contrast, if the behaviour elicits a stronger response by potential competitors (Muroyama and Thierry, 1998), this could suggest that the behaviours play a key role in a competitive environment. The effects of the social environment on the production of stress behaviours, and the subsequent responses to them, provides us with some insights about the social knowledge of our subjects. First, these data support the existing evidence suggesting primates can accurately distinguish between in-group and out-group members; as during looking-task experiments, attention was modulated by familiarity with the individual; with within-group individuals being monitored more than unknown individuals. Second, this data supports the evidence which suggest that non-human primates can effectively retain a social knowledge about those in their environment, and use their understanding of their relative social relationships to make decisions in the future (Bergman et al., 2013; Seyfarth and Cheney, 2011; Smuts et al., 1987); the degree to which subjects were socially bonded with the stimulus individual influenced attention. Lastly, our data suggest that the communicative role of scratching may be enhanced in a competitive environment. Barbary macaques attended to the stress behaviours of those with whom they were weakly bonded, and the response elicited in rhesus macaques was a reduction in likelihood of conflict. Responding to stress therefore, may be optimised around periods of social uncertainty, and could allow for individuals to better anticipate the behaviour of others where intentions are otherwise unpredictable.

6.2.4 Emotional signals within a predictive framework.

One way stress behaviours can be conceptualised, is similar to facial expressions; as expressions of emotion (Maestripieri et al., 1992). More recently, we are starting to consider the nonverbal behaviours, often called emotional expressions, outside of the framework of emotion, and instead more adaptively - as a predictor of potential future behaviour (Crivelli and Fridlund, 2018; Fridlund, 1994; Waller et al., 2016b). The ability to attend and respond to the emotions of others, although an arguably adaptive strategy in the maintenance of complex social systems (Clay and de Waal, 2013), may not represent the most parsimonious explanation for the evolution of emotional expression in animals. Instead, the ability to avoid harmful situations by predicting the likely behaviour of others could impose an enormous selection pressure on the evolution of behaviour throughout the animal kingdom. For example, signals that allow individuals to avoid interspecific and intraspecific conflict are extremely useful adaptations (eg. Alarm calling, Seyfarth et al., 1980; Reconciliation, de Waal and van Roosmalen, 1979). If emotional expressions themselves also reduce the likelihood of future conflict by allowing an individual to predict the future behaviour of others (which experimental data is beginning to suggest; Buttelmann et al., 2009; Morimoto and Fujita, 2012, 2011; Waller et al., 2016) this could be a more parsimonious explanation for their selection than the perception and processing of complex emotions alone. In this thesis, the responses to scratching by others may not represent an understanding of the emotional state of the individual, but instead, social partners may be better predicting the actions of stressed individuals. It could be, of course, that information regarding both the individual's emotional state and their future intentions have influenced the evolution of emotional expressions, and so it may be just as problematic to ignore emotion altogether. By bridging the gap between these two schools of thought, of both the functional and causal aspects of emotional expressions, we could develop an improved framework to fully understand these behaviours (Tinbergen, 1963; Waller et al., 2016a).

6.2.5 Scratching as a marker of stress: a word of caution.

One of the fundamental issues surrounding the use of scratching and/or other self-directed behaviours as a marker of stress, is that these behaviours are also observed in other, non-stressful contexts and are usually derived from pre-existing behaviour (Maestripieri et al., 1992). For example, scratching serves a hygienic function, and is impacted by other variables such as lice-load and environmental factors (e.g. rainfall, temperature, Duboscq et al., 2016) in addition to stress. Therefore, an increased rate of scratching can only provide an estimate of the level of stress experienced by an individual, but is not a definite indicator. In addition, there are now some data to suggest that scratching is not only increased during negative arousal, but also during positive arousal (Neal and Caine, 2015); suggesting that scratching could be a marker of arousal, without an attributed valence. Although collecting hormonal data to increase the certainty that behaviours are stress associated would be ideal, this in itself raises methodological issues. First, we can always observe a time-lag between the psychological and endocrine stress responses (Hellhammer et al., 2009), therefore attributing the measures of stress in endocrine samples (Gustison et al., 2012; Hanson et al., 1976) to a specific point in time with confidence, is problematic. This issue is exaggerated when we wish to attribute hormonal markers to specific behaviours. Second, as an important goal of this thesis was to measure spontaneous responses to the stress behaviours of others, approaching scratching individuals to attempt to collect samples compromises any subsequent social interaction that individual may have with others. The evidence that links scratching behaviours to stress is plentiful (Chapter 1.3.1), however, given the points above, we should always remain cautious when interpreting responses to scratching and other self-directed behaviours, as a response to stress specifically.

6.2.6 Scratching outside of the context of stress.

Scratching (the stress behaviour focused on throughout this thesis) has been hypothesised to have communicative functions outside of the context of stress in non-human primates. It has been proposed to communicate both the changing of behaviour (behavioural transitions, Diezinger and Anderson, 1986) and, to referentially direct the grooming efforts of others to specific scratched locations (directed scratching; Gupta and Sinha, 2016; Pika and Mitani, 2006). Although we found scratching to be highly associated with a preceding behavioural change (an association already quantified by others, Buckley and Semple, 2012; Diezinger and Anderson, 1986), further analysis of our data did not provide any convincing evidence that others used this association in a functional way. When looking at how scratching behaviours were produced and used when individuals were being groomed, the descriptive data suggests no change in observer's behaviour in response to scratching. Groomers did not seem to change grooming location to the scratched location, as observed in other studies (Gupta and Sinha, 2016; Pika and Mitani, 2006), and did not show similar patterns to groom solicitation behaviours (which did show positive responses from others in this thesis). Although scratching can be observed in these other contexts, these occurrences may not be completely disassociated from the explanation of stress. Scratching during behavioural transitions, could result from the stress of changing behaviour (e.g. moving away from more dominant individuals, or environmental stressors), or, that frequent behavioural change is in fact a consequence of stressful experience (e.g. restlessness, Higham et al., 2011). Additionally, grooming itself has the potential to cause stress (Semple et al., 2013), and the stress generated during a grooming interaction may explain why we observe scratching during these events.

6.2.7 Implications for a comparative approach.

Humans share many commonalities with non-human primates in how stress manifests itself in behaviour. Similarly to the non-human primate markers focused on in this thesis, experiences of stress in humans are linked to scratching (Mohiyeddini et al., 2013) among other behaviours such as yawning, lip biting, and face-touching (Mohiyeddini and Semple, 2013). Such similarities in the form and causation of stress behaviours between humans and macaques, could suggest a conserved function of these behaviours in humans too. Humans are extremely sensitive to visual displays of stress, and have both physiological (Ward et al., 2013) and behavioural (Dimitroff et al., 2017) responses to watching stressed individuals on video. Such responses to the stress of others in humans are attributed to empathy, which itself has been argued to have numerous adaptive functions such as group bonding, and parental care (Decety, 2015). The ability to recognise the emotions of others stems from associations with specific behavioural movements (Ekman, 1993), and is a cognitive skill which is likely to be of high importance during the evolution of empathy. Before sharing the emotional states with others, an individual needs to be able to recognise and process when these emotions are being expressed. The findings presented in this thesis, namely the evidence which suggests macaques can recognise and respond to the stress behaviours of others, could therefore represent an important evolutionary building block during the emergence of empathy in humans (and potentially other great apes, Campbell and de Waal, 2011; de Waal, 2008).

6.2.8 Welfare

Among the animals housed and bred in captivity, macaques (and in particular rhesus macaques) are very common. Many of these are supplied to laboratories and biomedical facilities for research (Buchanan-Smith, 2010). Institutions are required to maximise welfare, and incorporate the practices of the Three R’s (replacement and reduction and refinement) into the management of their facilities (Russel and Burch, 1959), therefore methods to measure the welfare of their animals is important. To monitor the welfare of their animals during day-to-day activities and invasive procedures, facilities will often use behavioural markers of stress, including displacement and stress behaviours, to assess for compromised welfare (JWGR, Joint Working Group on Refinement, 2009). If stress behaviours in non-human primates are perceived by conspecifics and elicit a response, then it could be important to consider not only the welfare of individuals, but also any potential observers that may be affected. For example, facilities could conduct stressful procedures on single individuals out of sight from others, which might help reduce the overall impact of the procedure on the animals around them. Alternatively, exposing individuals to the stress of others may be beneficial in facilitating social relationships between captive animals in some contexts, by making sure the causes of stress are visible to the rest of the group. Overall, developing a better understanding of stress, and the consequences of stress, will allow for the better management of captive populations, not only in laboratories, but also in zoological parks and rescue centres.

6.3 Future directions

Although the study of stress behaviour (and other displacement activities) has focused on non-human primate models in the recent years, such behaviours have been quantified in the past throughout many animal taxa; from birds and fish (Bradbury and Vehrencamp, 1998; Tinbergen, 1952), to non-vertebrates (Root-bernstein, 2010). To gain an accurate understanding of stress behaviours, and more specifically, the role of stress behaviours in a social environment, we could benefit from broadening our scope of subject species in the future. By comparing social responses to stress comparatively across species outside of the primates, we could develop more convincing hypotheses regarding the cognitive underpinnings of these responses, and the evolution of stress behaviour on the whole.

In addition, this area of research would benefit from further experimental research. Within the field of facial expression, researchers have developed paradigms to probe how non-human primates perceive expressions in terms of their associated valence (Parr, 2001), and the future behaviour of others (Waller et al., 2016b). In these studies, the subjects are trained to match images or videos, with other images of similar type. Subjects are then presented with meaningful communicative stimuli (e.g. a facial expression), and two options – one representing something positive (e.g. individuals grooming) and one representing something negative (e.g. individuals fighting). Subjects are then required to make a choice; to choose which option most closely matches the initial stimuli. This then allows us to see what stimuli subjects spontaneously match the communicative signal with, and therefore informs us what information an individual may be extracting from a signal. An approach like this, however, with stress behaviour, would allow us to confirm if the animals' perceive the behaviours as associated with negative context (and associated with stress). More importantly, it could help confirm that it is in fact the behavioural movements the animals are responding to in the first place, and not some other marker of stress occurring in synchrony to scratches and other self-directed behaviour.

6.4 Conclusions

By approaching the study of stress behaviour from the perspective of observers, I highlight the potential for these behaviours to have communicative function. My studies demonstrate that macaques respond to stress behaviours in a way that is comparable to other communicative signals; these elicit a functional response (aggression reducing) from others, and in a way that is flexible depending on the relationship between the sender and receiver. The adaptive value of these behaviours still remains relatively misunderstood, however, and here I propose an adaptive function that may help towards explaining their selection: to reduce uncertainty in others, allowing others to reliably predict future behaviour, and ultimately, to allow for more coordinated social interaction. The findings of this thesis provide a new framework to study stress and associated behaviour, and instead of approaching stress in terms of an individual’s experience, in the future we should also consider stress to be situated within a social environment.

References

Akinyi, M.Y., Tung, J., Jeneby, M., Patel, N.B., Altmann, J., Alberts, S.C., 2014. Role of Grooming in Reducing Tick Load in Wild Baboons (Papio cynocephalus). Anim. Behav. 85, 559–568. doi:10.1016/j.anbehav.2012.12.012.Role

Allen, A.P., Kennedy, P.J., Cryan, J.F., Dinan, T.G., Clarke, G., 2014. Biological and psychological markers of stress in humans: focus on the Trier Social Stress Test. Neurosci. Biobehav. Rev. 38, 94–124. doi:10.1016/j.neubiorev.2013.11.005

Altmann, J., 1974. Observational study of behaviour. Behaviour 49, 227–267.

Altmann, S., 1962. A Field Study of the Sociobiology of Rhesus Monkeys, Macaca mulatta. Ann. N. Y. Acad. Sci. 102, 338–435.

Anderson, J.R., Myowa-Yamakoshi, M., Matsuzawa, T., 2004. Contagious yawning in chimpanzees. Proc. Biol. Sci. 271 Suppl , S468–S470. doi:10.1098/rsbl.2004.0224

Anestis, S.F., 2010. Hormones and Social Behavior in Primates. Evol. Anthropol. 78, 66–78. doi:10.1002/evan.20253

Armstrong, E.A., 1950. The nature and function of displacement activities. Symp. Soc. Exp. Biol. 4, 361–387.

Aureli, F., Cords, M., van Schaik, C.P., 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. Anim. Behav. 64.

Aureli, F., Cozzolino, R., Cordishi, C., Scucchi, S., 1992. Kin-oriented redirection among Japanese macaques: an expression of a revenge system? Anim. Behav. 44, 283–291.

Aureli, F., de Waal, F., 2000. Natural Conflict Resolution. University of California Press.

Aureli, F., van Schaik, C.P., van Hoof, J.A.R.A.M., 1989. Functional aspects of reconciliation among captive long-tailed macaques (Macaca fascicularis). Am. J. Primatol. 19, 39–51.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2014. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw.

Bergman, T.J., Bergman, T.J., Beehner, J.C., Cheney, D.L., 2013. Hierarchical Classification by Rank and Kinship in Baboons. Science (80-.). 1234. doi:10.1126/science.1087513

Berridge, C.W., Mitton, E., Clark, W., Roth, R.H., 1999. Engagement in a Non-Escape (Displacement) Behavior Elicits a Selective and Lateralized Suppression of Frontal Cortical Dopaminergic Utilization in Stress. Synapse 197, 187–197.

Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of Animal Communication. Sinaur Associates, Sunderland, MA.

Bradshaw, R.H., 1993. Displacement Activities as Potential Covert Signals in Primates. Folia Primatol. 174–176.

Buchanan, T.W., Bagley, S.L., Stansfield, R.B., Preston, S.D., Louis, S., 2012. The empathic , physiological resonance of stress. Soc. Neurosci. 7, 1–11. doi:10.1080/17470919.2011.588723

Buchanan-Smith, H.M., 2010. Environmental enrichment for primates in laboratories. Adv. Sci. Res. 41–56. doi:10.5194/asr-5-41-2010

Buckley, V., Semple, S., 2012. Evidence that displacement activities facilitate behavioural transitions in ring-tailed lemurs. Behav. Processes 90, 433–5. doi:10.1016/j.beproc.2012.04.009

Buttelmann, D., Call, J., Tomasello, M., 2009. Do great apes use emotional expressions to infer desires? Dev. Sci. 12, 688–98. doi:10.1111/j.1467-7687.2008.00802.x

Byrne, R., Whiten, A., 1989. A Machiavellian Intelligence - Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Oxford University Press.

Call, J., Aureli, F., de Waal, F.B.., 2002. Postconflict third-party affiliation in stumptailed macaques. Anim. Behav. 63, 209–216. doi:10.1006/anbe.2001.1908

Call, J., Aureli, F., de Waal, F.B.M., 1999. Reconciliation patterns among stumptailed macaques: a multivariate approach. Anim. Behav. 58, 165–172.

Campbell, M.W., de Waal, F.B.M., 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. PLoS One 6, e18283. doi:10.1371/journal.pone.0018283

Carne, C., Wiper, S., Semple, S., 2011. Reciprocation and Interchange of Grooming, Agonistic Support, Feeding Tolerance, and Aggression in Semi-Free-Ranging Barbary Macaques. Am. J. Primatol. 73, 1127–1133. doi:10.1002/ajp.20979

Castles, D., Whiten, a, Aureli, F., 1999. Social anxiety, relationships and self-directed behaviour among wild female olive baboons. Anim. Behav. 58, 1207–1215. doi:10.1006/anbe.1999.1250

Cavigelli, S.A., Caruso, M.J., 2015. Sex , social status and physiological stress in primates : the importance of social and glucocorticoid dynamics. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 370, 20140103.

Chance, M.R.., 1962. An interpretation of some agonistic postures; the role of cut-off acts and postures In Evolutionary aspects of animal communications, 1961. Symp. Zool Soc London 8, 71–89.

Cheney, D.L., 2009. Stress and Coping Mechanisms in Female Primates, in: Wynne-Edwards, H., Brockmann, J., Snowdon, C., Roper, T., Naguib, M.K. (Eds.), Advances in the Study of Behavior. Academic Press, pp. 1–44. doi:10.1016/S0065-3454(09)39001-4

Chrousos, G.., 2009. Stress and disorders of the stress system. Nat. Rev. Endocrinol. 374–381.

Clay, Z., de Waal, F.B.M., 2013. Development of socio-emotional competence in bonobos. Proc. Natl. Acad. Sci. U. S. A. 110, 18121–6. doi:10.1073/pnas.1316449110

Clutton-brock, T.H., Albon, S.D., 1979. The Roaring of Red Deer and the Evolution of Honest Advertisement. Behaviour 69, 145–170.

Creel, S., Dantzer, B., Goymann, W., Rubenstein, D.R., 2013. The ecology of stress : effects of the social environment. Funct. Ecol. 27, 66–80. doi:10.1111/j.1365-2435.2012.02029.x

Crivelli, C., Fridlund, A.J., 2018. Facial Displays Are Tools for Social Influence. Cell 22. doi:10.1016/j.tics.2018.02.006

Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., Cheney, D.L., 2008. Social stressors and coping mechanisms in wild female baboons (Papio hamadryas ursinus). Horm. Behavor 53, 254–265. doi:10.1016/j.yhbeh.2007.10.007

Cronin, K.A., Jacobson, S.L., Bonnie, K.E., Hopper, L.M., 2017. Studying primate cognition in a social setting to improve validity and welfare : a literature review highlighting successful approaches. Peer J 5, e3649. doi:10.7717/peerj.3649

Czoty, P.., Gould, R.., Nader, M.., 2009. Relationship between Social Rank and Cortisol and Testosterone concentrations in Male Cynomolgus Monkeys (Macaca fascicularis). J. Endocrinol. 21, 68–76. doi:10.1111/j.1365-2826.2008.01800.x.Relationship

Darwin, C., 1872. The expression of the emotions in man and animals, 1st ed. John Murray, London, UK.

David, H.A., 1987. Ranking from unbalanced paired-comparison data. Biometrika 74, 432–436. doi:10.1093/biomet/74.2.432

De Waal, F., van Roosmalen, A., 1979. Reconciliation and consolation among chimpanzees. Behav. Ecol. Sociobiol. 5, 55–66.

De Waal, F., Yoshihara, D., 1983. Reconciliation and Redirected Affection in Rhesus Monkeys. Behaviour 85, 224–241.

De Waal, F.B.M., 2008. Putting the Altruism Back into Altruism : The Evolution of Empathy. Annu. Rev. Ecol. Syst. 59, 279–300. doi:10.1146/annurev.psych.59.103006.093625

Deaner, R.O., Khera, A. V, Platt, M.L., 2005. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. Curr. Biol. 15, 543–8. doi:10.1016/j.cub.2005.01.044

Decety, J., 2015. The neural pathways, development and functions of empathy. Curr. Opin. Behav. Sci. 3, 1–6. doi:10.1016/j.cobeha.2014.12.001

Delius, J.D., 1988. Preening and Associated Comfort Behavior in Birds. Ann. N. Y. Acad. Sci. 525, 40–55. doi:10.1111/j.1749-6632.1988.tb38594.x

Diezinger, F., Anderson, J.R., 1986. Starting From Scratch : A First Look at a “ Displacement Activity ” in Group-Living Rhesus Monkeys. Am. J. Primatol. 124, 117–124.

Dimitroff, S.J., Kardan, O., Necka, E.A., Decety, J., Berman, M.G., Norman, G.J., 2017. Physiological dynamics of stress contagion. Sci. Rep. 1–8. doi:10.1038/s41598-017-05811-1

Dobson, S.D., 2012. Coevolution of Facial Expression and Social Tolerance in Macaques. Am. J. Primatol. 74, 229–235. doi:10.1002/ajp.21991

Duboscq, J., Romano, V., Sueur, C., Macintosh, A.J.J., 2016. Scratch that itch : revisiting links between self-directed behaviour and parasitological , social and environmental factors in a free-ranging primate Subject Category : Subject Areas : R. Soc. Open Sci.

Dunbar, R., 1991. Functional Significance of Social Grooming in Primates. Folia Primatol. 57, 121–131. doi:10.1159/000156574

Dunbar, R.I.., Sharman, M., 1980. Is Social Grooming Altruistic? Ethology 64, 163–173.

Ekman, P., 1993. Facial Expression and Emotion. Am. Psychol. 43, 384–392.

Emery, N.J., Oram, M., Emery, N.J., Lorincz, E.N., Perrett, D.I., Oram, M.W., Baker, C.I., 1997. Gaze Following and Joint Attention in Rhesus Monkeys (Macaca mulatta) Gaze Following and Joint Attention in Rhesus Monkeys (Macaca mulatto). J. Comp. Psychol. 111, 286–293. doi:10.1037/0735-7036.111.3.286

Fedurek, P., Dunbar, R.I.M., Academy, B., 2009. What Does Mutual Grooming Tell Us About Why Chimpanzees. Ethology 115, 566–575. doi:10.1111/j.1439-0310.2009.01637.x

Feneran, A.N., O'Donnell, R., Press, A., Yosipovitch, G., Cline, M., Dugan, G., Papoiu, A.D.P., Nattkemper, L. a., Chan, Y.H., Shively, C. a., 2013. Monkey see, monkey do: Contagious itch in nonhuman primates. Acta Derm. Venereol. 93, 27–29. doi:10.2340/00015555-1406

Field, A., Miles, J., Field, Z., 2012. Discovering Statistics Using R. Sage Publications Ltd, London, UK.

Fooden, J., 1982. Ecogeographic segregation of macaque species. Primates 23, 574–579.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evoltion.

Fridlund, A.J., 1994. Human facial expression: An evolutionary view. Academic Press, San Diego, CA.

Gallup, A.C., Swartwood, L., Militello, J., Sackett, S., 2015. Experimental evidence of contagious yawning in budgerigars (Melopsittacus undulatus). Anim. Cogn. doi:10.1007/s10071-015-0873-1

Gazes, R.P., Emily, K.B., Basile, B.M., Hampton, R.R., 2013. Automated cognitive testing of monkeys in social groups yields results comparable to individual laboratory-based testing. Anim. Cogn. 16, 445–458. doi:10.1007/s10071-012-0585-8

Grueter, C.C., Bissonnette, A., Isler, K., Schaik, C.P. Van, 2013. Evolution and Human Behavior Grooming and group cohesion in primates : implications for the evolution of language. Evol. Hum. Behav. 34, 61–68. doi:10.1016/j.evolhumbehav.2012.09.004

Guilford, T., Dawkins, M.S., 1991. Receiver psychology and the evolution of animal signals. Anim. Behav. 42, 1–14. doi:10.1016/S0003-3472(05)80600-1

Gupta, S., Sinha, A., 2016. Not here, there! Possible referential gesturing during allogrooming by wild bonnet macaques, Macaca radiata. Anim. Cogn. 19, 1243–1248. doi:10.1007/s10071-016-1012-3

Gust, D.A., Gordon, T.P., Hambright, M.K., Wilson, M.., 1993. Relationship between Social Factors and Pituitary-Adrenocortical Activity in Female Rhesus Monkeys (Macaca mulatta). Horm. Behav. 27, 318–331.

Gustison, M.L., MacLarnon, A., Wiper, S., Semple, S., 2012. An experimental study of behavioural coping strategies in free-ranging female Barbary macaques (Macaca sylvanus). Stress 15, 608–17. doi:10.3109/10253890.2012.668589

Hanson, J.., Larson, M.., Snowdon, C.., 1976. The effects of control over high intensity noise on plasma cortisol levels in rhesus monkeysJohn D.HansonMark E.LarsonCharles T.Snowdon. Behav. Biol. 16, 333–340.

Heery, E.A., Kring, A.M., 2007. Interpersonal consequences of social anxiety. J. Abnorm. Psychol. 116, 125–134.

Hellhammer, D.H., Wu, S., Kudielka, B.M., 2009. Salivary cortisol as a biomarker in stress research. Psychoneuroendocrinology 34, 162–171. doi:10.1016/j.psyneuen.2008.10.026

Henkel, S., Lambides, A.R., Berger, A., Thomsen, R., 2015. Rhesus macaques (Macaca mulatta) recognize group membership via olfactory cues alone. Behav. Ecol. Sociobiol. 69, 2019–2034. doi:10.1007/s00265-015-2013-y

Hennessy, M.B., Foy, T., 1987. Nonedible material elicits chewing and reduces the plasma corticosterone response during novelty exposure in mice. Behav. Neurosci. 101, 237–245.

Higham, J.P., Heistermann, M., Maestripieri, D., 2011. The energetics of male-male endurance rivalry in free-ranging rhesus macaques, Macaca mulatta. Anim. Behav. 81, 1001–1007. doi:10.1016/j.anbehav.2011.02.001

Hobaiter, C., Byrne, R.W., 2014. The Meanings of Chimpanzee Gestures. Curr. Biol. 24, 1596–1600. doi:10.1016/j.cub.2014.05.066

Hopper, L.M., 2017. Cognitive research in zoos. Curr. Opin. Behav. Sci. 16, 100–110. doi:10.1016/j.cobeha.2017.04.006

Hoppitt, W., Laland, K.., 2013. Social Learning: An Introduction to Mechanisms, Methods, and Models. Princeton University Press.

ICUN, 2017. The IUCN Red List of Threatened Species. Version 2017-3. [WWW Document]. URL www.iucnredlist.org

Joly-Mascheroni, R.M., Senju, A., Shepherd, A.J., 2008. Dogs catch human yawns. Biol. Lett. 4, 446–8. doi:10.1098/rsbl.2008.0333

Judge, P.G., 2005. Conflict resolution, in: Maestripieri, D. (Ed.), Primate Psychology. Harvard University Press, Cambridge, pp. 41–48.

JWGR, 2009. Refinements in husbandry, care and common procedures for non-human primates: 9th report of the BVAAWF/FRAME/RSPCA/UFAW Joint Working Group on Refinement (M Jennings & MJ Prescott, eds). LAb Anmal 43 1–47.

Kappeler, P.M., Schaik, C.P. Van, Nunn, C.L., 2004. New and Comparative Perspectives Sexual selection and exaggerated sexual swellings of female primates, in: Sexual Selection in Primates. pp. 71–89.

Keverne, E.B., Martensz, N.D., Tuite, B., 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. Psychoneuroendocrinology 14, 155–161.

Koolhaas, J.., Bartolomucci, A., Buwalda, B., de Boer, S.., Flügge, G., Korte, S.M., Meerlo, P., Murison, R., Olivier, B., Palanza, P., Richter-Levin, G., Sgoifo, A., Steimer, T., Stiedl, O., van Dijk, G., Wöhr, M., Fuchs, E., 2011. Stress revisited: a critical evaluation of the stress concept. Neurosci. Biobehav. Rev. 35, 291–301.

Koolhaas, J.M., Bartolomucci, A., Buwalda, B., Boer, S.F. De, Flügge, G., Korte, S.M., Meerlo, P., Murison, R., Olivier, B., Palanza, P., Richter-levin, G., Sgoifo, A., Steimer, T., Stiedl, O., Dijk, G. Van, Wöhr, M., Fuchs, E., 2011. A critical evaluation of the stress concept. Neurosci. Biobehav. Rev. 35, 1291–1301. doi:10.1016/j.neubiorev.2011.02.003

Koolhaas, J.M., Korte, S.M., Boer, S.F. De, Vegt, B.J. Van Der, Reenen, C.G. Van, Hopster, H., De Jong, I.C., Ruis, M.A.., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 4.

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press.

Krebs, J.R., Davies, N.B., 1993. An Introduction to Behavioural Ecology. Blackwell Scientific Publications.

Krebs, J.R., Dawkins, R., 1978. Animal Signals: Mind-Reading and Manipulation, in: Krebs, J.R., Dawkins, R. (Eds.), Behavioural Ecology. An Evolutionary Approach. Blackwell Scientific Publications, Oxford, p. 381.

Kummer, H., 1968. Social Organization of Hamadryas Baboons. A Field Study. University of Chicago Press.

Laidre, M.E., Johnstone, R.A., 2013. Animal signals. Curr. Biol. 23, R829–833. doi:10.1016/j.cub.2013.07.070

Land, B.B., Seeley, T.D., 2004. The Grooming Invitation Dance of the Honey Bee. Ethology 10, 1–10.

Leavens, D.., Russell, J.L., Hopkins, W.D., 2007. Intentionality as Measured in the Persistence and Elaboration of Communication by Chimpanzees (Pan troglodytes). Child Dev. 76, 291–306.

Leavens, D.A., Aureli, F., Hopkins, W.D., Hyatt, C.W., 2001. Effects of cognitive challenge on self-directed behaviors by chimpanzees (Pan troglodytes). Am. J. Primatol. 55, 1–14.

Leavens, D.A., Hopkins, W.D., 1998. Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. Dev. Dev. Psychol. 34, 813–822.

Lehmann, H.E., 1979. Yawning. A homeostatic reflex and its psychological significance. Bull. Menninger Clin. 43, 123–6.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.., 2007. Group size, grooming and social cohesion in primates. Anim. Behav. 74, 1617–1629. doi:10.1016/j.anbehav.2006.10.025

Levin, S., Ursin, H., 1991. What is stress?, in: Brown, M.R., Koob, G.F., Rivier, C. (Eds.), Stress: Neurobiology and Neuroendocrinology. Marcel Dekker, Inc., New York, pp. 3–21.

Liebal, K., Call, J., 2012. The origins of non-human primates' manual gestures. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 367, 118–28. doi:10.1098/rstb.2011.0044

Liebal, K., Waller, B., Burrows, A.M., Slocombe, K.E., 2013. Primate Communication. A Multimodal Approach. Cambridge University Press, New York.

Maestripieri, D., 2010. Maternal Anxiety in Rhesus Macaques (Macaca mulatta). Ethology 95, 19–31.

Maestripieri, D., 2005. Gestural communication in three species of macaques (Macaca mulatta, M. nemestrina, M. arctoides). Gesture 5, 57–73.

Maestripieri, D., Schino, G., Aureli, F., Troisi, A., 1992. A modest proposal: displacement activities as an indicator of emotions in primates. Anim. Behav. 967–979.

Massen, J.J.M., Ritter, C., Bugnyar, T., 2015. Tolerance and reward equity predict cooperation in ravens (Corvus corax). Sci. Rep. 5, 15021. doi:10.1038/srep15021

McDonald, M., Johnson, S., 2014. “There”s an app for that’: a new program for the collection of behavioural field data. Anim. Behav. 95, 81–87. doi:10.1016/j.anbehav.2014.06.009

McEwen, B.S., 2007. Physiology and Neurobiology of Stress and Adaptation: Central Role of the Brain. Phyisological Rev. 87, 873–904.

McEwen, B.S., Sapolsky, R.M., 1995. Stress and cognitive function. Curr. Opin. Neurobiol. 5, 205–216. doi:10.1016/0959-4388(95)80028-X

Micheletta, J., Engelhardt, A., Matthews, L., Agil, M., Waller, B.M., 2013. Multicomponent and multimodal lipsmacking in crested macaques (Macaca nigra). Am. J. Primatol. 75, 763–73. doi:10.1002/ajp.22105

Micheletta, J., Waller, B.M., 2012. Friendship affects gaze following in a tolerant species of macaque, Macaca nigra. Anim. Behav. 83, 459–467. doi:10.1016/j.anbehav.2011.11.018

Micheletta, J., Waller, B.M., Panggur, M.R., Neumann, C., Duboscq, J., Agil, M., Engelhardt, A., 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaque, Macaca nigra. Proc. R. Soc. B Biol. Sci. 279, 4042–4050. doi:10.1098/rspb.2012.1470

Micheletta, J., Whitehouse, J., Parr, L. a, Waller, B.M., 2015. Facial expression recognition in crested macaques (Macaca nigra). Anim. Cogn. doi:10.1007/s10071-015-0867-z

Moberg, G.., 1999. When does stress become distress? Lab Anim. (NY). 28, 22–26.

Mohiyeddini, C., Bauer, S., Semple, S., 2015. Neuroticism and stress: the role of displacement behavior. Anxiety. Stress. Coping 28, 391–407. doi:10.1080/10615806.2014.1000878

Mohiyeddini, C., Bauer, S., Semple, S., 2013. Displacement behaviour is associated with reduced stress levels among men but not women. PLoS One 8, e56355. doi:10.1371/journal.pone.0056355

Mohiyeddini, C., Semple, S., 2013. Displacement behaviour regulates the experience of stress in men. Stress 16, 163–71. doi:10.3109/10253890.2012.707709

Morimoto, Y., Fujita, K., 2012. Capuchin monkeys (Cebus apella) use conspecifics' emotional expressions to evaluate emotional valence of objects. Anim. Cogn. 15, 341–7. doi:10.1007/s10071-011-0458-6

Morimoto, Y., Fujita, K., 2011. Capuchin monkeys (Cebus apella) modify their own behaviors according to a conspecific's emotional expressions. Primates. 52, 279–86. doi:10.1007/s10329-011-0249-3

Muroyama, Y., Thierry, B., 1998. Species Differences of Male Loud Calls and Their Perception in Sulawesi Macaques 39, 115–126.

Nakayama, K., 2004. Observing conspecifics scratching induces a contagion of scratching in Japanese monkeys (Macaca fuscata). J. Comp. Psychol. 118, 20–24. doi:10.1037/0735-7036.118.1.20

Neal, S.J., Caine, N.G., 2015. Scratching under positive and negative arousal in common marmosets (Callithrix jacchus). Am. J. Primatol. n/a–n/a. doi:10.1002/ajp.22498

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., 2011. Assessing dominance hierarchies : validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 1–11. doi:10.1016/j.anbehav.2011.07.016

Oller, D.K., Greibal, U., 2004. Evolution of communication systems: A comparative approach. Cambridge: The MIT Press.

Otte, D., 1974. Effects and functions in the evolution of signaling systems. Annu. Rev. Ecol. Syst. 5, 358–417.

Parr, L. a, Waller, B.M., 2006. Understanding chimpanzee facial expression: insights into the evolution of communication. Soc. Cogn. Affect. Neurosci. 1, 221–8. doi:10.1093/scan/nsl031

Parr, L.A., 2001. Cognitive and physiological markers of emotional awareness in chimpanzees (Pan troglodytes). Anim. Cogn. 4, 223–9. doi:10.1007/s100710100085

Parr, L.A., Heintz, M., 2009. Facial expression recognition in rhesus monkeys, Macaca mulatta. Anim. Behav. 77, 1507–1513. doi:10.1016/j.anbehav.2009.02.024.Facial

Paukner, A., Anderson, J.R., 2006. Video-induced yawning in stumptail macaques (Macaca arctoides). Biol. Lett. 2, 36–8. doi:10.1098/rsbl.2005.0411

Pavani, S., Maestripieri, D., Schino, G., Turillazzi, P.G., Schucci, S., 1991. Factors Influencing Scratching Behaviour in Long-Tailed Macaques (Macaca fascicularis). Am. J. Primatol. 57, 34–38.

Peignot, P., Jankowski, F., Anderson, J.R., 2004. On self-scratching in captive mandrills (Mandrillus sphinx). Folia Primatol. (Basel). 75, 160–4. doi:10.1159/000078307

Pelagi, E., Leone, A., Mancini, G., Ferrari, P.F., 2009. Contagious yawning in gelada baboons as a possible expression of empathy. Proc. Natl. Acad. Sci. U. S. A. 106, 19262–19267.

Pellis, S.M., Pellis, V.C., 1996. On knowing it's only play: The role of play signals in play fighting. Aggress. Violent Behav. 1, 249–268.

Pika, S., Mitani, J., 2006. Referential gestural communication in wild chimpanzees (Pan troglodytes). Curr. Biol. 16, R191–2. doi:10.1016/j.cub.2006.02.037

Preuschoft, S., van Schaik, C.P., 2000. Dominance and Communication, in: Natural Conflict Resolution. University of California Press, London, UK.

Romero, T., Castellanos, M.A., de Waal, F.B.M., 2010. Consolation as possible expression of sympathetic concern among chimpanzees. Proc. Natl. Acad. Sci. U. S. A. 107, 12110–5. doi:10.1073/pnas.1006991107

Root-bernstein, M., 2010. Displacement activities during the honeybee transition from waggle dance to foraging. Anim. Behav. 79, 935–938. doi:10.1016/j.anbehav.2010.01.010

Rowe, C., 1999. Receiver psychology and the evolution of multicomponent signals. Anim. Behav. 58, 921–931.

Ruby, S., Buchanan-Smith, H.M., 2015. The effects of individual cubicle research on the social interactions and individual behavior of brown capuchin monkeys (Sapajus apella). Am. J. Primatol. 1–12. doi:10.1002/ajp.22444

Russel, W., Burch, R., 1959. The principles of humane experimental technique. Universities Federation of Animal Welfare, Wheathampstead, UK.

Sapolsky, R.M., 1996. Stress, Glucocorticoids, and Damage to the Nervous System: The Current State of Confusion. Stress Int. J. Biol. Stress 1, 1–19.

Sato, N., Tan, L., Tate, K., Okada, M., 2015. Rats demonstrate helping behavior toward a soaked conspecific. Anim. Cogn. 18, 1039–47. doi:10.1007/s10071-015-0872-2

Schino, G., Maestripieri, D., Scucchi, S., Turillazzi, P.G., 1990. Social Tension in Familiar and Unfamiliar Pairs of Long-Tailed Macaques. Behaviour 113, 264–272. doi:10.1163/156853990X00518

Schino, G., Troisi, A., Perretta, G., Monaco, V., 1991. Measuring anxiety in nonhuman primates: effect of lorazepam on macaque scratching. Pharmacol. Biochem. Behav. 38, 889–891.

Scott-phillips, T.C., Blythe, R.A., Gardner, A., West, S.A., 2012. How do communication systems emerge? 1943–1949. doi:10.1098/rspb.2011.2181

Searcy, W.., 2005. The Evolution of Animal Communication: Reliability and Deception in Signaling Systems. Princeton University Press.

Semple, S., Harrison, C., Lehmann, J., 2013. Grooming and Anxiety in Barbary Macaques. Ethology 119, 779–785. doi:10.1111/eth.12119

Semple, S., Higham, J.P., 2013. Primate signals: current issues and perspectives. Am. J. Primatol. 75, 613–20. doi:10.1002/ajp.22139

Seyfarth, R.M., Cheney, D.L., 2011. The Evolutionary Origins of Friendship. Annu. Rev. Psychol. 63, 153–177.

Seyfarth, R.M., Cheney, D.L., Marler, P., 1980. Vervet Monkey Alarm Calls: Semantic Communication in a Free-Ranging Primate. Science (80-.). 210, 801–803. doi:10.1016/S0003-3472(80)80097-2

Silk, J., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195.

Silk, J.B., 2002. The Form and Function of Reconciliation in Primates. Annu. Rev. Anthropol. 31, 21–44. doi:10.1146/annurev.anthro.31.032902.101743

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. Behav. Ecol. Sociobiol. 61, 183–195. doi:10.1007/s00265-006-0249-2

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010. Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. Curr. Biol. 20, 1359–1361. doi:10.1016/j.cub.2010.05.067

Slocombe, K.E., Kaller, T., Turman, L., Townsend, S.W., Papworth, S., Squibbs, P., Zuberbühler, K., 2010. Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. Behav. Ecol. Sociobiol. 64, 1959–1966. doi:10.1007/s00265-010-1006-0

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R., Struhsaker, T.T., 1987. Primate Societies, 1st ed. University of Chicago Press, Chicago.

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R., Struhsaker, T.T., 1987. Primate Societies. University of Chicago Press.

Sosa, S., 2016. The Influence of Gender, Age, Matriline and Hierarchical Rank on Individual Social Position, Role and Interactional Patterns in Macaca sylvanus at “La Forêt des Singes”: A Multilevel Social Network Approach. Front. Psychol. 7, 529. doi:10.3389/fpsyg.2016.00529

Sueur, C., Petit, O., De Marco, a., Jacobs, a. T., Watanabe, K., Thierry, B., 2011. A comparative network analysis of social style in macaques. Anim. Behav. 82, 845–852. doi:10.1016/j.anbehav.2011.07.020

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection , multimodel inference and model averaging in behavioural ecology using Akaike ' s information criterion 13–21. doi:10.1007/s00265-010-1037-6

Team, R. core, 2014. R: A Language and Environment for Statistical Computing.

Thierry, B., 2007. Unity in Diversity : Lessons From Macaque Societies. Evol. Anthropol. 238, 224–238. doi:10.1002/evan.20147

Thierry, B., Aureli, F., 2006. Barbary but not barbarian: social relations in a tolerant macaque, in: Hodges, J.K., Cortes, J. (Eds.), The Barbary Macaque: Biology, Management and Conservation. Nottingham University PRess, Nottingham, pp. 29–45.

Thierry, B., Bynum, E.L., Baker, S., Kinnaird, M.F., Matsumura, S., Muroyama, Y., O'Brien, T.G., Petit, O., Watanabe, K., 2000. The Social Repertoire of Sulawesi Macaques. Primate Res. 16, 203–226. doi:10.2354/psj.16.203

Thierry, B., Singh, M., Kaumanns, W., 2004. Macaque Societies: A Model for the Study of Social Organization. Cambridge University Press.

Tinbergen, 1952. “Derived” Activities; Their Causation, Biological Significance, Origin, and Emancipation During Evolution. Q. Rev. Biol. 27, 1–32.

Tinbergen, N., 1963. On aims and methods of ethology. Z. Tierpsychol. 410–433.

Tinbergen, N., 1952. “Derived” Activities: Their Causation, Biological Significance, Origin, and Emancipation During Evolution. Q. Rev. Biol. 27, 1–32.

Tod, E., Brander, D., Waran, N., 2005. Efficacy of dog appeasing pheromone in reducing stress and fear related behaviour in shelter dogs. Appl. Anim. Behav. Sci. 93, 295–308. doi:10.1016/j.applanim.2005.01.007

Tomasello, M., 2010. Origins of Human Communication. MIT Press.

Tomasello, M., 2008. Origins of Human Communication. MIT Press, London, UK.

Townsend, S.W., Manser, M.B., 2013. Functionally Referential Communication in Mammals : The Past , Present and the Future 119, 1–11. doi:10.1111/eth.12015

Troisi, A., 2002. Displacement Activities as a Behavioral Measure of Stress in Nonhuman Primates and Human Subjects. Stress Int. J. Biol. Stress 5, 47–54.

Troisi, A., 1999. Ethological research in clinical psychiatry: the study of nonverbal behavior during interviews. Neurosci. Biobehav. Rev. 23, 905–913. doi:10.1016/S0149-7634(99)00024-X

Tsukahara, T., 1990. Initiation and Solicitation in Male-female Grooming in a Wild Japanese Macaque Troop on Yakushima Island The University of Tokyo. Primates 31, 147–148.

Ueno, M., Yamada, K., 2014. The effect of solicitations on grooming exchanges among female Japanese macaques at Katsuyama. Primates 55, 81–87. doi:10.1007/s10329-013-0371-5

Vail, A.L., Manica, A., Bshary, R., 2014. Fish choose appropriately when and with whom to collaborate. Curr. Biol. 24, R791–3. doi:10.1016/j.cub.2014.07.033

Van Zeeland, Y.R. a., Spruit, B.M., Rodenburg, T.B., Riedstra, B., van Hierden, Y.M., Buitenhuis, B., Korte, S.M., Lumeij, J.T., 2009. Feather damaging behaviour in parrots: A review with consideration of comparative aspects. Appl. Anim. Behav. Sci. 121, 75–95. doi:10.1016/j.applanim.2009.09.006

Virgin, C.E., Sapolsky, R.M., 1997. Styles of Male Social Behavior and Their Endocrine Correlates Among Low-Ranking Baboons 39, 25–39.

Waitt, C., Gerald, M.S., Little, A.C., Kraiselburd, E., 2006. Selective attention toward female secondary sexual color in male rhesus macaques. Am. J. Primatol. 68, 738–44. doi:10.1002/ajp.20264

Walker, R.H., King, A.J., Mcnutt, J.W., Jordan, N.R., Walker, R.H., 2017. Sneeze to leave: African wild dogs (Lycaon pictus) use variable quorum thresholds facilitated by sneezes in collective decisions. Proc. R. Soc. B Biol. Sci. 284.

Waller, B.M., 2013. Facial Expression in Nonhuman Animals. doi:10.1177/1754073912451503

Waller, B.M., Dunbar, R.I.M., 2005. Differential Behavioural Effects of Silent Bared Teeth Display and Relaxed Open Mouth Display in Chimpanzees (Pan troglodytes). Ethology 142, 129–142.

Waller, B.M., Micheletta, J., 2013. Facial Expression in Nonhuman Animals. Emot. Rev. 5, 54–59. doi:10.1177/1754073912451503

Waller, B.M., Misch, a, Whitehouse, J., Herrmann, E., 2014. Children, but not chimpanzees, have facial correlates of determination. Biol. Lett. 10, 20130974. doi:10.1098/rsbl.2013.0974

Waller, B.M., Warmelink, L., Liebal, K., Micheletta, J., Slocombe, K.E., 2013. Pseudoreplication: a widespread problem in primate communication research. Anim. Behav. 86, 483–488. doi:10.1016/j.anbehav.2013.05.038

Waller, B.M., Whitehouse, J., Micheletta, J., 2016a. Rethinking primate facial expression: A predictive framework. Neurosci. Biobehav. Rev. doi:10.1016/j.neubiorev.2016.09.005

Waller, B.M., Whitehouse, J., Micheletta, J., 2016b. Macaques can predict social outcomes from facial expressions. Anim. Cogn. doi:10.1007/s10071-016-0992-3

Ward, J., Burckhardt, V., Holle, H., 2013. Contagious scratching: shared feelings but not shared body locations. Front. Hum. Neurosci. 7, 122. doi:10.3389/fnhum.2013.00122

Watson, K.K., Ghodasra, J.H., Furlong, M. a, Platt, M.L., 2012. Visual preferences for sex and status in female rhesus macaques. Anim. Cogn. 15, 401–7. doi:10.1007/s10071-011-0467-5

Watson, S.K., Townsend, S.W., West, V., Slocombe, K.E., Watson, S.K., Townsend, S.W., Schel, A.M., Wilke, C., Wallace, E.K., Cheng, L., West, V., Slocombe, K.E., 2015. Report Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. Curr. Biol. 25, 495–499. doi:10.1016/j.cub.2014.12.032

Watson, S.L., Ward, J.P., Davis, K.B., Stavisky, R.C., 1999. Scent-Marking and Cortisol Response in the Small-Eared Bushbaby (Otolemur garnettii) 66, 695–699.

Whitehouse, J., Mi, J., Waller, B.M., 2017. Stress behaviours buffer macaques from aggression 1–9. doi:10.1038/s41598-017-10754-8

Whitehouse, J., Micheletta, J., Kaminski, J., Waller, B.M., 2016. Macaques attend to scratching in others. Anim. Behav. 122, 169–175. doi:10.1016/j.anbehav.2016.10.020

Whitehouse, J., Micheletta, J., Powell, L.E., Bordier, C., Waller, B.M., 2013. The impact of cognitive testing on the welfare of group housed primates. PLoS One 8.

Wilz, K.J., 1970. Self-regulation of Motivation in the Three-spined Stickleback (Gasterosteus aculeatus L.). Nature 226, 465–466.

Winters, S., Dubuc, C., Higham, J.P., 2015. Perspectives: The Looking Time Experimental Paradigm in Studies of Animal Visual Perception and Cognition. Ethology 121, 625–640. doi:10.1111/eth.12378

Young, C., Majolo, B., Heistermann, M., Schülke, O., Ostner, J., 2014. Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proc. Natl. Acad. Sci. U. S. A. 111, 18195–200. doi:10.1073/pnas.1411450111

Appendices

Appendix 1. List of focals and observation time for Chapters 3,4, and 5. All focal follows where approximately 30 minutes; if subject went out of sight after 20 minutes and could not be found, the focal data was kept. Therefore not all focal follows were exactly 30 minutes long.

Focal	Sex	Num Focals	Obv time (sec)	Out of sight (sec)	Total Obv time (sec)	Total Obv time (Min)
120	M	10	17075	640	16435	273.92
00V	F	10	16446	154	16292	271.53
0E3	M	10	18000	205	17795	296.58
0F0	F	10	16034	199	15835	263.92
0G1	M	10	16755	142	16613	276.88
0K0	F	10	17490	1384	16106	268.43
18I	M	10	18000	240	17760	296.00
19T	M	10	16812	301	16511	275.18
1B0	F	10	18000	325	17675	294.58
1F2	M	10	15830	177	15653	260.88
1G0	F	10	16789	221	16568	276.13
1G1	F	10	17516	0	17516	291.93
1K1	F	10	16131	74	16057	267.62
1K2	F	10	17789	300	17489	291.48
25R	M	10	16695	82	16613	276.88
2C9	M	7	12276	224	12052	200.87
2E4	F	10	16096	146	15950	265.83
2F8	M	10	16696	159	16537	275.62
2G2	F	10	17748	84	17664	294.40
2G3	F	10	16866	100	16766	279.43
2G4	F	10	17516	569	16947	282.45
33t	M	10	17537	350	17187	286.45
3b9	M	10	17527	381	17146	285.77
3D9	F	10	16526	537	15989	266.48
3H0	F	10	16883	74	16809	280.15
3k1	M	10	17076	32	17044	284.07
45Z	F	10	17594	232	17362	289.37
4C5	F	10	17629	210	17419	290.32
4C9	F	10	18000	118	17882	298.03

4E2	M	9	15288	65	15223	253.72
4J4	F	10	16922	47	16875	281.25
51A	M	10	18000	194	17806	296.77
53Z	F	10	17617	28	17589	293.15
5E6	M	10	18000	378	17622	293.70
5E8	F	10	17101	126	16975	282.92
5L7	F	10	17559	236	17323	288.72
73S	M	10	17035	12	17023	283.72
7A2	M	10	17146	119	17027	283.78
7F5	M	10	17791	74	17717	295.28
7k8	F	10	17800	2361	15439	257.32
85T	F	10	17625	48	17577	292.95
98K	M	10	17777	275	17502	291.70
9C1	F	10	17162	21	17141	285.68
9E3	M	10	17685	290	17395	289.92
9I9	M	10	17786	39	17747	295.78

Appendix 2. Elo-rating data group R, data used in Chapter 3,4,5. Elo-rating was calculated using all agonistic interactions. Data includes focal animals (Appendix 1) and non-focal animals. Absolute rank is calculated by ordering the highest to lowest Elo-rating, individuals with higher the Elo-ratings (and lower Absolute ranks) were considered to be more dominant individuals. If an individual has an Elo-rating of NA, the animal was never observed in an agonistic interaction, and therefore rank could not be estimated.

Focal	Final Elo-rating	Absolute rank	**Focal**	Final Elo-rating	Absolute rank
120	1391	1	**2K0**	991	51
51A	1340	2	**98J**	991	52
98K	1338	3	**2K6**	986	53
19T	1338	4	**51Z**	983	54
4E2	1314	5	**3I6**	970	55
2e4	1286	6	**1G6**	969	56
25R	1250	7	**2G2**	965	57
7L8	1243	8	**3B0**	961	58
81O	1231	9	**4G8**	954	59
1B1	1222	10	**52z**	950	60
33T	1213	11	**5J1**	949	61
2K4	1201	12	**04T**	943	62
1K1	1182	13	**93T**	939	63
61R	1161	14	**1G4**	934	64
3B9	1152	15	**1F2**	931	65
18I	1151	16	**404**	927	66
8A9	1149	17	**3H0**	922	67
7C4	1148	18	**15E**	916	68
7G1	1140	19	**2F8**	914	69
00v	1137	20	**78I**	912	70
3J7	1133	21	**2G4**	909	71
2K5	1129	22	**2I3**	890	72
8D8	1118	23	**0K0**	889	73
14E	1108	24	**7F5**	889	74
5B0	1099	25	**4J4**	888	75
5e6	1094	26	**5L7**	876	76
32Z	1089	27	**1I5**	871	77
0F0	1081	28	**4C5**	868	78
5K3	1076	29	**0G1**	858	79

47Z	1069	30	**bear**	857	80
0M1	1055	31	**4C9**	854	81
2K3	1051	32	**73S**	851	82
0M8	1050	33	**3K1**	846	83
2K1	1048	34	**0E3**	845	84
5N5	1046	35	**7K8**	842	85
37N	1043	36	**5L8**	840	86
77I	1037	37	**1G0**	837	87
5C6	1037	38	**2G3**	820	88
90T	1034	39	**1K2**	815	89
1G1	1030	40	**3D9**	813	90
SPOT	1028	41	**5E8**	811	91
4D4	1026	42	**9E3**	806	92
9C1	1025	43	**1B0**	805	93
53Z	1022	44	**85T**	802	94
4D3	1016	45	**45Z**	799	95
5K8	1014	46	**9P3**	794	96
0T9	1013	47	**2C9**	786	97
9e8	1001	48	**7A2**	720	98
1I6	1001	49	**9I9**	685	99
2F8	NA	NA	**3I5**	617	100

Appendix 3. Composite sociality index (CSI) data, group R, used in Chapter 3,4,5. Data includes only focal animals (Appendix 1). CSI data was calculated using grooming and proximity data. A higher CSI represents a more bonded dyad, a lower CSI represents a less bonded dyad.

Focal	Dyad	CSI	Focal	Dyad	CSI	Focal	Dyad	CSI	Focal	Dyad	CSI
_00V	_00V		**_1B0**	_7K8	2.40	**_2F8**	_5E8	0.00	**_45Z**	_4E2	3.01
_00V	_0E3	0.71	**_1B0**	_85T	3.01	**_2F8**	_5L7	2.18	**_45Z**	_4J4	1.54
_00V	_0F0	1.57	**_1B0**	_98K	3.09	**_2F8**	_73S	0.74	**_45Z**	_51A	2.26
_00V	_0G1	0.00	**_1B0**	_9C1	0.00	**_2F8**	_7A2	0.73	**_45Z**	_53Z	0.72
_00V	_0K0	2.99	**_1B0**	_9E3	0.00	**_2F8**	_7F5	0.00	**_45Z**	_5E6	8.40
_00V	_120	13.35	**_1B0**	_9I9	0.00	**_2F8**	_7K8	0.00	**_45Z**	_5E8	2.85
_00V	_18I	5.28	**_1F2**	_00V	0.82	**_2F8**	_85T	0.79	**_45Z**	_5L7	0.69
_00V	_19T	0.00	**_1F2**	_0E3	0.00	**_2F8**	_98K	0.00	**_45Z**	_73S	2.21
_00V	_1B0	0.00	**_1F2**	_0F0	0.79	**_2F8**	_9C1	0.79	**_45Z**	_7A2	0.00
_00V	_1F2	0.82	**_1F2**	_0G1	0.00	**_2F8**	_9E3	1.57	**_45Z**	_7F5	0.72
_00V	_1G0	3.72	**_1F2**	_0K0	0.00	**_2F8**	_9I9	0.00	**_45Z**	_7K8	0.00
_00V	_1G1	5.24	**_1F2**	_120	0.82	**_2G2**	_00V	3.63	**_45Z**	_85T	3.57
_00V	_1K1	1.52	**_1F2**	_18I	1.63	**_2G2**	_0E3	0.00	**_45Z**	_98K	3.58
_00V	_1K2	2.23	**_1F2**	_19T	10.18	**_2G2**	_0F0	3.80	**_45Z**	_9C1	4.39
_00V	_25R	3.83	**_1F2**	_1B0	0.82	**_2G2**	_0G1	0.00	**_45Z**	_9E3	0.00
_00V	_2C9	0.00	**_1F2**	_1F2		**_2G2**	_0K0	1.49	**_45Z**	_9I9	0.00
_00V	_2E4	0.64	**_1F2**	_1G0	0.00	**_2G2**	_120	2.25	**_4C5**	_00V	0.76
_00V	_2F8	1.52	**_1F2**	_1G1	0.00	**_2G2**	_18I	1.44	**_4C5**	_0E3	2.13
_00V	_2G2	3.63	**_1F2**	_1K1	0.00	**_2G2**	_19T	1.44	**_4C5**	_0F0	0.00
_00V	_2G3	1.39	**_1F2**	_1K2	0.00	**_2G2**	_1B0	5.96	**_4C5**	_0G1	0.00
_00V	_2G4	20.71	**_1F2**	_25R	1.60	**_2G2**	_1F2	1.44	**_4C5**	_0K0	1.44
_00V	_33T	1.46	**_1F2**	_2C9	0.82	**_2G2**	_1G0	5.18	**_4C5**	_120	2.87
_00V	_3B9	1.52	**_1F2**	_2E4	0.82	**_2G2**	_1G1	2.83	**_4C5**	_18I	2.17
_00V	_3D9	0.00	**_1F2**	_2F8	0.79	**_2G2**	_1K1	3.03	**_4C5**	_19T	0.00
_00V	_3H0	0.74	**_1F2**	_2G2	1.44	**_2G2**	_1K2	1.44	**_4C5**	_1B0	2.26
_00V	_3K1	0.00	**_1F2**	_2G3	0.82	**_2G2**	_25R	0.72	**_4C5**	_1F2	0.00
_00V	_45Z	3.71	**_1F2**	_2G4	1.46	**_2G2**	_2C9	0.00	**_4C5**	_1G0	2.18
_00V	_4C5	0.76	**_1F2**	_33T	3.91	**_2G2**	_2E4	3.28	**_4C5**	_1G1	0.69
_00V	_4C9	0.00	**_1F2**	_3B9	0.00	**_2G2**	_2F8	1.57	**_4C5**	_1K1	0.76
_00V	_4E2	0.85	**_1F2**	_3D9	1.62	**_2G2**	_2G2		**_4C5**	_1K2	2.87
_00V	_4J4	1.52	**_1F2**	_3H0	0.00	**_2G2**	_2G3	0.72	**_4C5**	_25R	11.27
_00V	_51A	0.76	**_1F2**	_3K1	0.00	**_2G2**	_2G4	6.52	**_4C5**	_2C9	0.00
_00V	_53Z	8.45	**_1F2**	_45Z	0.00	**_2G2**	_33T	0.00	**_4C5**	_2E4	5.36
_00V	_5E6	0.00	**_1F2**	_4C5	0.00	**_2G2**	_3B9	1.52	**_4C5**	_2F8	0.00
_00V	_5E8	2.97	**_1F2**	_4C9	0.00	**_2G2**	_3D9	0.72	**_4C5**	_2G2	2.16

_00V	_5L7	1.39	**_1F2**	_4E2	1.70	**_2G2**	_3H0	11.67	**_4C5**	_2G3	4.96
_00V	_73S	4.48	**_1F2**	_4J4	0.82	**_2G2**	_3K1	0.79	**_4C5**	_2G4	1.44
_00V	_7A2	0.00	**_1F2**	_51A	0.00	**_2G2**	_45Z	3.59	**_4C5**	_33T	2.90
_00V	_7F5	3.63	**_1F2**	_53Z	0.77	**_2G2**	_4C5	2.16	**_4C5**	_3B9	0.76
_00V	_7K8	3.83	**_1F2**	_5E6	1.63	**_2G2**	_4C9	0.69	**_4C5**	_3D9	0.00
_00V	_85T	2.08	**_1F2**	_5E8	1.39	**_2G2**	_4E2	2.55	**_4C5**	_3H0	1.44
_00V	_98K	11.76	**_1F2**	_5L7	0.82	**_2G2**	_4J4	3.70	**_4C5**	_3K1	0.72
_00V	_9C1	5.97	**_1F2**	_73S	4.54	**_2G2**	_51A	2.16	**_4C5**	_45Z	4.31
_00V	_9E3	0.00	**_1F2**	_7A2	0.73	**_2G2**	_53Z	3.65	**_4C5**	_4C5	
_00V	_9I9	0.00	**_1F2**	_7F5	0.82	**_2G2**	_5E6	3.89	**_4C5**	_4C9	1.44
_0E3	_00V	0.71	**_1F2**	_7K8	0.00	**_2G2**	_5E8	0.69	**_4C5**	_4E2	0.72
_0E3	_0E3		**_1F2**	_85T	0.69	**_2G2**	_5L7	2.11	**_4C5**	_4J4	2.26
_0E3	_0F0	0.00	**_1F2**	_98K	0.00	**_2G2**	_73S	2.95	**_4C5**	_51A	2.98
_0E3	_0G1	0.00	**_1F2**	_9C1	0.82	**_2G2**	_7A2	1.45	**_4C5**	_53Z	0.77
_0E3	_0K0	1.41	**_1F2**	_9E3	2.50	**_2G2**	_7F5	5.02	**_4C5**	_5E6	0.00
_0E3	_120	1.63	**_1F2**	_9I9	0.82	**_2G2**	_7K8	0.80	**_4C5**	_5E8	1.44
_0E3	_18I	0.73	**_1G0**	_00V	3.72	**_2G2**	_85T	0.72	**_4C5**	_5L7	2.85
_0E3	_19T	1.45	**_1G0**	_0E3	3.72	**_2G2**	_98K	4.97	**_4C5**	_73S	2.92
_0E3	_1B0	1.48	**_1G0**	_0F0	0.79	**_2G2**	_9C1	2.23	**_4C5**	_7A2	0.00
_0E3	_1F2	0.00	**_1G0**	_0G1	0.74	**_2G2**	_9E3	1.67	**_4C5**	_7F5	5.72
_0E3	_1G0	3.72	**_1G0**	_0K0	1.49	**_2G2**	_9I9	0.00	**_4C5**	_7K8	2.32
_0E3	_1G1	2.10	**_1G0**	_120	4.46	**_2G3**	_00V	1.39	**_4C5**	_85T	0.72
_0E3	_1K1	1.52	**_1G0**	_18I	0.00	**_2G3**	_0E3	0.00	**_4C5**	_98K	0.71
_0E3	_1K2	2.14	**_1G0**	_19T	0.00	**_2G3**	_0F0	0.00	**_4C5**	_9C1	2.18
_0E3	_25R	0.00	**_1G0**	_1B0	3.00	**_2G3**	_0G1	3.09	**_4C5**	_9E3	1.44
_0E3	_2C9	0.00	**_1G0**	_1F2	0.00	**_2G3**	_0K0	2.13	**_4C5**	_9I9	0.00
_0E3	_2E4	0.64	**_1G0**	_1G0		**_2G3**	_120	0.00	**_4C9**	_00V	0.00
_0E3	_2F8	4.40	**_1G0**	_1G1	0.74	**_2G3**	_18I	0.00	**_4C9**	_0E3	0.71
_0E3	_2G2	0.00	**_1G0**	_1K1	2.98	**_2G3**	_19T	0.74	**_4C9**	_0F0	0.79
_0E3	_2G3	0.00	**_1G0**	_1K2	5.13	**_2G3**	_1B0	1.39	**_4C9**	_0G1	5.02
_0E3	_2G4	1.44	**_1G0**	_25R	2.29	**_2G3**	_1F2	0.82	**_4C9**	_0K0	9.23
_0E3	_33T	0.71	**_1G0**	_2C9	0.00	**_2G3**	_1G0	11.56	**_4C9**	_120	2.33
_0E3	_3B9	1.52	**_1G0**	_2E4	0.00	**_2G3**	_1G1	2.08	**_4C9**	_18I	1.43
_0E3	_3D9	0.00	**_1G0**	_2F8	0.00	**_2G3**	_1K1	2.78	**_4C9**	_19T	0.74
_0E3	_3H0	1.45	**_1G0**	_2G2	5.18	**_2G3**	_1K2	1.39	**_4C9**	_1B0	3.01
_0E3	_3K1	0.79	**_1G0**	_2G3	11.56	**_2G3**	_25R	0.69	**_4C9**	_1F2	0.00
_0E3	_45Z	1.42	**_1G0**	_2G4	0.74	**_2G3**	_2C9	0.00	**_4C9**	_1G0	2.23
_0E3	_4C5	2.13	**_1G0**	_33T	2.98	**_2G3**	_2E4	0.69	**_4C9**	_1G1	0.00
_0E3	_4C9	0.71	**_1G0**	_3B9	2.25	**_2G3**	_2F8	1.48	**_4C9**	_1K1	0.00
_0E3	_4E2	1.56	**_1G0**	_3D9	3.95	**_2G3**	_2G2	0.72	**_4C9**	_1K2	0.00
_0E3	_4J4	4.63	**_1G0**	_3H0	5.21	**_2G3**	_2G3		**_4C9**	_25R	0.00
_0E3	_51A	5.07	**_1G0**	_3K1	0.00	**_2G3**	_2G4	0.00	**_4C9**	_2C9	1.39
_0E3	_53Z	1.48	**_1G0**	_45Z	0.00	**_2G3**	_33T	0.69	**_4C9**	_2E4	1.39
_0E3	_5E6	0.00	**_1G0**	_4C5	2.18	**_2G3**	_3B9	2.15	**_4C9**	_2F8	2.27
_0E3	_5E8	1.40	**_1G0**	_4C9	2.23	**_2G3**	_3D9	2.30	**_4C9**	_2G2	0.69

_0E3	_5L7	2.10	**_1G0**	_4E2	7.33	**_2G3**	_3H0	4.37	**_4C9**	_2G3	2.78
_0E3	_73S	5.06	**_1G0**	_4J4	2.23	**_2G3**	_3K1	0.00	**_4C9**	_2G4	0.73
_0E3	_7A2	2.87	**_1G0**	_51A	0.77	**_2G3**	_45Z	2.78	**_4C9**	_33T	2.81
_0E3	_7F5	0.71	**_1G0**	_53Z	1.49	**_2G3**	_4C5	4.96	**_4C9**	_3B9	1.39
_0E3	_7K8	0.00	**_1G0**	_5E6	3.12	**_2G3**	_4C9	2.78	**_4C9**	_3D9	3.90
_0E3	_85T	0.71	**_1G0**	_5E8	2.18	**_2G3**	_4E2	2.93	**_4C9**	_3H0	2.13
_0E3	_98K	0.00	**_1G0**	_5L7	4.37	**_2G3**	_4J4	5.63	**_4C9**	_3K1	1.57
_0E3	_9C1	0.00	**_1G0**	_73S	0.00	**_2G3**	_51A	0.77	**_4C9**	_45Z	10.51
_0E3	_9E3	0.00	**_1G0**	_7A2	0.00	**_2G3**	_53Z	2.08	**_4C9**	_4C5	1.44
_0E3	_9I9	0.00	**_1G0**	_7F5	6.66	**_2G3**	_5E6	0.00	**_4C9**	_4C9	
_0F0	_00V	1.57	**_1G0**	_7K8	0.00	**_2G3**	_5E8	0.00	**_4C9**	_4E2	1.70
_0F0	_0E3	0.00	**_1G0**	_85T	1.39	**_2G3**	_5L7	8.33	**_4C9**	_4J4	2.08
_0F0	_0F0		**_1G0**	_98K	0.00	**_2G3**	_73S	0.74	**_4C9**	_51A	2.85
_0F0	_0G1	2.49	**_1G0**	_9C1	0.00	**_2G3**	_7A2	0.00	**_4C9**	_53Z	3.09
_0F0	_0K0	3.14	**_1G0**	_9E3	0.00	**_2G3**	_7F5	0.00	**_4C9**	_5E6	2.78
_0F0	_120	1.63	**_1G0**	_9I9	0.00	**_2G3**	_7K8	1.60	**_4C9**	_5E8	0.69
_0F0	_18I	4.66	**_1G1**	_00V	5.24	**_2G3**	_85T	0.00	**_4C9**	_5L7	0.69
_0F0	_19T	0.00	**_1G1**	_0E3	2.10	**_2G3**	_98K	2.11	**_4C9**	_73S	0.69
_0F0	_1B0	1.57	**_1G1**	_0F0	1.39	**_2G3**	_9C1	0.00	**_4C9**	_7A2	0.73
_0F0	_1F2	0.79	**_1G1**	_0G1	0.00	**_2G3**	_9E3	0.00	**_4C9**	_7F5	4.19
_0F0	_1G0	0.79	**_1G1**	_0K0	10.12	**_2G3**	_9I9	0.00	**_4C9**	_7K8	1.50
_0F0	_1G1	1.39	**_1G1**	_120	18.06	**_2G4**	_00V	20.71	**_4C9**	_85T	0.69
_0F0	_1K1	13.08	**_1G1**	_18I	13.49	**_2G4**	_0E3	1.44	**_4C9**	_98K	1.39
_0F0	_1K2	0.79	**_1G1**	_19T	0.00	**_2G4**	_0F0	4.50	**_4C9**	_9C1	0.00
_0F0	_25R	1.60	**_1G1**	_1B0	1.39	**_2G4**	_0G1	0.73	**_4C9**	_9E3	0.00
_0F0	_2C9	0.00	**_1G1**	_1F2	0.00	**_2G4**	_0K0	0.00	**_4C9**	_9I9	0.00
_0F0	_2E4	7.72	**_1G1**	_1G0	0.74	**_2G4**	_120	8.56	**_4E2**	_00V	0.85
_0F0	_2F8	0.00	**_1G1**	_1G1		**_2G4**	_18I	9.50	**_4E2**	_0E3	1.56
_0F0	_2G2	3.80	**_1G1**	_1K1	0.00	**_2G4**	_19T	0.74	**_4E2**	_0F0	0.85
_0F0	_2G3	0.00	**_1G1**	_1K2	1.41	**_2G4**	_1B0	0.00	**_4E2**	_0G1	0.85
_0F0	_2G4	4.50	**_1G1**	_25R	2.99	**_2G4**	_1F2	1.46	**_4E2**	_0K0	0.00
_0F0	_33T	0.73	**_1G1**	_2C9	1.39	**_2G4**	_1G0	0.74	**_4E2**	_120	1.67
_0F0	_3B9	0.00	**_1G1**	_2E4	0.69	**_2G4**	_1G1	5.77	**_4E2**	_18I	0.00
_0F0	_3D9	0.00	**_1G1**	_2F8	0.00	**_2G4**	_1K1	0.00	**_4E2**	_19T	2.55
_0F0	_3H0	0.74	**_1G1**	_2G2	2.83	**_2G4**	_1K2	0.73	**_4E2**	_1B0	5.40
_0F0	_3K1	0.00	**_1G1**	_2G3	2.08	**_2G4**	_25R	3.06	**_4E2**	_1F2	1.70
_0F0	_45Z	3.80	**_1G1**	_2G4	5.77	**_2G4**	_2C9	0.00	**_4E2**	_1G0	7.33
_0F0	_4C5	0.00	**_1G1**	_33T	1.43	**_2G4**	_2E4	2.19	**_4E2**	_1G1	0.00
_0F0	_4C9	0.79	**_1G1**	_3B9	0.00	**_2G4**	_2F8	0.73	**_4E2**	_1K1	0.00
_0F0	_4E2	0.85	**_1G1**	_3D9	1.60	**_2G4**	_2G2	6.52	**_4E2**	_1K2	32.03
_0F0	_4J4	2.33	**_1G1**	_3H0	0.69	**_2G4**	_2G3	0.00	**_4E2**	_25R	2.50
_0F0	_51A	8.58	**_1G1**	_3K1	0.00	**_2G4**	_2G4		**_4E2**	_2C9	0.00
_0F0	_53Z	1.56	**_1G1**	_45Z	0.72	**_2G4**	_33T	3.65	**_4E2**	_2E4	0.85
_0F0	_5E6	0.00	**_1G1**	_4C5	0.69	**_2G4**	_3B9	0.73	**_4E2**	_2F8	0.00
_0F0	_5E8	3.05	**_1G1**	_4C9	0.00	**_2G4**	_3D9	0.00	**_4E2**	_2G2	2.55

_0F0	_5L7	0.00
_0F0	_73S	3.06
_0F0	_7A2	0.79
_0F0	_7F5	0.79
_0F0	_7K8	3.99
_0F0	_85T	0.00
_0F0	_98K	0.71
_0F0	_9C1	6.74
_0F0	_9E3	0.00
_0F0	_9I9	0.00
_0G1	_00V	0.00
_0G1	_0E3	0.00
_0G1	_0F0	2.49
_0G1	_0G1	
_0G1	_0K0	0.85
_0G1	_120	1.63
_0G1	_18I	0.00
_0G1	_19T	1.49
_0G1	_1B0	2.39
_0G1	_1F2	0.00
_0G1	_1G0	0.74
_0G1	_1G1	0.00
_0G1	_1K1	0.00
_0G1	_1K2	0.72
_0G1	_25R	0.00
_0G1	_2C9	3.98
_0G1	_2E4	0.00
_0G1	_2F8	0.00
_0G1	_2G2	0.00
_0G1	_2G3	3.09
_0G1	_2G4	0.73
_0G1	_33T	0.00
_0G1	_3B9	0.85
_0G1	_3D9	0.80
_0G1	_3H0	2.34
_0G1	_3K1	2.36
_0G1	_45Z	0.85
_0G1	_4C5	0.00
_0G1	_4C9	5.02
_0G1	_4E2	0.85
_0G1	_4J4	0.00
_0G1	_51A	0.77
_0G1	_53Z	0.00
_0G1	_5E6	1.70
_0G1	_5E8	0.00
_1G1	_4E2	0.00
_1G1	_4J4	0.00
_1G1	_51A	0.00
_1G1	_53Z	3.70
_1G1	_5E6	3.59
_1G1	_5E8	1.39
_1G1	_5L7	0.00
_1G1	_73S	1.39
_1G1	_7A2	1.46
_1G1	_7F5	2.78
_1G1	_7K8	0.00
_1G1	_85T	0.69
_1G1	_98K	1.39
_1G1	_9C1	2.78
_1G1	_9E3	0.00
_1G1	_9I9	0.00
_1K1	_00V	1.52
_1K1	_0E3	1.52
_1K1	_0F0	13.08
_1K1	_0G1	0.00
_1K1	_0K0	3.75
_1K1	_120	1.57
_1K1	_18I	0.76
_1K1	_19T	1.52
_1K1	_1B0	1.52
_1K1	_1F2	0.00
_1K1	_1G0	2.98
_1K1	_1G1	0.00
_1K1	_1K1	
_1K1	_1K2	0.00
_1K1	_25R	1.60
_1K1	_2C9	0.00
_1K1	_2E4	4.60
_1K1	_2F8	2.27
_1K1	_2G2	3.03
_1K1	_2G3	2.78
_1K1	_2G4	0.00
_1K1	_33T	3.00
_1K1	_3B9	0.76
_1K1	_3D9	0.00
_1K1	_3H0	2.23
_1K1	_3K1	0.00
_1K1	_45Z	1.44
_1K1	_4C5	0.76
_1K1	_4C9	0.00
_2G4	_3H0	0.74
_2G4	_3K1	0.00
_2G4	_45Z	0.72
_2G4	_4C5	1.44
_2G4	_4C9	0.73
_2G4	_4E2	0.73
_2G4	_4J4	0.73
_2G4	_51A	2.19
_2G4	_53Z	10.60
_2G4	_5E6	0.00
_2G4	_5E8	0.69
_2G4	_5L7	0.00
_2G4	_73S	0.74
_2G4	_7A2	0.00
_2G4	_7F5	3.63
_2G4	_7K8	2.26
_2G4	_85T	0.69
_2G4	_98K	3.63
_2G4	_9C1	12.61
_2G4	_9E3	0.00
_2G4	_9I9	0.00
_33T	_00V	1.46
_33T	_0E3	0.71
_33T	_0F0	0.73
_33T	_0G1	0.00
_33T	_0K0	1.49
_33T	_120	1.63
_33T	_18I	0.00
_33T	_19T	1.48
_33T	_1B0	0.00
_33T	_1F2	3.91
_33T	_1G0	2.98
_33T	_1G1	1.43
_33T	_1K1	3.00
_33T	_1K2	2.16
_33T	_25R	5.12
_33T	_2C9	0.00
_33T	_2E4	1.46
_33T	_2F8	0.79
_33T	_2G2	0.00
_33T	_2G3	0.69
_33T	_2G4	3.65
_33T	_33T	
_33T	_3B9	1.49
_33T	_3D9	4.67
_4E2	_2G3	2.93
_4E2	_2G4	0.73
_4E2	_33T	0.73
_4E2	_3B9	1.61
_4E2	_3D9	12.31
_4E2	_3H0	11.05
_4E2	_3K1	0.00
_4E2	_45Z	3.01
_4E2	_4C5	0.72
_4E2	_4C9	1.70
_4E2	_4E2	
_4E2	_4J4	2.55
_4E2	_51A	0.00
_4E2	_53Z	0.00
_4E2	_5E6	0.00
_4E2	_5E8	0.00
_4E2	_5L7	4.86
_4E2	_73S	1.49
_4E2	_7A2	0.00
_4E2	_7F5	0.71
_4E2	_7K8	0.00
_4E2	_85T	0.00
_4E2	_98K	6.08
_4E2	_9C1	2.44
_4E2	_9E3	0.00
_4E2	_9I9	0.00
_4J4	_00V	1.52
_4J4	_0E3	4.63
_4J4	_0F0	2.33
_4J4	_0G1	0.00
_4J4	_0K0	0.77
_4J4	_120	0.00
_4J4	_18I	0.77
_4J4	_19T	0.00
_4J4	_1B0	1.54
_4J4	_1F2	0.82
_4J4	_1G0	2.23
_4J4	_1G1	0.00
_4J4	_1K1	0.77
_4J4	_1K2	0.00
_4J4	_25R	1.54
_4J4	_2C9	0.00
_4J4	_2E4	1.54
_4J4	_2F8	0.79
_4J4	_2G2	3.70

_0G1	_5L7	6.87	**_1K1**	_4E2	0.00	**_33T**	_3H0	0.74	**_4J4**	_2G3	5.63
_0G1	_73S	2.55	**_1K1**	_4J4	0.77	**_33T**	_3K1	0.00	**_4J4**	_2G4	0.73
_0G1	_7A2	0.00	**_1K1**	_51A	9.88	**_33T**	_45Z	1.44	**_4J4**	_33T	0.00
_0G1	_7F5	1.41	**_1K1**	_53Z	6.17	**_33T**	_4C5	2.90	**_4J4**	_3B9	0.76
_0G1	_7K8	0.00	**_1K1**	_5E6	0.00	**_33T**	_4C9	2.81	**_4J4**	_3D9	0.80
_0G1	_85T	0.00	**_1K1**	_5E8	3.03	**_33T**	_4E2	0.73	**_4J4**	_3H0	4.63
_0G1	_98K	1.70	**_1K1**	_5L7	0.69	**_33T**	_4J4	0.00	**_4J4**	_3K1	0.77
_0G1	_9C1	0.74	**_1K1**	_73S	1.52	**_33T**	_51A	0.00	**_4J4**	_45Z	1.54
_0G1	_9E3	0.00	**_1K1**	_7A2	0.00	**_33T**	_53Z	1.50	**_4J4**	_4C5	2.26
_0G1	_9I9	0.00	**_1K1**	_7F5	0.00	**_33T**	_5E6	1.55	**_4J4**	_4C9	2.08
_0K0	_00V	2.99	**_1K1**	_7K8	1.56	**_33T**	_5E8	17.03	**_4J4**	_4E2	2.55
_0K0	_0E3	1.41	**_1K1**	_85T	1.45	**_33T**	_5L7	2.78	**_4J4**	_4J4	
_0K0	_0F0	3.14	**_1K1**	_98K	1.46	**_33T**	_73S	3.72	**_4J4**	_51A	1.54
_0K0	_0G1	0.85	**_1K1**	_9C1	3.77	**_33T**	_7A2	0.73	**_4J4**	_53Z	2.31
_0K0	_0K0		**_1K1**	_9E3	0.00	**_33T**	_7F5	3.65	**_4J4**	_5E6	0.82
_0K0	_120	1.56	**_1K1**	_9I9	0.00	**_33T**	_7K8	0.00	**_4J4**	_5E8	0.00
_0K0	_18I	0.73	**_1K2**	_00V	2.23	**_33T**	_85T	5.08	**_4J4**	_5L7	2.08
_0K0	_19T	0.00	**_1K2**	_0E3	2.14	**_33T**	_98K	1.46	**_4J4**	_73S	1.52
_0K0	_1B0	0.00	**_1K2**	_0F0	0.79	**_33T**	_9C1	0.00	**_4J4**	_7A2	1.50
_0K0	_1F2	0.00	**_1K2**	_0G1	0.72	**_33T**	_9E3	0.00	**_4J4**	_7F5	2.31
_0K0	_1G0	1.49	**_1K2**	_0K0	0.00	**_33T**	_9I9	0.00	**_4J4**	_7K8	1.57
_0K0	_1G1	10.12	**_1K2**	_120	3.27	**_3B9**	_00V	1.52	**_4J4**	_85T	0.77
_0K0	_1K1	3.75	**_1K2**	_18I	2.89	**_3B9**	_0E3	1.52	**_4J4**	_98K	2.89
_0K0	_1K2	0.00	**_1K2**	_19T	0.74	**_3B9**	_0F0	0.00	**_4J4**	_9C1	0.74
_0K0	_25R	0.00	**_1K2**	_1B0	4.36	**_3B9**	_0G1	0.85	**_4J4**	_9E3	0.77
_0K0	_2C9	1.04	**_1K2**	_1F2	0.00	**_3B9**	_0K0	1.52	**_4J4**	_9I9	0.00
_0K0	_2E4	0.64	**_1K2**	_1G0	5.13	**_3B9**	_120	0.00	**_51A**	_00V	0.76
_0K0	_2F8	0.00	**_1K2**	_1G1	1.41	**_3B9**	_18I	0.00	**_51A**	_0E3	5.07
_0K0	_2G2	1.49	**_1K2**	_1K1	0.00	**_3B9**	_19T	0.76	**_51A**	_0F0	8.58
_0K0	_2G3	2.13	**_1K2**	_1K2		**_3B9**	_1B0	0.00	**_51A**	_0G1	0.77
_0K0	_2G4	0.00	**_1K2**	_25R	0.00	**_3B9**	_1F2	0.00	**_51A**	_0K0	2.29
_0K0	_33T	1.49	**_1K2**	_2C9	0.00	**_3B9**	_1G0	2.25	**_51A**	_120	0.00
_0K0	_3B9	1.52	**_1K2**	_2E4	0.00	**_3B9**	_1G1	0.00	**_51A**	_18I	0.00
_0K0	_3D9	0.00	**_1K2**	_2F8	1.57	**_3B9**	_1K1	0.76	**_51A**	_19T	0.00
_0K0	_3H0	1.49	**_1K2**	_2G2	1.44	**_3B9**	_1K2	1.44	**_51A**	_1B0	0.00
_0K0	_3K1	0.79	**_1K2**	_2G3	1.39	**_3B9**	_25R	0.00	**_51A**	_1F2	0.00
_0K0	_45Z	2.21	**_1K2**	_2G4	0.73	**_3B9**	_2C9	0.76	**_51A**	_1G0	0.77
_0K0	_4C5	1.44	**_1K2**	_33T	2.16	**_3B9**	_2E4	0.00	**_51A**	_1G1	0.00
_0K0	_4C9	9.23	**_1K2**	_3B9	1.44	**_3B9**	_2F8	0.76	**_51A**	_1K1	9.88
_0K0	_4E2	0.00	**_1K2**	_3D9	7.76	**_3B9**	_2G2	1.52	**_51A**	_1K2	0.72
_0K0	_4J4	0.77	**_1K2**	_3H0	13.91	**_3B9**	_2G3	2.15	**_51A**	_25R	0.80
_0K0	_51A	2.29	**_1K2**	_3K1	0.00	**_3B9**	_2G4	0.73	**_51A**	_2C9	0.00
_0K0	_53Z	1.52	**_1K2**	_45Z	1.44	**_3B9**	_33T	1.49	**_51A**	_2E4	5.52
_0K0	_5E6	0.00	**_1K2**	_4C5	2.87	**_3B9**	_3B9		**_51A**	_2F8	0.00
_0K0	_5E8	2.18	**_1K2**	_4C9	0.00	**_3B9**	_3D9	0.00	**_51A**	_2G2	2.16

_0K0	_5L7	0.69	**_1K2**	_4E2	32.03	**_3B9**	_3H0	0.74	**_51A**	_2G3	0.77
_0K0	_73S	1.49	**_1K2**	_4J4	0.00	**_3B9**	_3K1	0.00	**_51A**	_2G4	2.19
_0K0	_7A2	0.00	**_1K2**	_51A	0.72	**_3B9**	_45Z	2.27	**_51A**	_33T	0.00
_0K0	_7F5	4.46	**_1K2**	_53Z	0.77	**_3B9**	_4C5	0.76	**_51A**	_3B9	3.07
_0K0	_7K8	0.00	**_1K2**	_5E6	2.35	**_3B9**	_4C9	1.39	**_51A**	_3D9	2.31
_0K0	_85T	3.62	**_1K2**	_5E8	0.72	**_3B9**	_4E2	1.61	**_51A**	_3H0	0.77
_0K0	_98K	1.41	**_1K2**	_5L7	3.50	**_3B9**	_4J4	0.76	**_51A**	_3K1	0.00
_0K0	_9C1	1.49	**_1K2**	_73S	1.46	**_3B9**	_51A	3.07	**_51A**	_45Z	2.26
_0K0	_9E3	0.00	**_1K2**	_7A2	0.72	**_3B9**	_53Z	2.27	**_51A**	_4C5	2.98
_0K0	_9I9	0.00	**_1K2**	_7F5	2.86	**_3B9**	_5E6	0.00	**_51A**	_4C9	2.85
_120	_00V	13.35	**_1K2**	_7K8	1.52	**_3B9**	_5E8	0.76	**_51A**	_4E2	0.00
_120	_0E3	1.63	**_1K2**	_85T	0.72	**_3B9**	_5L7	0.00	**_51A**	_4J4	1.54
_120	_0F0	1.63	**_1K2**	_98K	3.54	**_3B9**	_73S	3.75	**_51A**	_51A	
_120	_0G1	1.63	**_1K2**	_9C1	0.74	**_3B9**	_7A2	2.25	**_51A**	_53Z	2.31
_120	_0K0	1.56	**_1K2**	_9E3	0.00	**_3B9**	_7F5	0.71	**_51A**	_5E6	3.22
_120	_120		**_1K2**	_9I9	2.84	**_3B9**	_7K8	0.00	**_51A**	_5E8	2.08
_120	_18I	8.64	**_25R**	_00V	3.83	**_3B9**	_85T	1.39	**_51A**	_5L7	0.00
_120	_19T	0.82	**_25R**	_0E3	0.00	**_3B9**	_98K	2.22	**_51A**	_73S	3.86
_120	_1B0	3.27	**_25R**	_0F0	1.60	**_3B9**	_9C1	0.00	**_51A**	_7A2	0.00
_120	_1F2	0.82	**_25R**	_0G1	0.00	**_3B9**	_9E3	0.83	**_51A**	_7F5	2.12
_120	_1G0	4.46	**_25R**	_0K0	0.00	**_3B9**	_9I9	0.00	**_51A**	_7K8	1.60
_120	_1G1	18.06	**_25R**	_120	2.42	**_3D9**	_00V	0.00	**_51A**	_85T	2.24
_120	_1K1	1.57	**_25R**	_18I	4.74	**_3D9**	_0E3	0.00	**_51A**	_98K	1.48
_120	_1K2	3.27	**_25R**	_19T	0.00	**_3D9**	_0F0	0.00	**_51A**	_9C1	10.61
_120	_25R	2.42	**_25R**	_1B0	0.00	**_3D9**	_0G1	0.80	**_51A**	_9E3	0.00
_120	_2C9	0.00	**_25R**	_1F2	1.60	**_3D9**	_0K0	0.00	**_51A**	_9I9	0.00
_120	_2E4	0.00	**_25R**	_1G0	2.29	**_3D9**	_120	1.60	**_53Z**	_00V	8.45
_120	_2F8	0.00	**_25R**	_1G1	2.99	**_3D9**	_18I	0.80	**_53Z**	_0E3	1.48
_120	_2G2	2.25	**_25R**	_1K1	1.60	**_3D9**	_19T	0.00	**_53Z**	_0F0	1.56
_120	_2G3	0.00	**_25R**	_1K2	0.00	**_3D9**	_1B0	1.60	**_53Z**	_0G1	0.00
_120	_2G4	8.56	**_25R**	_25R		**_3D9**	_1F2	1.62	**_53Z**	_0K0	1.52
_120	_33T	1.63	**_25R**	_2C9	0.00	**_3D9**	_1G0	3.95	**_53Z**	_120	5.58
_120	_3B9	0.00	**_25R**	_2E4	0.00	**_3D9**	_1G1	1.60	**_53Z**	_18I	2.27
_120	_3D9	1.60	**_25R**	_2F8	0.00	**_3D9**	_1K1	0.00	**_53Z**	_19T	0.00
_120	_3H0	1.56	**_25R**	_2G2	0.72	**_3D9**	_1K2	7.76	**_53Z**	_1B0	1.54
_120	_3K1	0.00	**_25R**	_2G3	0.69	**_3D9**	_25R	4.81	**_53Z**	_1F2	0.77
_120	_45Z	0.00	**_25R**	_2G4	3.06	**_3D9**	_2C9	0.00	**_53Z**	_1G0	1.49
_120	_4C5	2.87	**_25R**	_33T	5.12	**_3D9**	_2E4	0.00	**_53Z**	_1G1	3.70
_120	_4C9	2.33	**_25R**	_3B9	0.00	**_3D9**	_2F8	4.81	**_53Z**	_1K1	6.17
_120	_4E2	1.67	**_25R**	_3D9	4.81	**_3D9**	_2G2	0.72	**_53Z**	_1K2	0.77
_120	_4J4	0.00	**_25R**	_3H0	0.00	**_3D9**	_2G3	2.30	**_53Z**	_25R	0.00
_120	_51A	0.00	**_25R**	_3K1	0.00	**_3D9**	_2G4	0.00	**_53Z**	_2C9	0.00
_120	_53Z	5.58	**_25R**	_45Z	0.00	**_3D9**	_33T	4.67	**_53Z**	_2E4	3.09
_120	_5E6	0.82	**_25R**	_4C5	11.27	**_3D9**	_3B9	0.00	**_53Z**	_2F8	0.00
_120	_5E8	4.08	**_25R**	_4C9	0.00	**_3D9**	_3D9		**_53Z**	_2G2	3.65

_120	_5L7	2.08	**_25R**	_4E2	2.50	**_3D9**	_3H0	1.60	**_53Z**	_2G3	2.08
_120	_73S	0.00	**_25R**	_4J4	1.54	**_3D9**	_3K1	0.80	**_53Z**	_2G4	10.60
_120	_7A2	0.00	**_25R**	_51A	0.80	**_3D9**	_45Z	3.59	**_53Z**	_33T	1.50
_120	_7F5	0.00	**_25R**	_53Z	0.00	**_3D9**	_4C5	0.00	**_53Z**	_3B9	2.27
_120	_7K8	0.80	**_25R**	_5E6	0.00	**_3D9**	_4C9	3.90	**_53Z**	_3D9	0.00
_120	_85T	0.69	**_25R**	_5E8	0.00	**_3D9**	_4E2	12.31	**_53Z**	_3H0	0.74
_120	_98K	4.68	**_25R**	_5L7	1.60	**_3D9**	_4J4	0.80	**_53Z**	_3K1	0.00
_120	_9C1	2.23	**_25R**	_73S	2.35	**_3D9**	_51A	2.31	**_53Z**	_45Z	0.72
_120	_9E3	0.83	**_25R**	_7A2	0.80	**_3D9**	_53Z	0.00	**_53Z**	_4C5	0.77
_120	_9I9	0.00	**_25R**	_7F5	0.80	**_3D9**	_5E6	0.00	**_53Z**	_4C9	3.09
_18I	_00V	5.28	**_25R**	_7K8	0.80	**_3D9**	_5E8	0.00	**_53Z**	_4E2	0.00
_18I	_0E3	0.73	**_25R**	_85T	0.00	**_3D9**	_5L7	0.00	**_53Z**	_4J4	2.31
_18I	_0F0	4.66	**_25R**	_98K	4.33	**_3D9**	_73S	0.80	**_53Z**	_51A	2.31
_18I	_0G1	0.00	**_25R**	_9C1	3.09	**_3D9**	_7A2	2.33	**_53Z**	_53Z	
_18I	_0K0	0.73	**_25R**	_9E3	0.00	**_3D9**	_7F5	3.01	**_53Z**	_5E6	0.77
_18I	_120	8.64	**_25R**	_9I9	0.00	**_3D9**	_7K8	1.60	**_53Z**	_5E8	2.93
_18I	_18I		**_2C9**	_00V	0.00	**_3D9**	_85T	2.30	**_53Z**	_5L7	2.08
_18I	_19T	0.00	**_2C9**	_0E3	0.00	**_3D9**	_98K	2.31	**_53Z**	_73S	0.00
_18I	_1B0	0.73	**_2C9**	_0F0	0.00	**_3D9**	_9C1	0.74	**_53Z**	_7A2	0.00
_18I	_1F2	1.63	**_2C9**	_0G1	3.98	**_3D9**	_9E3	0.00	**_53Z**	_7F5	2.18
_18I	_1G0	0.00	**_2C9**	_0K0	1.04	**_3D9**	_9I9	0.00	**_53Z**	_7K8	1.54
_18I	_1G1	13.49	**_2C9**	_120	0.00	**_3H0**	_00V	0.74	**_53Z**	_85T	0.00
_18I	_1K1	0.76	**_2C9**	_18I	0.00	**_3H0**	_0E3	1.45	**_53Z**	_98K	5.91
_18I	_1K2	2.89	**_2C9**	_19T	2.53	**_3H0**	_0F0	0.74	**_53Z**	_9C1	0.77
_18I	_25R	4.74	**_2C9**	_1B0	1.54	**_3H0**	_0G1	2.34	**_53Z**	_9E3	0.00
_18I	_2C9	0.00	**_2C9**	_1F2	0.82	**_3H0**	_0K0	1.49	**_53Z**	_9I9	0.00
_18I	_2E4	1.46	**_2C9**	_1G0	0.00	**_3H0**	_120	1.56	**_5E6**	_00V	0.00
_18I	_2F8	0.79	**_2C9**	_1G1	1.39	**_3H0**	_18I	0.00	**_5E6**	_0E3	0.00
_18I	_2G2	1.44	**_2C9**	_1K1	0.00	**_3H0**	_19T	0.74	**_5E6**	_0F0	0.00
_18I	_2G3	0.00	**_2C9**	_1K2	0.00	**_3H0**	_1B0	29.76	**_5E6**	_0G1	1.70
_18I	_2G4	9.50	**_2C9**	_25R	0.00	**_3H0**	_1F2	0.00	**_5E6**	_0K0	0.00
_18I	_33T	0.00	**_2C9**	_2C9		**_3H0**	_1G0	5.21	**_5E6**	_120	0.82
_18I	_3B9	0.00	**_2C9**	_2E4	0.00	**_3H0**	_1G1	0.69	**_5E6**	_18I	3.01
_18I	_3D9	0.80	**_2C9**	_2F8	0.00	**_3H0**	_1K1	2.23	**_5E6**	_19T	0.00
_18I	_3H0	0.00	**_2C9**	_2G2	0.00	**_3H0**	_1K2	13.91	**_5E6**	_1B0	0.77
_18I	_3K1	0.00	**_2C9**	_2G3	0.00	**_3H0**	_25R	0.00	**_5E6**	_1F2	1.63
_18I	_45Z	5.08	**_2C9**	_2G4	0.00	**_3H0**	_2C9	0.00	**_5E6**	_1G0	3.12
_18I	_4C5	2.17	**_2C9**	_33T	0.00	**_3H0**	_2E4	0.74	**_5E6**	_1G1	3.59
_18I	_4C9	1.43	**_2C9**	_3B9	0.76	**_3H0**	_2F8	0.79	**_5E6**	_1K1	0.00
_18I	_4E2	0.00	**_2C9**	_3D9	0.00	**_3H0**	_2G2	11.67	**_5E6**	_1K2	2.35
_18I	_4J4	0.77	**_2C9**	_3H0	0.00	**_3H0**	_2G3	4.37	**_5E6**	_25R	0.00
_18I	_51A	0.00	**_2C9**	_3K1	1.57	**_3H0**	_2G4	0.74	**_5E6**	_2C9	0.00
_18I	_53Z	2.27	**_2C9**	_45Z	1.76	**_3H0**	_33T	0.74	**_5E6**	_2E4	0.00
_18I	_5E6	3.01	**_2C9**	_4C5	0.00	**_3H0**	_3B9	0.74	**_5E6**	_2F8	0.00
_18I	_5E8	1.46	**_2C9**	_4C9	1.39	**_3H0**	_3D9	1.60	**_5E6**	_2G2	3.89

_18I	_5L7	2.85	**_2C9**	_4E2	0.00	**_3H0**	_3H0		**_5E6**	_2G3	0.00
_18I	_73S	0.73	**_2C9**	_4J4	0.00	**_3H0**	_3K1	0.79	**_5E6**	_2G4	0.00
_18I	_7A2	0.00	**_2C9**	_51A	0.00	**_3H0**	_45Z	1.44	**_5E6**	_33T	1.55
_18I	_7F5	2.19	**_2C9**	_53Z	0.00	**_3H0**	_4C5	1.44	**_5E6**	_3B9	0.00
_18I	_7K8	0.73	**_2C9**	_5E6	0.00	**_3H0**	_4C9	2.13	**_5E6**	_3D9	0.00
_18I	_85T	7.27	**_2C9**	_5E8	0.00	**_3H0**	_4E2	11.05	**_5E6**	_3H0	0.74
_18I	_98K	7.82	**_2C9**	_5L7	0.00	**_3H0**	_4J4	4.63	**_5E6**	_3K1	0.82
_18I	_9C1	0.00	**_2C9**	_73S	0.00	**_3H0**	_51A	0.77	**_5E6**	_45Z	8.40
_18I	_9E3	2.30	**_2C9**	_7A2	0.00	**_3H0**	_53Z	0.74	**_5E6**	_4C5	0.00
_18I	_9I9	0.00	**_2C9**	_7F5	0.00	**_3H0**	_5E6	0.74	**_5E6**	_4C9	2.78
_19T	_00V	0.00	**_2C9**	_7K8	0.00	**_3H0**	_5E8	0.74	**_5E6**	_4E2	0.00
_19T	_0E3	1.45	**_2C9**	_85T	1.74	**_3H0**	_5L7	5.65	**_5E6**	_4J4	0.82
_19T	_0F0	0.00	**_2C9**	_98K	1.75	**_3H0**	_73S	1.49	**_5E6**	_51A	3.22
_19T	_0G1	1.49	**_2C9**	_9C1	0.00	**_3H0**	_7A2	0.00	**_5E6**	_53Z	0.77
_19T	_0K0	0.00	**_2C9**	_9E3	10.83	**_3H0**	_7F5	0.74	**_5E6**	_5E6	
_19T	_120	0.82	**_2C9**	_9I9	7.03	**_3H0**	_7K8	1.49	**_5E6**	_5E8	0.69
_19T	_18I	0.00	**_2E4**	_00V	0.64	**_3H0**	_85T	0.00	**_5E6**	_5L7	2.45
_19T	_19T		**_2E4**	_0E3	0.64	**_3H0**	_98K	0.00	**_5E6**	_73S	0.00
_19T	_1B0	1.49	**_2E4**	_0F0	7.72	**_3H0**	_9C1	0.00	**_5E6**	_7A2	0.82
_19T	_1F2	10.18	**_2E4**	_0G1	0.00	**_3H0**	_9E3	0.00	**_5E6**	_7F5	2.45
_19T	_1G0	0.00	**_2E4**	_0K0	0.64	**_3H0**	_9I9	0.00	**_5E6**	_7K8	0.00
_19T	_1G1	0.00	**_2E4**	_120	0.00	**_3K1**	_00V	0.00	**_5E6**	_85T	2.90
_19T	_1K1	1.52	**_2E4**	_18I	1.46	**_3K1**	_0E3	0.79	**_5E6**	_98K	0.82
_19T	_1K2	0.74	**_2E4**	_19T	0.00	**_3K1**	_0F0	0.00	**_5E6**	_9C1	0.00
_19T	_25R	0.00	**_2E4**	_1B0	1.54	**_3K1**	_0G1	2.36	**_5E6**	_9E3	0.00
_19T	_2C9	2.53	**_2E4**	_1F2	0.82	**_3K1**	_0K0	0.79	**_5E6**	_9I9	0.71
_19T	_2E4	0.00	**_2E4**	_1G0	0.00	**_3K1**	_120	0.00	**_5E8**	_00V	2.97
_19T	_2F8	0.00	**_2E4**	_1G1	0.69	**_3K1**	_18I	0.00	**_5E8**	_0E3	1.40
_19T	_2G2	1.44	**_2E4**	_1K1	4.60	**_3K1**	_19T	0.00	**_5E8**	_0F0	3.05
_19T	_2G3	0.74	**_2E4**	_1K2	0.00	**_3K1**	_1B0	0.79	**_5E8**	_0G1	0.00
_19T	_2G4	0.74	**_2E4**	_25R	0.00	**_3K1**	_1F2	0.00	**_5E8**	_0K0	2.18
_19T	_33T	1.48	**_2E4**	_2C9	0.00	**_3K1**	_1G0	0.00	**_5E8**	_120	4.08
_19T	_3B9	0.76	**_2E4**	_2E4		**_3K1**	_1G1	0.00	**_5E8**	_18I	1.46
_19T	_3D9	0.00	**_2E4**	_2F8	0.00	**_3K1**	_1K1	0.00	**_5E8**	_19T	1.44
_19T	_3H0	0.74	**_2E4**	_2G2	3.28	**_3K1**	_1K2	0.00	**_5E8**	_1B0	1.54
_19T	_3K1	0.00	**_2E4**	_2G3	0.69	**_3K1**	_25R	0.00	**_5E8**	_1F2	1.39
_19T	_45Z	0.00	**_2E4**	_2G4	2.19	**_3K1**	_2C9	1.57	**_5E8**	_1G0	2.18
_19T	_4C5	0.00	**_2E4**	_33T	1.46	**_3K1**	_2E4	0.00	**_5E8**	_1G1	1.39
_19T	_4C9	0.74	**_2E4**	_3B9	0.00	**_3K1**	_2F8	0.00	**_5E8**	_1K1	3.03
_19T	_4E2	2.55	**_2E4**	_3D9	0.00	**_3K1**	_2G2	0.79	**_5E8**	_1K2	0.72
_19T	_4J4	0.00	**_2E4**	_3H0	0.74	**_3K1**	_2G3	0.00	**_5E8**	_25R	0.00
_19T	_51A	0.00	**_2E4**	_3K1	0.00	**_3K1**	_2G4	0.00	**_5E8**	_2C9	0.00
_19T	_53Z	0.00	**_2E4**	_45Z	0.64	**_3K1**	_33T	0.00	**_5E8**	_2E4	7.32
_19T	_5E6	0.00	**_2E4**	_4C5	5.36	**_3K1**	_3B9	0.00	**_5E8**	_2F8	0.00
_19T	_5E8	1.44	**_2E4**	_4C9	1.39	**_3K1**	_3D9	0.80	**_5E8**	_2G2	0.69

_19T	_5L7	2.08	**_2E4**	_4E2	0.85	**_3K1**	_3H0	0.79	**_5E8**	_2G3	0.00
_19T	_73S	0.00	**_2E4**	_4J4	1.54	**_3K1**	_3K1		**_5E8**	_2G4	0.69
_19T	_7A2	0.00	**_2E4**	_51A	5.52	**_3K1**	_45Z	0.00	**_5E8**	_33T	17.03
_19T	_7F5	0.00	**_2E4**	_53Z	3.09	**_3K1**	_4C5	0.72	**_5E8**	_3B9	0.76
_19T	_7K8	0.00	**_2E4**	_5E6	0.00	**_3K1**	_4C9	1.57	**_5E8**	_3D9	0.00
_19T	_85T	0.69	**_2E4**	_5E8	7.32	**_3K1**	_4E2	0.00	**_5E8**	_3H0	0.74
_19T	_98K	0.00	**_2E4**	_5L7	0.00	**_3K1**	_4J4	0.77	**_5E8**	_3K1	0.00
_19T	_9C1	0.00	**_2E4**	_73S	2.13	**_3K1**	_51A	0.00	**_5E8**	_45Z	2.85
_19T	_9E3	0.00	**_2E4**	_7A2	0.73	**_3K1**	_53Z	0.00	**_5E8**	_4C5	1.44
_19T	_9I9	2.98	**_2E4**	_7F5	0.00	**_3K1**	_5E6	0.82	**_5E8**	_4C9	0.69
_1B0	_00V	0.00	**_2E4**	_7K8	0.00	**_3K1**	_5E8	0.00	**_5E8**	_4E2	0.00
_1B0	_0E3	1.48	**_2E4**	_85T	0.64	**_3K1**	_5L7	0.79	**_5E8**	_4J4	0.00
_1B0	_0F0	1.57	**_2E4**	_98K	0.00	**_3K1**	_73S	0.00	**_5E8**	_51A	2.08
_1B0	_0G1	2.39	**_2E4**	_9C1	3.95	**_3K1**	_7A2	0.00	**_5E8**	_53Z	2.93
_1B0	_0K0	0.00	**_2E4**	_9E3	0.00	**_3K1**	_7F5	0.00	**_5E8**	_5E6	0.69
_1B0	_120	3.27	**_2E4**	_9I9	0.00	**_3K1**	_7K8	0.00	**_5E8**	_5E8	
_1B0	_18I	0.73	**_2F8**	_00V	1.52	**_3K1**	_85T	0.00	**_5E8**	_5L7	0.69
_1B0	_19T	1.49	**_2F8**	_0E3	4.40	**_3K1**	_98K	0.71	**_5E8**	_73S	0.00
_1B0	_1B0		**_2F8**	_0F0	0.00	**_3K1**	_9C1	0.00	**_5E8**	_7A2	0.73
_1B0	_1F2	0.82	**_2F8**	_0G1	0.00	**_3K1**	_9E3	0.00	**_5E8**	_7F5	2.81
_1B0	_1G0	3.00	**_2F8**	_0K0	0.00	**_3K1**	_9I9	4.48	**_5E8**	_7K8	1.39
_1B0	_1G1	1.39	**_2F8**	_120	0.00	**_45Z**	_00V	3.71	**_5E8**	_85T	1.39
_1B0	_1K1	1.52	**_2F8**	_18I	0.79	**_45Z**	_0E3	1.42	**_5E8**	_98K	5.60
_1B0	_1K2	4.36	**_2F8**	_19T	0.00	**_45Z**	_0F0	3.80	**_5E8**	_9C1	2.13
_1B0	_25R	0.00	**_2F8**	_1B0	0.79	**_45Z**	_0G1	0.85	**_5E8**	_9E3	2.50
_1B0	_2C9	1.54	**_2F8**	_1F2	0.79	**_45Z**	_0K0	2.21	**_5E8**	_9I9	0.00
_1B0	_2E4	1.54	**_2F8**	_1G0	0.00	**_45Z**	_120	0.00	**_5L7**	_00V	1.39
_1B0	_2F8	0.79	**_2F8**	_1G1	0.00	**_45Z**	_18I	5.08	**_5L7**	_0E3	2.10
_1B0	_2G2	5.96	**_2F8**	_1K1	2.27	**_45Z**	_19T	0.00	**_5L7**	_0F0	0.00
_1B0	_2G3	1.39	**_2F8**	_1K2	1.57	**_45Z**	_1B0	1.54	**_5L7**	_0G1	6.87
_1B0	_2G4	0.00	**_2F8**	_25R	0.00	**_45Z**	_1F2	0.00	**_5L7**	_0K0	0.69
_1B0	_33T	0.00	**_2F8**	_2C9	0.00	**_45Z**	_1G0	0.00	**_5L7**	_120	2.08
_1B0	_3B9	0.00	**_2F8**	_2E4	0.00	**_45Z**	_1G1	0.72	**_5L7**	_18I	2.85
_1B0	_3D9	1.60	**_2F8**	_2F8		**_45Z**	_1K1	1.44	**_5L7**	_19T	2.08
_1B0	_3H0	29.76	**_2F8**	_2G2	1.57	**_45Z**	_1K2	1.44	**_5L7**	_1B0	0.69
_1B0	_3K1	0.79	**_2F8**	_2G3	1.48	**_45Z**	_25R	0.00	**_5L7**	_1F2	0.82
_1B0	_45Z	1.54	**_2F8**	_2G4	0.73	**_45Z**	_2C9	1.76	**_5L7**	_1G0	4.37
_1B0	_4C5	2.26	**_2F8**	_33T	0.79	**_45Z**	_2E4	0.64	**_5L7**	_1G1	0.00
_1B0	_4C9	3.01	**_2F8**	_3B9	0.76	**_45Z**	_2F8	0.79	**_5L7**	_1K1	0.69
_1B0	_4E2	5.40	**_2F8**	_3D9	4.81	**_45Z**	_2G2	3.59	**_5L7**	_1K2	3.50
_1B0	_4J4	1.54	**_2F8**	_3H0	0.79	**_45Z**	_2G3	2.78	**_5L7**	_25R	1.60
_1B0	_51A	0.00	**_2F8**	_3K1	0.00	**_45Z**	_2G4	0.72	**_5L7**	_2C9	0.00
_1B0	_53Z	1.54	**_2F8**	_45Z	0.79	**_45Z**	_33T	1.44	**_5L7**	_2E4	0.00
_1B0	_5E6	0.77	**_2F8**	_4C5	0.00	**_45Z**	_3B9	2.27	**_5L7**	_2F8	2.18
_1B0	_5E8	1.54	**_2F8**	_4C9	2.27	**_45Z**	_3D9	3.59	**_5L7**	_2G2	2.11

_1B0	_5L7	0.69	**_2F8**	_4E2	0.00	**_45Z**	_3H0	1.44	**_5L7**	_2G3	8.33
_1B0	_73S	2.23	**_2F8**	_4J4	0.79	**_45Z**	_3K1	0.00	**_5L7**	_2G4	0.00
_1B0	_7A2	2.92	**_2F8**	_51A	0.00	**_45Z**	_45Z		**_5L7**	_33T	2.78
_1B0	_7F5	2.96	**_2F8**	_53Z	0.00	**_45Z**	_4C5	4.31	**_5L7**	_3B9	0.00

Appendix 4. Maternal relatedness. Maternal relatedness was known, but paternal relatedness was not. Maternal relatedness was quantified through a coefficient of relatedness (r) index that represents the probability that two individuals will have copies of the same gene50. Mother-offspring pairs have an r of 0.5, grandmother-grandchildren pairs have an r of 0.25, siblings have an r of 0.25, and maternally unrelated individuals have an r of 0. Data includes focal animals (Appendix 1) and non-focal animals.

Focal	Mother	r	Focal	Mother	r	Focal	Mother	r
04T	96G	0.5	**4D3**	31G	0.5	**9K9**	06A	0.5
06O	19A	0.5	**_4E2**	67G	0.5	**_00V**	30J	0.5
_0E3	L19	0.5	**4G8**	73B	0.5	**_0F0**	31L	0.5
_0G1	K00	0.5	**4K7**	3E7	0.5	**_0K0**	15E	0.5
0I9	_85T	0.5	**4L1**	81B	0.5	**0M3**	1B3	0.5
0J4	16Z	0.5	**4L6**	28A	0.5	**0M4**	14E	0.5
0L4	16Z	0.5	**_51A**	K04	0.5	**13H**	J41	0.5
OM1	13H	0.5	**5B0**	81I	0.5	**14E**	L49	0.5
12E	J92	0.5	**5E6**	78T	0.5	**15E**	J41	0.5
_120	I56	0.5	**5I3**	56R	0.5	**_1B0**	99J	0.5
_18I	L80	0.5	**5I5**	30O	0.5	**_1G0**	25N	0.5
_19T	V05	0.5	**5J1**	4C2	0.5	**_1G1**	48S	0.5
1B1	360	0.5	**5K8**	28G	0.5	**1G4**	_85T	0.5
_1F2	81I	0.5	**5L0**	61K	0.5	**1G6**	52Z	0.5
1L9	V80	0.5	**5L4**	3D1	0.5	**1I5**	01R	0.5
_25R	V44	0.5	**61R**	07A	0.5	**1I6**	51Z	0.5
28B	J28	0.5	**6K4**	90P	0.5	**1I7**	13H	0.5
_2F8	08Z	0.5	**_73S**	29B	0.5	**1K1**	31L	0.5
2K0	51Z	0.5	**73V**	T83	0.5	**1K2**	99J	0.5
2K3	90T	0.5	**77I**	S97	0.5	**_2E4**	29J	0.5
2K4	_2E4	0.5	**_7A2**	28N	0.5	**_2G2**	81E	0.5
2K5	52Z	0.5	**_7F5**	76J	0.5	**_2G3**	47Z	0.5
2K6	_9C1	0.5	**7G1**	39F	0.5	**_2G4**	_00V	0.5
2L0	3A2	0.5	**7L8**	40Z	0.5	**2I3**	_52Z	0.5
32Z	J91	0.5	**7L9**	_1B0	0.5	**2K1**	98J	0.5
_33T	89K	0.5	**81O**	02A	0.5	**_3D9**	T03	0.5

36V	35B	0.5	**8A7**	46K	0.5	**_3H0**	_1B0	0.5
_3B9	150	0.5	**8A9**	13A	0.5	**_45Z**	20C	0.5
3I6	61A	0.5	**8D8**	60R	0.5	**47Z**	31G	0.5
3I9	6A4	0.5	**8K1**	6C2	0.5	**_4C5**	T03	0.5
3J7	47Z	0.5	**8L5**	3A9	0.5	**_4C9**	20C	0.5
_3K1	14L	0.5	**_98K**	74B	0.5	**_4J4**	90T	0.5
3L4	48J	0.5	**_9E3**	56E	0.5	**51Z**	97J	0.5
4D3	31G	0.5	**_9I9**	360	0.5	_52Z	78I	0.5
93T	L66	0.5	**78I**	13B	0.5	53Z	30J	0.5
98J	13A	0.5	**7C4**	13B	0.5	5C6	31L	0.5
_9C1	67F	0.5	**_7K8**	13B	0.5	_5E8	78I	0.5
9E8	L66	0.5	**_85T**	98J	0.5	_5L7	81E	0.5
T03	845	0.5	**90T**	79I	0.5	5L8	_4C5	0.5

Focal	Sibling	r	Shared Mother	**Focal**	Offspring	r
9I9	1b1	0.25	360	**85T**	0I9	0.5
1b1	9I9	0.25	360	**2e4**	2k1	0.5
1G4	0I9	0.25	85T	**9C1**	2K6	0.5
7K8	7C4	0.25	13B	**2G4**	00v	0.5
7C4	7K8	0.25	13B	**00v**	2G4	0.5
7K8	78I	0.25	13B	**52Z**	2I5	0.5
78I	7K8	0.25	13B	**1B0**	3H0	0.5
45Z	4C9	0.25	20C	**3H0**	1B0	0.5
4C9	45Z	0.25	20C	**4j4**	90T	0.5
00V	53Z	0.25	30J	**52Z**	78I	0.5
53Z	00V	0.25	30J	**4c5**	5L8	0.5
0F0	1K1	0.25	31L	**85t**	98J	0.5
1K1	0F0	0.25	31L			
0F0	5C6	0.25	31L			
1k1	5C6	0.25	31L			
52z	5e8	0.25	78i			
5e8	52z	0.25	78i			
2g2	5l7	0.25	81E			
5l7	2g2	0.25	81E			
1F2	5b0	0.25	81L			
85T	2K1	0.25	98J			
1B0	1K2	0.25	99J			
1K2	1B0	0.25	99J			
3D9	4C5	0.25	T03			
4C5	3D9	0.25	T03			