

UNIVERSIDADE DE SÃO PAULO

INSTITUTO DE PSICOLOGIA

CAMILA GALHEIGO COELHO

**SOCIAL DYNAMICS AND DIFFUSION OF NOVEL BEHAVIOUR
PATTERNS IN WILD CAPUCHIN MONKEYS (*Sapajus libidinosus*)
INHABITING THE SERRA DA CAPIVARA NATIONAL PARK.**

São Paulo

2015

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*Tese apresentada para o Instituto de Psicologia da
Universidade de São Paulo, como parte dos requisitos para a
obtenção do título de Doutor em Ciências.*

Área de Concentração: Psicologia Experimental

Orientador: Prof. Dr. Eduardo B. Ottoni

Co-orientador: Prof. Dr. Rachel L; Kendal

AUTORIZO A REPRODUÇÃO E DIVULGAÇÃO TOTAL OU PARCIAL DESTES
TRABALHO, POR QUALQUER MEIO CONVENCIONAL OU ELETRÔNICO, PARA
FINS DE ESTUDO E PESQUISA, DESDE QUE CITADA A FONTE.

Catálogo na publicação

Biblioteca Dante Moreira Leite

Instituto de Psicologia da Universidade de São Paulo

Coelho, Camila Galheigo.

Dinâmica social e difusão de novos padrões comportamentais em macacos-prego (*Sapajus libidinosus*) que habitam o Parque Nacional da Serra da Capivara / Camila Galheigo Coelho; orientador Eduardo B. Ottoni. -- São Paulo, 2015.

187 f.

Tese (Doutorado – Programa de Pós-Graduação em Psicologia. Área de Concentração: Psicologia Experimental) – Instituto de Psicologia da Universidade de São Paulo.

1. *Sapajus libidinosus* 2. Tradições comportamentais 3. Aprendizagem social 4. Análise de redes sociais I. Título.

QL737.P925

NOME: Camila Galheigo Coelho

TÍTULO: Dinâmica social e difusão de novos padrões comportamentais em macacos-prego (*Sapajus libidinosus*) que habitam o Parque Nacional da Serra da Capivara

TITLE: Social Dynamics and Diffusion of Novel Behaviour Patterns in Wild Capuchin Monkeys (*Sapajus Libidinosus*) Inhabiting the Serra da Capivara National Park.

Tese apresentada para o Instituto de Psicologia da Universidade de São Paulo, como parte dos requisitos para a obtenção do título de Doutor em Ciências.

Aprovado em: ___ / ___ / ___

Banca Examinadora:

Prof. Dr. _____

Instituição: _____

Assinatura: _____

ACKNOWLEDGEMENTS

Agradecimentos:

Ao meu orientador Prof. Dr. Eduardo Ottoni, por tudo que me ensinou, pela oportunidade de trabalhar com os macacos-prego e por uma orientação construtiva.

À FAPESP e ao CNPq pela concessão de bolsa e auxílio de pesquisa.

Ao Parque Nacional da Serra da Capivara, às guariteiras e aos funcionários do Parque por todo o apoio.

À Fumdhm, pelo apoio logístico e por disponibilizar a moradia.

Ao ICMBio pela concessão da autorização para a realização da pesquisa de campo no Parque Nacional da Serra da Capivara

Ao Parque Ecológico do Tietê por ter me permitido desenvolver o estudo piloto com os macacos das ilhas e da área de proteção, e por todo apoio.

À Dra. Briseida Resende e ao Dr. Tiago Falótico pelas críticas e sugestões durante a qualificação, e por todo o apoio.

Aos funcionários do IPUSP in particular ao Noel pela engenhosidade na preparação do aparato experimental. E à Sonia pelo cuidado com as questões administrativas.

Ao Chico pela labuta com os macacos, pelas conversas, pela companhia, pelas histórias que me contou, por me ensinar tudo o que sei sobre a caatinga e a tecer cesta de cipó e, acima de tudo pela amizade. Ao George pela assistência no

A special thanks:

To Rachel Kendal, my co-supervisor, for the kind words and invaluable supervision, guiding me every step of the way. And for the warm welcome and hospitality during my time at Durham.

To Clara Corat, Bruce Rawlings, Marta Miguel, and Indikha Smith, this thesis would have never been possible were it not for your dedicated work in collecting and coding the data herein. Also for the friendship and company whether during the sweaty harsh fieldwork or the hard long hours on excel and R programming.

To Dan Franks and Will Hoppitt for their instructive advices on social network analysis and statistical modeling.

To Edinburgh Zoo for allowing me to conduct research with the Living Links capuchins, to all the staff for their help and support.

To the CCBC group at Durham University for the stimulating readings and debates.

To the staff at Durham University and Ustinov College for receiving me so well and accommodating my academic and personal needs, for all the support.

To all my colleagues at Durham University, especially those who braved the challenges of thesis writing together in 337 and 338. To Klara and Claudia for the providential walks in the forest, Julian, Samy, Pina, Jim, Tom, Diana, Chris, Natália, Bia for the support and fun times.

campo e pela companhia. E à Teresinha e Cleo por cuidarem de mim em SRN.

Aos amigos do Piauí, Amelie, Rafael, Elver, Jessica, Marina e Antoine, Bianca, Fernando e Clarinha. Pela companhia desbravando o PNSC.

Aos colegas Clara, Rachel, Lucas, Irene, Marcelo, Anna Penna, Zé, Mari Fogaça, MariLee, Olivia Mendonça, MariXá, Marcola, Yarka, Michelle, Tiago, Raphael, Bia, Noemi, Marcos.

Aos amigos da Biologia e da vida, especialmente Luara, Maissa, Talitha, Carol, Ilana, Talita, Nina, Sandy, Fer, Lia, Fernanda, Anna...

À minha família, velhos e novos integrantes.

Aos meus pais e meu irmão, por tudo, em especial pela companhia nessa grande viagem que têm sido nossas vidas; you are and will always be home to me.

To the Wild Brazil team (BBC) for taking an interest in my research and portraying the incredible monkeys at Capivara so well. It was a pleasure sharing this experience with you all.

To Ted Giffords and Emily Walmsly for the lovely time spent in our field set-up in Sítio do Mocó, for the many conversations on monkey behaviour and for the insight to the capuchins would made possible by the amazing images filmed.

To my British family, the Appleyards, Brighton friends, Bronnie and Aggie, and all at BFS colleagues, especially Rakel.

To Flávia, for safeguarding my wishes for a better way of living

To Maurice Said for the love, support, friendship, patience, for all the stimulating conversations and words of encouragement. In special, for the affection, companionship and for sharing with me the journey, that is living.

ABSTRACT

The existence of behavioural traditions – that is, cross-generational socially mediated learning of a behaviour - in non-human animals has been the subject of intense debate in the last decade. To classify as a behavioural tradition, a behaviour must be acquired by naïve individuals through learning that must in some way be mediated or facilitated by the behaviour of a conspecific. The overarching aim of this thesis is to further our understanding of behavioural traditions in capuchin monkeys. To do so I examine the acquisition of new behaviours via socially-biased learning in two groups of wild bearded capuchin monkeys (*Sapajus libidinosus*) inhabiting the *Serra da Capivara National Park*, Piauí, Brazil. More specifically, the thesis answers three main questions: (1) what are the opportunities of social learning; (2) how can social learning be identified in wild populations and (3) how do social biases in the transmission of information affect the final behavioural repertoire of the groups. To address the first question I describe the social context in which the capuchin monkeys live as a means to characterise the opportunities monkeys have of learning from one another. My findings confirm Coussi-Korbel & Fragaszy's (1995) predictions that capuchin monkeys have relationships conducive of both non-specific social learning and directed social learning. Using social network analysis I portray the groups' social structures based on different measures of relationships and describe how patterns of association (social proximity, co-feeding) depict opportunities for non-specific social learning, while interactions (grooming, social play) are conducive to directed social learning. The second question is answered by implementing an open-diffusion field experiment and the application of novel data analysis methodologies (NBDA: Franz & Nunn 2009 and Option-bias: Kendal et al 2009) designed for studying social learning in wild populations. NBDA found that when the social transmission model was informed by observation networks, it presented a better fit to the diffusion data, thus providing evidence for social learning of the foraging tasks. Moreover, only observation from shorter distances produced these results, indicating that observation of the task, from close up, was needed for the behaviour to be acquired. Other social networks also provided evidence for social learning in both groups, predominantly those based on grooming relations for the lift-pull task and co-feeding relations for the tube-task. To address the third question I examine possible transmission biases, addressing, in particular, frequency-dependent and model-based transmission biases. Given the homogeneity of behavioural variants for solving foraging task, rigorous conclusions regarding frequency-dependent biases were not possible. The model-based bias revealed a selective attention towards proficient individuals, resonating with what has been described for tool-aided nut cracking in semi-free capuchin (*Sapajus spp.*: Ottoni et al 2005, Coelho et al, 2015) and wild capuchin monkeys (*Sapajus libidinosus*: Coelho et al 2008). Considering opportunities of social learning and transmission biases together allows us to further the understanding of the dynamics involved in the establishment and maintenance of shared practices and of the spread of behavioural traditions across populations.

RESUMO

A existência de tradições comportamentais – comportamentos transgeracionais adquiridos por aprendizagem socialmente mediada - em animais não-humanos tem sido objeto de intenso debate na última década. Para classificar uma tradição como comportamental, um comportamento deve ser adquirido por indivíduos inexperientes através da aprendizagem que deve, de alguma forma, ser mediada ou facilitada pelo comportamento de uma mesma espécie. O objetivo central desta tese é avançar nossa compreensão acerca das tradições comportamentais em macacos-prego. Para fazer isso, eu analiso a aquisição de novos comportamentos através da aprendizagem socialmente mediada em dois grupos de macacos-prego selvagens (*Sapajus libidinosus*) que habitam o Parque Nacional da Serra da Capivara, Piauí, Brasil. Mais especificamente, a tese responde a três perguntas principais: (1) quais são as oportunidades de aprendizagem social; (2) como a aprendizagem social pode ser identificada em populações selvagens e (3) como os vieses sociais na transmissão de informações afetam o repertório comportamental final dos grupos. Para abordar a primeira pergunta eu descrevo o contexto social em que os macacos-prego vivem como forma de caracterizar as oportunidades que os macacos têm de aprender uns com os outros. Meus achados confirmam as hipóteses de Coussi-Korbel & Fragaszy (1995) de que os macacos-prego têm relacionamentos propícios tanto para a *aprendizagem social não-específica* como para a *aprendizagem social dirigida*. Usando a análise de redes sociais eu descrevo as estruturas sociais dos grupos com base em diferentes medidas de associações e interações sociais. Descrevo como os padrões de associação (proximidade social, co-alimentação) representam oportunidades para *aprendizagem social não-específica*, enquanto as interações (catação, brincadeira) são propícias a *aprendizagem social dirigida*. A segunda pergunta é respondida através da implementação de um experimento de campo em difusão aberta e a aplicação de novas metodologias de análise de dados (NBDA: Franz & Nunn 2009 e Option-viés: Kendal et al 2009), concebidas para estudar a aprendizagem social em populações selvagens. NBDA revelam que, quando o modelo de transmissão social foi informado por redes de observação, apresentou um melhor ajuste aos dados de difusão, proporcionando assim evidência de aprendizado social das tarefas de forrageamento. Além disso, apenas a observação de distâncias mais curtas produziram esses resultados, indicando que a observação de perto, era necessária para o comportamento a ser adquirido. Outras redes sociais também forneceram evidências para a aprendizagem social em ambos os grupos, predominantemente aqueles baseados em dados de catação referentes ao experimento *lift-pull task* e de dados de co-alimentação ao que se refere ao experimento *tubo-task*. Para abordar a terceira questão eu examino possíveis *vieses de transmissão* (transmission biases), em particular, *vieses de transmissão baseados no modelo* e *vieses de transmissão frequência-dependentes*. Dada a homogeneidade das variantes comportamentais, não foi possível se chegar a conclusões consistentes referentes aos *vieses de transmissão frequência-dependentes*. O *viés de transmissão baseado no modelo* revelou uma atenção seletiva para os indivíduos proficientes, em consonância com o que foi descrito para a quebra de cocos por uso de ferramenta macacos-prego semi-livres (*Sapajus spp*: Ottoni et al 2005, Coelho et al, 2015) e macacos-prego selvagens (*Sapajus libidinosus*: Coelho et al 2008). Considerando-se as oportunidades de aprendizagem social e os vieses de transmissão, em conjunto, permitenos avançar na compreensão da dinâmica envolvida no estabelecimento e manutenção de práticas compartilhadas e da disseminação das tradições comportamentais entre populações.

TABLE OF CONTENTS

LIST OF FIGURES	i
LIST OF TABLES	v

CHAPTER 1. INTRODUCTION	1
--------------------------------------	---

CHAPTER 2. METHODS	19
2.1 Study species	20
2.2 Study sites and focal subjects	22
2.2.1 Serra da Capivara Nacional Park (SCNP)	22
2.2.2 Tiete Ecological Park (TEP)	26
2.2.3 Edinburgh Zoo - Living Links	27
2.3 Experiments	28
2.3.1 Lift-pull task	28
2.3.2 Tube task	34
2.3.3 Novel objects	35
2.4 Social context data collection	37
2.4.1 Behavioural data sampling	37
2.4.2 Social networks	40
2.5 Data Analysis	42
2.5.1 Network-based diffusion analysis	42
2.5.2 Option-bias analysis	44
2.5.3 Social Network Analysis	45
2.5.4 Standard inferential statistics	46

CHAPTER 3. THE SOCIAL CONTEXT OF LEARNING: DIRECTED SOCIAL LEARNING AND SOCIAL NETWORK ANALYSIS	47
3.1 Introduction	48
3.2 Methods	52
3.2.1 Behavioural data sampling	52
3.2.2 Social Networks	53
3.2.2 Social network analysis and statistical methods	55

3.3 Results.....	57
3.3.1 Focal samples and frequency of behavioural coordination.....	57
3.3.2 Graphical representation of networks	58
3.3.3 Social network analysis: cohesion measures	67
3.3.4 Assortative mixing.....	71
3.3.5 Flow betweenness and network centralization index.....	76
3.4 Discussion.....	80

CHAPTER 4. IDENTIFYING SOCIAL LEARNING IN WILD BEARDED CAPUCHIN MONKEYS (SAPAJUS LIBIDINOSUS): AN OPEN DIFFUSION EXPERIMENT WITH TWO FORAGING TASKS 84

4.1 Introduction.....	85
4.2 Methods.....	89
4.2.1 Study site and subjects	89
4.2.2 Experimental set-up and procedures	89
4.2.3 Behavioural observations.....	96
4.2.4 Statistical methods	97
4.3 Results.....	100
4.3.1 Lift-pull task.....	100
4.3.2 Tube task.....	105
4.4 Discussion.....	108

CHAPTER 5. TRANSMISSION BIASES IN WILD BEARDED CAPUCHIN MONKEYS (SAPAJUS LIBIDINOSUS) 113

5.1 Introduction.....	114
5.2 Methods.....	117
5.2.1 Observation records and first successful manipulations.....	117
5.2.2 Frequency dependent social learning strategies.....	118
5.2.3 Model-based social learning strategies	119
5.3 Results.....	120
5.3.1 Observation records and first successful manipulations.....	120
5.3.2 Frequency-dependent social learning strategies	122
5.3.3 Whom do naïve individuals observe? Model-based biases	124
5.4 Discussion.....	127

CHAPTER 6. GENERAL DISCUSSION	129
The social context: on opportunities of social learning	130
Identifying learning influenced by the social context: on the importance of choosing social networks representative of the relationships underlying diffusion	134
On the group repertoire and social learning strategies.....	137
On integrating social context, learning processes and transmission biases	140
On tolerance, social learning and behavioural traditions.....	142
Future directions	144
REFERENCES	145
APPENDIX A – Dominance Hierarchy and Ranking	155
APPENDIX B – Novel objects experiment: measuring neophobia.....	160
APPENDIX C – Supplementary material for NBDA.....	163
APPENDIX D - Supplementary material Tube task experiment.....	166
APPENDIX E – GLM analysis chapter 5	169

LIST OF FIGURES

Figure 1.1 Three dimensions of behavioural coordination, in space, in time and in space-time, according to Coussi-Korbel & Fragasy (1995).....	10
Figure 2.1 Schematic representation of home ranges for Jurubeba (orange) and Pedra Furada (purple) in the Serra da Capivara National Park.....	23
Figure 2.2 Diagram of the lift-pull task: (A) frontal view, (B) side view of lift option to solve the task and (C) side view of pull option to solve the task.....	29
Figure 2.3 Schematic representation of home range for Jurubeba group and the locations where the experiments were conducted. (A) Boqueirão da Baixa Grande, (B) Boqueirão dos Oitenta and (C) Boqueirão do Gato (near Casinha do Isaias).....	33
Figure 2.4 Schematic representation of home range for Pedra Furada group and the locations where the experiments were conducted. (A) Sítio do Carlindo, (B) Baixão da Esperança and (C) near cashew trees at the end of the Boqueirão da Pedra Furada.....	33
Figure 2.5 (A) close up on the lift-pull apparatus and (B) the experimental set-up at the Boqueirão dos Oitenta.....	34
Figure 2.6 Novel objects and individuals interacting with these objects. (A) Juvenile male (Lim) rolls the ball around, (B) adult female (Gor) pushes the sink plunger over and (C) adult female (Moc) approaching fluffy toy, later she pokes the toys eyes.....	36
Figure 3.1 Activity of individuals during behavioural coordination within 1 meter, compiled for both groups. Values represent the percent of focal points for each activity.....	57
Figure 3.2 Graph representation of <i>social proximity within 1m</i> networks. Nodes coloured red indicate individuals that are part of the main component. Thickness of edges represents the strength of association.....	59
Figure 3.3 Graph representations of <i>co-feeding</i> networks. Nodes coloured red indicate individuals who are part of the main component. Thickness of edges represents the strength of association.....	60

Figure 3.4 Graph representation of *grooming* networks. Nodes coloured red indicate individuals that are part of the main component. Other components in green and isolated individuals in blue. Thickness of edges represents the frequency of interactions.....62

Figure 3.5 Graph representation of *social play* network. Nodes coloured red indicate individuals, part of the main component. Isolated individuals in blue. Thickness of edges represents the frequency of interactions.....63

Figure 3.6 Graph representation of *observation up to 10 meters* network. Nodes coloured red indicate individuals, part of the main component. In green other smaller components. Thickness of edges represents the frequency of observations.....65

Figure 3.7 Graph representation of *observation within 5 meter* network. Nodes coloured red and purple part of the main components. In green other smaller components. Isolated individuals in blue. Thickness of edges represents the frequency of observations.....66

Figure 3.8 Comparison of network metrics Density and Component ratio, between the three types of networks: Association, Interaction and Observation. * significant differences in Density between network types. ** significant differences in Component ratio between network types.....68

Figure 3.9 Comparison of network metric Density between different networks.....69

Figure 3.10 Comparison of network metric Component ration between different networks..70

Figure 3.11 Mean Clustering coefficient for each of the social networks.....71

Figure 3.12 Assortativity by (A) sex, (B) age and (C) dominance rank in social networks for each group, Jurubeba (in orange) and Pedra Furada (in purple).....72

Figure 3.13 Assortative mixing between classes of individuals, by average tie strength, for grooming network in Jurubeba group. Groomer-groomee (e.g. M-F: indicates male grooms female).....73

Figure 3.14 Assortative mixing by sex (A; B) and age (C; D). Average tie strength for social play networks in Jurubeba (A; C) and Pedra Furada (B; D).....74

Figure 3.15 Assortative mixing by dominance rank. Average tie strength for observation within 10 meters networks in Jurubeba (A) and Pedra Furada (B).....75

Figure 3.16 Flow betweenness centralization index each of the social networks.....76

Figure 3.17 Flow betweenness of each individual for the several networks: on the left, Jurubeba group (in orange); on the right Pedra Furada group (in purple).....78

Figure 3. 18 Average Flow Betweenness from co-feeding, grooming, social play, and observation networks for each member of the groups, Jurubeba and Pedra Furada.....79

Figure 4.1 – The Lift-Pull task set up with JB group. A juvenile male solving the task by (A) option *lift* and (B) option *pull*. Food reward slides down a shaft into the tray at the bottom of the task. (C) within a 5-meter radius of box, an adult male (LOI) solves the task using *lift*. At the moment the food reward was released three other monkeys (an adult female, TOP, and two juvenile males, QUE and MIN) were observing.....91

Figure 4.2 Tube task experiment with the Pedra Furada group: (A) adult male (Nic) trying to reach the mango pulp with his hands, without success, (B) adult female (Ali), with infant on her back, using tail-dipping technique, successfully, (C) dominant male (Tor) using a stick probe to solve the task successfully while being observed by conspecifics.....95

Figure 4.3 Proportion of informed individuals over time elapsed of experimentation for Jurubeba (N=40) and Pedra Furada (N=30). Dotted line indicates when open diffusion began.....100

Figure 4.4 Percentage of options used to solve the lift-pull task, per individual, for both wild groups.....101

Figure 4.5 Results of the Option-bias analysis for the lift-pull task experiment. Red line indicates the observed chi-square metric value which does not fall within the upper tail of the null distributions of the chi-square values, created by the randomised simulations.....102

Figure 4.6 Observation networks within 5 meters. Edge thickness is proportional to the frequency of observation. Node size is proportional to the degree (number of arriving (observed) and leaving (observing) from node) Pie chart on nodes represents proportion of options used to solve the task successfully: blue for lift and green for pull options. In black

are monkeys that never solved the task successfully. Panel A for Jurubeba group and panel B for Pedra Furada group.....103

4.7 Results of the Option-bias analysis for the tube task experiment. Panel A depicts the observed percentages of options used to solve the tube task, per individual, for both wild groups. Panel B shows that the observed chi-square metric value (red line) falls within the upper tail of the null distributions of the chi-square values created by the randomised simulations. Thus the null hypothesis is rejected and evidence of social learning present..106

Figure 5.1 Proportion of *lift* (blue) and *pull* (green) actions performed by monkeys in both groups when solving the lift-pull task successfully. * indicates individuals who originally solved the task using the alternative option (*pull*) but shifted to the group prevailing option (*lift*). ** indicates individual who continued to use the alternative option (*pull*).....121

Figure 5.2 Regression of Proportion of actions observed and Proportion of actions produced, throughout the open diffusion, for juveniles (N=8) and adults (N=18) for data on both wild groups (JB and PF) together.....123

Figure 5.3 Observation within 5-meter radius networks for (A) Jurubeba and (B) Pedra Furada. Size of nodes indicates in-degree centrality (i.e. frequency that a monkey was observed by a naïve conspecific, while it solved the task). Colour of nodes code for success ratio: stronger tones for higher success ratios in solving the lift-pull task. Node shapes indicate sex of monkey, *circle*=female and *square*=male.....161

LIST OF TABLES

Table 2.1 Composition of Jurubeba group inhabiting Serra da Capivara National Park. ¥ Dominant male. Date of birth displayed to the infant’s name.....	25
Table 2.2 Composition of Pedra Furada group inhabiting Serra da Capivara National Park. ¥ Dominant male. Date of birth displayed to the infant’s name.....	26
Table 2.3 Composition of captive capuchins of the East and West groups at the Living Links – Edinburgh Zoo - Scotland.....	27
Table 2.4 Novel objects and order of presentation to each group.....	35
Table 2.5 Description of behaviours displayed by the capuchin monkeys examined in this study and how these were recorded and categorised for analysis.....	38-9
Table 3.1 Composition of groups Jurubeba (JB) and Pedra Furada (PF).....	52
Table 3.2 Summary of Social Network Analysis measures applied (based on Borgatti et al. 2013).....	56
Table 4.1 Definitions of actions on extractive foraging apparatus.....	90
Table 4.2 Results for Time of acquisition diffusion analysis (TADA). Observation networks for data on observation of manipulations of the lift-pull task by conspecifics, at different distances from task.....	104
Table 4.3 Results for Time of acquisition diffusion analysis (TADA) of solving the <u>lift-pull task</u> with the social model informed by social networks (proximity, co-feeding, play and grooming).....	105
Table 4.4 Results for Time of acquisition diffusion analysis (TADA). Observation networks for data on observation of manipulations of the tube task by conspecifics.....	107
Table 4.5 Results for Time of acquisition diffusion analysis (TADA) of solving the <u>tube task</u> with the social model informed by social networks (proximity, co-feeding, play and grooming).....	108

Table 5.1 Results for the generalized linear model analysis, testing for frequency dependent bias, *copy variant lift*, in the lift-pull task.....122

Table 5.2 Results for the generalized linear model analysis, testing for conformity bias in the lift-pull task.....124

Table 5.3 Results for the generalized linear model analysis, testing for model-based biases in the choice of observational targets during the lift-pull task experiment.....125

CHAPTER 1:

INTRODUCTION

This thesis is organised around three main chapters. The over-arching theme of this thesis is the acquisition of new behaviours by wild bearded capuchin monkeys (*Sapajus libidinosus*) via socially-biased learning. In the first results chapter (chapter 3), I compare different types of affiliative relationships between members of two different groups of wild capuchin monkeys in order to describe the social context in which the monkeys may learn from one another. In the second results chapter (chapter 4), I empirically identify socially-biased learning by means of an open-diffusion field experiment and the application of novel data analysis methodologies designed for studying social learning in wild populations. In the third and final results chapter (chapter 5), I examine transmission biases, addressing, in particular, frequency-dependent and model-based transmission biases. Each of the results chapters contain a brief discussion section specifically attuned to the topic therein. A broader discussion, dialoguing the finding in this thesis with the current literature, is presented in the general discussion (chapter 6), to avoid unnecessary repetition.

I begin the introduction to this thesis by exploring how the field of social learning has developed over time and how social learning and behavioural traditions have been studied in capuchin monkeys to date. I outline how methodological advancements are helping researchers to describe primate social structures and to detect social learning in wild populations, thus, setting the stage for the chapters to follow.

As with most themes in the Life Sciences, the discussion about social learning in animals was already present in Darwin's questioning. Anecdotes from Darwin's contemporaries recount instances in which animals, after seeing another animal behave in a certain way, performed the same action or behaviour, thus having advantage over those 'cunning enough' to copy. Romanes (1882, cited Shettleworth, 2010), as well as Darwin himself, defended the existence of a mental continuity that followed sequentially from "lower animals" up to man. Within this anthropocentric perspective of the age, the first enquiries in this field of research focused on whether animals could reproduce that which they seen being done, an 'imitative' ability. Perhaps the most relevant contribution to the field of social learning came from Thorndike (1911, cited Shettleworth, 2010) in the beginning of the twentieth century, when he proposed the classic experiment of a 'problem box'. Thorndike greatly enriched this line of study, providing a means of empirically testing for 'imitation' in

animals by means of a controlled experimental set-up. From his experiments he concluded animals lacked imitative abilities.

Thorndike's experiment with the 'problem box' was the first in a long line of experiments based on the model-observer paradigm. Generally, a subject is trained to perform a task and, once proficient, it is placed in front of a naïve individual who observes the model's performance. Next, the observer is given a chance to solve the task. If the animal solves the task in the same way as it observed the model solving it, then copying is said to have occurred. For decades, experiments based on this paradigm have been refined and an extensive terminology has accumulated to describe various types of social learning mechanisms. Among these are: stimulus or local enhancement¹ (Campbell et al, 1999), emulation, and various kinds of imitation² (Ham & Whiten, 1992; Call & Tomasello, 1997; Byrne & Russon, 1998). In general, studies have shown that animals learned the new task, but that imitation – i.e. copying the *action* after seeing it being done - was rare in non-human animal species. In most cases, the acquisition of a new behaviour occurred primarily by other forms of social learning or simply by trial and error (for a recent review on social learning mechanism see chapter 4 from Hoppitt & Laland, 2013).

Two-action task: a two action paradigm for studying social learning mechanisms

Studies on social learning mechanisms require experiments to control the environmental and social variables. This methodology, pioneered by Dawson & Foss (1965), usually consists of two-action task experimental set-ups conducted with animals in captivity. These are similar to the experiments described above, however now the problem box can be solved in two discrete ways. The model is trained, in isolation, to solve the problem with one of two possible actions. Once the model has reached a required proficiency in solving the task, s/he is paired with a naïve observer, demonstrating to her/him the trained action several times. Finally, the observer is given the chance to solve the task, which can be done by two different means, only one of which it has observed previously. This procedure is repeated

¹ Campbell et al (1999, p. 151) define stimulus and local enhancement as “when a naïve animal learns about the presence, location and/or value of stimuli, objects or events in the environment”

²The concept of imitation is still hotly debated among academics. Broadly, it refers to situations where an individual replicates the exact movements of another individual after having observed it (Tomasello & Call, 1997) or the functional structure of other individual's behavior ("imitation at program level," Byrne & Russon 1998). "Emulation", on the other hand, does not require that the movements are accurate and, therefore, the individual need only manipulating elements in an idiosyncratic way as long as it leads to the expected result (Whiten & Ham, 1992).

with N observers; if they reproduce the option that was seen being done by the demonstrator, then there is basis to affirm that social learning is occurring. Conversely, if the observers solved the task without a bias towards the demonstrated method, then no imitation has occurred. Moreover, the level of fidelity in the reproduction of behaviour and the elements that have been reproduced may indicate the type of learning process (imitation, emulation, stimulus enhancement, among others). There are countless studies of two-action tasks conducted with a wide range of animal species (starlings: Campbell et al, 1999; parakeets: Heyes & Saggerson, 2002; marmosets and tamarins: Voelkl & Huber, 2000, Day et al, 2003, Caldwell & Whiten, 2004; orangutans: Custance et al., 2001; chimpanzees: Whiten et al, 2005, Hopper et al, 2007; capuchin monkeys: Custance et al, 1999, Dindo et al, 2007 - to name a few). Here I shall focus primarily on the set of studies conducted with capuchin monkeys and on methodologies, which have in one way or another, advanced the field in its attempts to identify social learning in animals.

Custance and colleagues (1999) designed an apparatus (called and ‘artificial fruit’) that could be opened by a total of four different actions (poking the front of a rod, twisting front of a rod, turning a handle or pulling a handle). Succeeding in opening the ‘artificial fruit’ resulted in the animal finding a reward. The task was presented to 11 adult capuchin monkeys bred in captivity, using a human care-taker as a demonstrator. The care-taker solved the task using one of the four actions in front of each monkey separately. After re-baiting and assembling the box out of sight from the subjects, the apparatus was given to the monkeys for a total of two minutes each. Independent researchers (who had not taken part in the experiment) coded video recordings of the actions used by the monkeys attempting to solve the task. These researchers were able to correctly identify the action witnessed by the capuchins, based on the types of manipulations the monkeys performed on the apparatus. A micro-analysis of videos revealed that capuchin monkeys even reproduced the direction in which the rods were removed, and the authors conclude that it is likely the monkeys were learning to solve the task by object movement re-enactment (a form of emulation). However, these capuchin monkeys have a high level of acculturation, as they were raised within human families as part of an aid project for people with disabilities. Enculturated primates are more attentive to human movements and so may even have learned more subtle aspects of object relationship / hand movement than might be expected from wild or captive but non-enculturated primates (Bard & Gardner, 1996). So enculturated capuchin monkeys were able to copy the actions of a human demonstrator, but could uncultured capuchin monkeys learn from other capuchins?

Dindo and collaborators (2007) tested captive capuchin monkeys with a two-action task in an experimental set-up in which models and observers were conspecifics. This study used a diffusion chain paradigm to investigate whether capuchin monkeys would be able to learn a new foraging task by observing a conspecific solving the task using one of the two available actions. To do so, two monkeys were isolated from their respective social groups and trained to solve the two-action task, each with one of two possible actions (lift or slide). Once these had reached the desired level of proficiency, each of the demonstrators was paired with a naive observer who, after observing 20 demonstrations, was tested alone with the task to see which action it would use. The observer, having learned to solve the task (irrespective of the action used), was then assigned as a demonstrator, and solved the task before a naïve conspecific. This procedure was repeated along a chain of individuals. Two chains were produced, each having started with one of the actions (lift or slide). Dyads were chosen based on social tolerance information (assessed through co-feeding and social interaction data) collected before the experiment. In doing so, researchers created an ideal tolerance context, with demonstrators being slightly dominant over observers, thus guaranteeing that the information of how to solve this foraging task was transmitted along the chains, representing ‘pseudo-generations’. By including conspecific models this experimental set-up was an improvement on previous ones. However, the pairing of dyads based on perfect social tolerance is lacking in ecological validity; studies with more natural social contexts would be desired.

As part of Dindo’s et al (2007) research four monkeys were used as controls, and given the task without having received any training or having observed any demonstrations of how to solve the task. Three out of the four control monkeys managed to solve the task (two used lift and one used slide), indicating that the behavior was easy enough that it could be innovated several times. However, fidelity in the use of the variants indicates some form of social learning. Dindo and colleagues (2007) avoid making statements on the mechanisms behind the acquisition of the new behavior; they simply state that the fidelity in the use of the options is a sign of some ability to copy the action (lifting or sliding the door by imitation) or as the result of the object’s movement (door on top vs. door to the side, a sign of emulation).

Socially-biased learning: moving away from social learning mechanisms and towards a greater focus on the social context of learning

An emerging field that could greatly contribute to the understanding of the mechanisms underlying social learning is the research on mirror neurons. The Mirror Neurons System

(SNE) was originally described in the premotor cortex of rhesus monkeys and consist of neurons that are activated both when an individual performs an action and when an individual observes the same action being performed by a conspecific. This neural representation common to both perception and enactment of a behaviour, has led to the proposition of the direct-matching hypothesis. This hypothesis offers an explanation of the proximal mechanisms behind neonatal imitation, imitation, and theory of mind, among others aspects of cognition. The direct-matching hypothesis advocates that our understanding of the actions of others stems from a matching process in which the action observed is matched to the equivalent mental representation that the individual has of its own actions (Rizzolatti & Craighero, 2004).

When the action observed is not present in the individual's motor repertoire, it is interpreted by other brain areas. However, when the action is known to the observer, the motor neuron system automatically resonates in response to the action being observed. Existing studies point to a need for prior action by the individual before it can perceive the actions or objectives of others. Infants were only able to recognize the purpose of the actor (e.g. reach for an object) when they already had experience with that same action. (Kanakogi & Itakura, 2010). Little is known about the development of the direct-matching mechanism and studies about its ontogeny are needed. Neonatal imitation studies, however, point to the possibility that the mirror neurons are active from birth (Ferrari et al, 2006) (see Gariépy et al, 2014, for a review on social learning and neural basis).

The perception-action mechanism as described above appears to be the neural basis for transforming an observed behaviour into the enactment of a similar behaviour in human and nonhuman primates. Furthermore, this theoretical framework is in line with current thinking that social and asocial learning depend on the same basic mechanisms of associative learning. What makes learning distinctively social is that the input is somehow biased by other agents, via perceptual, attentional or motivational processes (Heyes, 2012).

The findings described above are also in agreement with the proposal made by Frigaszy and Visalberghi in their 2001 paper, "Recognizing the Swan: Socially-biased Learning". In this paper the authors suggest we adopt the term socially-biased learning instead of "social learning", given that, ultimately, learning is always an individual endeavour. The metaphor of the swan was adopted to portray the elegance in the simplicity of the mechanisms involved in socially-biased learning as proposed by them, namely associative learning, subject to biases that social context can produce. The authors predict that socially-biased learning is likely to occur in a broad spectrum of animals since it is not

the result of specific cognitive processes but depends on the same basic learning mechanisms present in most animals.

In the same article, Fragaszy & Visalberghi (2001) criticize the idea that imitation is necessary for behavioural traditions and state that new behaviours can become group-wide shared practices maintained over time by a simpler mechanism, such as, socially-biased learning. The “ugly duckling” in there analogy are the simpler mechanisms, such as stimulus enhancement, which nevertheless can foster social learning. The authors emphasize that, to understand how these traditions are maintained, we must conceive of individuals as dynamic and engaged with social and non-social elements of their environment, not simply agents capable of transforming visual information into motor output. Throughout this thesis, I often employ the term "social learning" for convenience, but I am not assuming any mechanism other than standard associative learning that is particular because of the social context in which it occurs.

Diffusion studies in captive nonhuman primates: using the two-action task paradigm to studying social transmission

The two-action two-group paradigm has more recently been used to study social transmission through groups rather than dyads. Interested in the possibility of generating differing traditions in social groups, these studies were also conducted in captivity and selected individuals to be trained as models, based on the most desirable attributes of a model. This experimental set-up gained ecological validity, since, after the trained model had acquired the desired proficiency, it was returned to its social group, where it could freely demonstrate the task solution to the other naïve group members within their usual enclosure. Whereas previously individuals were isolated and paired two by two, now learning was allowed to take place in a more naturalistic social setting. To ascertain that social learning is occurring, the task is presented to two groups, so that the model in the second group demonstrates the alternative solution to that presented by the model in the first group; thus the groups function as a control of each other. Furthermore, by doing so, we can establish that one of the options is not more likely to be adopted than the other.

Dindo and colleagues (2009) were the first to conduct an open diffusion experiment with capuchin monkeys in captivity. In a previous study (described above) Dindo et al (2007) had shown that capuchin monkeys were capable of accurately copying the foraging activity of a conspecific in a controlled dyadic experimental condition. In their 2009 paper the authors report a replication of the previous study, now in a more naturalistic context, where all

members have access to the experimental apparatus. An open diffusion set-up allows us to study the spread of socially transmitted behaviour with greater ecological validity. In this study, the alpha males of two groups of captive capuchin monkeys were trained, in isolation, to solve a two-action task; one with the option lift and the other with the option slide. The models were then returned to their social group, where they were able to monopolize the device for the first five days, demonstrating the trained option and thus seeding one option in each group. No scrounging or manipulation of the task (other than by the trained models) was allowed during the observation phase; if a naive individual approached the task, the apparatus was removed by the researcher from the experimental area. During the subsequent phase, the open diffusion, 13 of the 14 capuchins who observed the model using lift used the option lift when solving the task themselves, while 8 of the 11 capuchins who observed the model using slide exhibited slide; other individuals did not learn to solve the task. Although most individuals eventually solved the task using both the techniques (lift and slide) they all exhibited 76.8% fidelity to the option seeded in the group by the trained demonstrator.

The final two-action task, social learning experiment I address here is a study conducted by Crast et al (2010) with captive capuchin monkeys. This study added another layer to its naturalistic approach by incorporating a developmental approach to investigate how infants acquire the group typical behaviour. An apparatus with two possible means of obtaining a resource (orange juice) was placed in an environment that only infants had access to, called the "nursery". Initially, both options for obtaining juice were available to the infants, who eventually learnt to drink using both options. The apparatus was then offered to all members of the social group, however, in each of the social groups only one of the options produced rewards; thus, adults exhibited only one of the alternatives. Two years later, the apparatus was made available again (now with both options rewarding); in this reproduction of the experiment, infants used the option used by the adults in their respective social groups, despite having originally learned that both options were rewarding. The authors conclude that the social context played an important role in the acquisition of a new foraging technique among young captive capuchin monkeys and that their results support the existence of traditions in wild populations.

Here I presented a short re-count of some relevant social learning studies with capuchin monkeys that lead up to the experimental set-up I adopted for the research conducted for this thesis. This is by no means an extensive review of the social learning studies, even within the capuchin monkeys. For a review on animal social diffusion experiments refer to Whiten & Mesoudi (2008). Reader & Biro (2010) make an extensive review of experimental

identification of social learning in the wild, while Lonsdorf & Bonnie (2010) emphasize the importance of including developmental factors when studying social learning. Furthermore, there is an extensive body of literature on capuchin monkey problem solving abilities (reviewed in Frigaszy et al, 2004) and more recent branches from the social learning area into the subjects of cumulative learning and cooperation, which are beyond the scope of this thesis.

The importance of the social context of learning in the field of behavioural traditions

Most of the studies on social learning have focused on the mechanisms of social learning and were conducted in highly controlled settings, usually between dyads in isolated cubicles (Kendal et al, 2010). These studies required experiments to be conducted with such control of environmental and social variables that often, little or no resemblance of the natural social dynamics of the species remained. Recent studies of social diffusion went a step further, incorporating some of the social dynamics, even if the social conditions of captive groups differed from the natural social context found in wild populations. Still, all these studies manipulated the choices of models that were trained individually, or the individuals (or class of individuals) that have access to the task. The experiment could be applied on consecutive days and scrounging controlled. An added advantage is that experiments conducted in enclosures make keeping record of who observed what, and thus measuring social learning, easier.

If on one hand, these studies have the advantages that come with controlling the experimental set-up, on the other hand, studying wild populations has the advantage of working with the complex ecological and social context in which socially-biased learning actually occurs. Coussi-Korbel & Frigaszy (1995) were amongst the first to point out how the social learning field has been dominated by controlled dyadic studies. They emphasize the need to give due attention to the specific social context in which a particular social animal lives, as this reflects the propensity they have of learning from conspecifics: many social animals live within a structured social context and this context influences their opportunities for social learning.

An aspect that few studies have taken into consideration, and which Coussi-Korbel and Frigaszy (1995) emphasize, is the coordination of behavior between group members as a principle common to all forms of social learning. Behavioural coordination can be described in terms of its occurrence in time and space (Figure 1.1). When a naïve individual learns by interacting with parts of the environment that have been modified by a conspecific, or has its

attention drawn to essential characteristics of the environment because others had previously interacted with it, then, *behavioural coordination in space* is said to be occurring. *Behavioural coordination in time* occurs when individuals are not in close proximity but simultaneously perform a behaviour (e.g. foraging) because it is a certain time of day or the group is in a certain environment where a given resource is available. Behavioural coordination involving physical proximity between conspecifics is restricted to the third dimension of behavioural coordination, *coordination in space and time*, where individuals are in the same space at the same time. Different types of behavioural coordination are posited to support the acquisition of different kinds of information, although all three forms of behavioural coordination can facilitate social learning (Coussi-Korbel & Fragaszy, 1995).

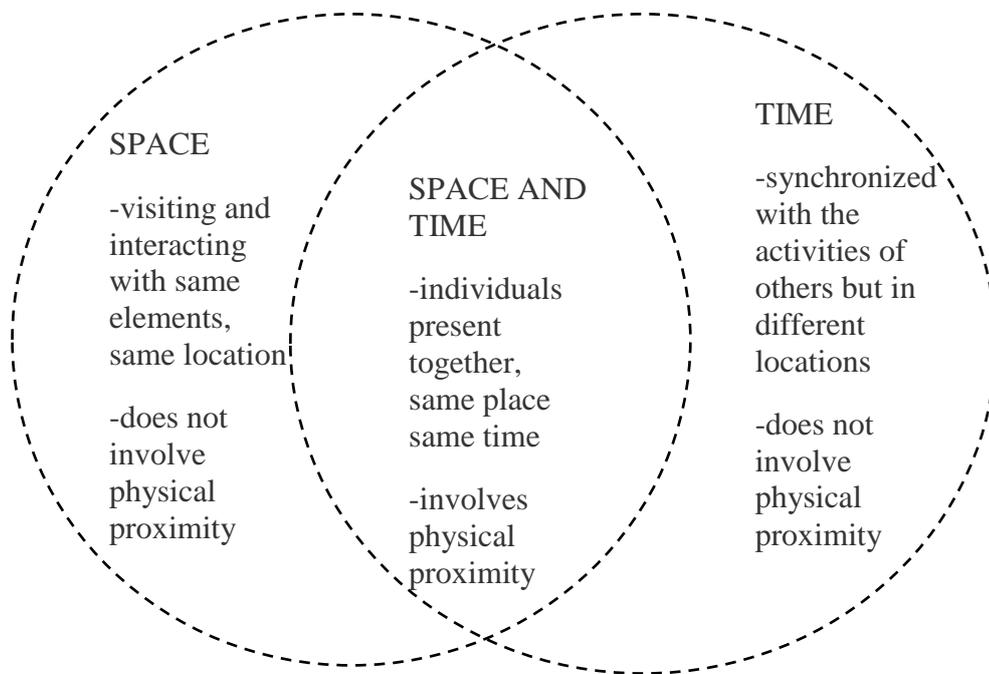


Figure 1.1 Three dimensions of behavioural coordination, in space, in time and in space-time, according to Coussi-Korbel & Fragaszy (1995)

In the first results chapter in this thesis (chapter 3), I use behavioural coordination as a means of describing the opportunities the monkeys have of learning from each other, as a reflection of the structure of relationships present between group members. I mostly focus on behavioural coordination in both time and space as it enables individuals to acquire more specific information (e.g. how to solve a task) by close observation of the activities of others.

As argued previously in the text, observational learning, and likewise behavioural coordination in time-and-space, are not prerequisites for the establishment of behavioural traditions. Similarly, the idea that complex behaviours, such as tool-use, require imitation is also not held. Here I do not equate observational learning to imitation, as no assumptions concerning mechanisms of social learning are made in this thesis. Rather, I consider that through observation, the monkeys can acquire information that, coupled with other forms of social learning, such as learning from interacting with the products of conspecifics, can lead to the dissemination of a novel behavioural trait among members of the social group.

It is important to note, however, that behavioural coordination is not always conducive to social learning. As such, Coussi-Korbel & Fragaszy (1995) further characterize coordination into two types, with very different outcomes:

(i) *isomorphic coordination*, defined as “when one individual’s activities channels the attention of its conspecific(s) to an activity or element in the environment, such that behavioural similarity between the two individuals increases.” (pg. 1443,); typical of model/observer, knowledgeable/naïve relationships.

(ii) *complementary coordination*: when individuals engage in asymmetrical behaviours, such as producer/scrounger or dominant/subordinate relationships, which generally inhibit rather than support the transmission of information.

The dissemination of social information can be actively interrupted by the dynamic between dominant and subordinate individuals. Subordinate individuals might avoid approaching a resource and/or task or solving the task in front of dominant individuals if they are likely to have the resources usurped (Brown & Laland 2002; Kendal et al 2010b). This inhibition to display the behaviour before group members might disrupt its spread via social learning, and makes it difficult for researchers to assess whether the experimental subjects have learned to solve the task. For this reason, many social learning experiments chose the models and observers based on their social position, with models usually being slightly more dominant than observers (Drea & Wallen, 1999; Hopper et al, 2013; Kendal et al, 2015), enough to ensure that the model will have the opportunity to demonstrate the new behaviour sufficiently and that observers will pay attention to demonstrations.

Classifying behaviours into isomorphic and complementary coordination, however, might not be this straightforward. The literature shows, for example, that producer/scrounger

relationships do not always inhibit social learning, quite the contrary (e.g. Caldwell & Whiten 2003, Coelho et al 2015). Furthermore, scrounging is better considered in light of a dynamic trade-off in a scrounger-producer frequency-dependent game (Koops & Giraldeau, 1996, Barta & Giraldeau, 1998). Likewise, behavioural coordination involving socio-positive relationships such as grooming might be thought of as always contributing to social learning, however, dominance effects, such as ‘groom up the hierarchy’ (Tiddi et al, 2012) might affect the social learning context negatively.

In elaborating on the relations between social dynamics and social learning, in the same article, Coussi-Korbel & Frigaszy (1995) make predictions regarding how different social systems in different species may influence the diffusion of behaviour. According to the model presented, in some types of societies a greater directionality in the dissemination of information within the group would be expected. The authors predict that, in more egalitarian societies, the even distribution of aggression and affiliation between dyads would result in an even transmission of socially acquired information between members of a group. The similar proximity between individuals would result in the predominance of *non-specific social learning*, that is, independent of the identity of the models and observers. Consistent with this, Day et al (2003) did not detect any consistent order of dissemination of information within groups of Callitrichid monkeys (egalitarian species) based on either the identity of individuals nor classes of individuals. Finally, *non-specific social learning* is also predicted to generate behavioural homogeneity within groups and allow information to spread rapidly through the entire group.

In contrast, in more despotic societies the high degree of asymmetry in relationships, in terms of both aggression and frequency of affiliative interaction, would make non-specific social learning unlikely. This is because social constraints ensure only certain dyads frequently tolerate each other’s proximity. Consequently, socially acquired information would not spread evenly in time or extent through the social group, but would flow through subsections of the group, as a function of the identity (e.g. age, sex, social status) of the knowledgeable individual, resulting in *directed social learning*. Such *directed social learning* would likely result in within group variation of behaviour characterised by a relatively slow and uneven spread of information through the group (Coussi-Korbel & Frigaszy, 1995).

Capuchin monkeys, present an example of intermediate societies given that they have dominance hierarchies that are non-linear and aggression is distributed asymmetrically between the dyads; concurrently there is plenty of tolerance among other dyads (Ferreira et al, 2006; Izar et al, 2006; Izar et al, 2012). Coussi-Korbel and Frigaszy (1995) suggest that

where a species is intermediate on the egalitarian-despotic spectrum, specific behavioural skills (which would require more accurate observation) will spread according to the identity of the individual involved (*directed social learning*). Other types of information, however, that do not require a high degree of behavioural coordination, could spread through social learning independent of the identity of individuals (*non-specific social learning*).

Social networks analysis (SNA) has immense potential to enrich studies of the social animals by allowing us to integrate social relationships at the dyadic level in to a group-level representation of the social structure (Sih, et al, 2009; Krause et al, 2009; Sueur et al, 2011). Thus, SNA can be an important tool for furthering our understanding of social structure, cooperation, dominance hierarchy, social learning and dynamic aspects of social structure, to list a few (Krause, et al 2009; Sih, et al 2009). A more detailed description of SNA can be found in the first results chapter of this thesis (chapter 3) where I draw on established social network metrics to describe the opportunities the capuchin monkeys have of learning from each other, within the framework of behavioural coordination and directed social learning put forth by Coussi-Korbel and Fragaszy (1995).

Identifying social learning in the wild

In a special issue of Learning and Behaviour (Kendal et al., 2010) several authors came together to discuss how to study social learning in wild groups of non-human animals. Kendal et al (2010a) describe how methods for identify social learning fall along a continuum between studies in captivity with controlled dyadic set-ups on one side, and natural open diffusion in wild groups on the other side. At one end of the spectrum, studies have enough control and provide a good understanding of social learning processes, but relatively little ecological validity. In contrast, at the other end of the spectrum studies will have high ecological and social validity, but little power to identify the processes underlying the spread of behaviour. Kendal et al (2010) produce a review of the methods used to date for studying social learning, and the implication the different experimental set-ups have on the results they present; thus this paper proves to be an important guide helping researchers to navigate among the growing range of methods available for studying social learning in natural contexts. Here, once more, open diffusion experiments are recommended because these allow us to factor in physical and social aspects of the natural environment in which learning occurs. In the same special edition, Lonsdorf and Bonnie (2010) point out the need to incorporate ontogenetic aspects to studies of social learning and thus take into consideration

the trajectory of acquisition of complex behaviours, such as tool-use, by young individuals in wild primate groups. They conclude by stating that greater attention should be given to social factors, such as the different social systems of primates, so as to better evaluate the dynamics in model-observers relationships.

The use of experimental approaches, such as two-action task experiment, with wild primates is very recent, few have been the studies to adopt this approach: vervet monkeys (van de Waal et al, 2010) and lemurs (Kendal et al, 2010b; Schnoell & Fichtel, 2012). I shall present these studies in greater detail in the general discussion (chapter 6), when I relate my findings to the findings of these studies. The main scientific challenge that these studies - and my doctorate research – face, is how to identify social learning based on data collected from the apparent diffusion of a new behaviour in a naturalistic context. New data analysis methodologies (Franz & Nunn, 2009; Hoppitt & Laland, 2011; Kendal et al, 2009) have been developed to help researchers identify biases in social learning in the wild. Below, I present some of these methodologies, giving some information on why they were developed and the logic on which they operate. Further details on these analytical methodologies can be found in chapter 4 where I address them more specifically with regards to my data.

Data analysis methodologies for studying the diffusion of novel behaviours

Diffusion curve analysis is a mathematical approach commonly applied in studies of human traditions and present in theoretical studies of social learning in animals (see Reader, 2004 for a review). According to this approach, one can distinguish between social and asocial learning curves based on the shape of the learning curve. The probability that a naïve individual will adopt the group typical behaviour occurs as a function between the number of naïve individuals and the number of experienced individuals in the group. Thus, typically, social learning would generate sigmoidal curves, S format, while asocial learning (i.e. learning independent from the social context) would describe a curve in the R format.

Empirical studies and theoretical modelling have recently criticized diffusion curve analysis, by showing that when aspects of the social contexts, or of the complex conditions in which a new behaviour is acquired, are taken into consideration, the assumptions of curve format are not sustained. Hoppitt et al (2010), for example, alert researchers to false positives (S curves resulting from asocial learning) and false negatives (R curves that result from social learning), that can result from how the social context is characterised (i.e. learning opportunities based on relationships) or based on the structure of the task and the phases present in acquiring a new behavioural trait. Laland & Kendal (2003) warn researchers that,

given the rarity of documenting the onset (innovation) of a new behavioural trait and its initial spread, sometimes researchers might describe, from their data, learning curves that appear to be slowing down (R format), when in fact they are describing the spread in its final stage only - a false negative of social learning.

In a meta-analysis of food innovations in primates, Lefebvre (1995) concluded that in general there was a tendency to confirm that these behaviours were acquired by cultural diffusion based on accelerated learning curves; he points out, however, that scrounging can have the effect of slowing the learning curve down (a false negative). Lefebvre also shows that if the individual learning latencies present a normal distribution, then even the acquisition of behaviour via "trial and error" (i.e. without social bias) could, at the population level, describe a broadcast curve in S format (a false positive). Hoppitt et al (2010) also describe cases of false positive identification of social learning by simulating how different social learning mechanisms might affect the diffusion data. They found that, processes such as neophobia and reinforcement by completed sub-steps could result in diffusion curves in an S format even in situations where no social bias in learning was present. An S curve might be described if, at first, less neophobic individuals interact with the task resulting in a rapid increase in the an rate of acquisition and then subsequent slowing down of the diffusion speed as gradually more neophobic individuals come to interact with the task, Similarly, task that require several steps to be learned sequentially could portray and overall different pattern for the rate of diffusion based on the slowing down caused by added steps to the acquisition of the behaviour.

Among the criticism to the diffusion curve analysis, one which is of particular interest - given that the present thesis is mostly concerned with the social context of learning - is the assumption that all individuals have the same probability of interacting with each other. Clearly this assumption of diffusion curve analysis does not match the real context in which most social animals learn. In line with the arguments made previously, it is important that any analysis take into account the complex social context in which a particular animal lives and learns. A recent approach, namely Network-Based Diffusion Analysis (NBDA), solves this problem by incorporating data describing the social context when analysing diffusion patterns. NBDA was developed by Franz & Nunn (2009), and seeks to determine whether the diffusion pattern of a given behaviour is better described by paths of association between individuals in the social network. Further details regarding NBDA can be found in the second results chapter in this thesis (chapter 4).

In the same chapter I describe the behavioural repertoire established in each group once the diffusion of an introduced behaviour (using a novel two-action foraging task) has reached saturation level. Option-bias analysis (OBA) (Kendal et al, 2009) is a statistical methodology developed for identifying social learning based on the group behavioural repertoire (as opposed to those previously described which are based on the rate, or pattern, of diffusion). The main assumption of OBA is that, when social learning is occurring, a greater homogeneity in the variants of a behaviour will be found within each social group. Both NBDA and OBA offer promising means of advancing the field of social learning and will be discussed in further detail in chapter 4, where I present my own findings after having applied the techniques to my data

Tufted capuchin monkeys (*Sapajus sp*): tool-use, socially-biased learning and claims for behavioural traditions

Naturalistic studies with semi-free and wild capuchin monkeys were (and still are) important to the advancement of our understanding of the dynamic social context in which learning occurs, and which is the hard evidence needed to ascertain whether certain behavioural traits constitute behavioural traditions.

Multiple regional differences in the repertoire of tool use by wild capuchin monkeys (*Sapajus spp*) have been described by Ottoni & Izar (2008) and represent candidate behaviours of behavioural traditions in these neotropical primates. The populations of *Sapajus libidinosus* inhabiting the *caatinga* of the Serra da Capivara National Park (SCNP) (the same population studied for this thesis) have the largest "tool-kit" described for capuchin monkeys (Mannu & Ottoni, 2009; Falótico & Ottoni, 2013; Haslam & Falótico, 2015). Capuchin monkeys at SCNP manufacture probes from plant structures (usually branches) which they use to access food or water in holes or crevices. Stones tools are used in more than one motor pattern and to perform various functions, including: (i) as a "hammer" to crack open encapsulated fruit or seed, (ii) as a "hammer" to loosen the soil and as a "hoe" to dig for roots, tubers and arthropods nests, (iii) to break rotten wood (in search of larvae and arthropods), (iv) as an "axe" to crush invertebrates, roots, tubers and cactus, (v) to dislodge other stones trapped in sedimentary conglomerates, (vi) to pulverize quartz, which is then licked, smelled, and/or rubbed on their body (the purpose of this behaviour being unclear: Mannu & Ottoni, 2009) and (vii) as projectiles thrown by females as part of sexual display (Falótico, 2011).

The use of tools in capuchin monkeys was, however, first described in a semi-free population that inhabits the Tiete Ecological Park (Ottoni & Mannu, 2001). A study of the ontogeny of tool-aided nut-cracking behavior (Resende et al, 2008; Resende, 2004) indicated how behaviour patterns develop from: (i) general manipulation of objects by infants (such as striking closed nuts against the substrate or hitting the hammer against the substrate), followed by (ii) inept attempts of associating the stone hammer and the nuts (such as positioning nuts on top of hammers, or rolling hammers over nut), until the final (iii) functional association of the three elements (hammer, anvil and nut) in the necessary temporal and spatial order, thereby obtaining access to nutritious nut endosperm. The whole process resembles that seen in infant chimpanzees (Inoue-Nakamura & Matzusawa, 1997), but with some differences in the difficulty of acquiring different stages of the sequence being learned. Young chimpanzees have greatest difficulty beginning to use stones percussively, which is an unusual action in their foraging repertoire, while young capuchin monkeys exhibit greatest difficulty in learning to position the nut on the anvil, possibly as the result of the risk of losing an object by dropping it; a greater concern for arboreal species such as capuchins (Resende et al, 2008).

Adult capuchin monkeys are extremely tolerant of infants and juveniles, allowing them to observe most activities, including nut-cracking, from a short distance. The young capuchins are also allowed access to nuts and stone tools ("hammers") and scrounging is often tolerated (Coelho 2009). Such tolerance provides social opportunities which can facilitate the learning of naïve individuals, leading to social transmission of tool using behaviour. Ottoni et al (2005) investigated which social factors could be biasing the choice of which monkeys the naïve individuals observed and found no significant correlation with age, social proximity or the hierarchical position of the observation target. A significant relationship, however, was found between the frequency an individual was observed by conspecifics and its proficiency at cracking open nuts. Ottoni et al (2005) hypothesised that a simple mechanism, such as optimizing scrounging opportunities could be mediating the choice of observing the most proficient individuals; this in turn would have the positive feed-back of optimising the possibilities of social transmission of information. A subsequent study (Coelho et al, 2015) sought to investigate this hypothesis further and its results confirmed that the choice of observational targets was an active one: monkeys were not simply observing those who they are socially close to but also monkeys with higher nut-cracking productivity rates, who were tolerant of scroungers; further supporting the scrounging hypothesis. Finally, in this paper transmission biases are described, showing how young capuchin monkeys choose to observe

older, more proficient and dominant individuals during nut-cracking bouts. In the last results chapter of this thesis (chapter 5), I look at possible biases in the transmission of how to solve the two-action task experiment, namely I investigate frequency-dependent and model-based transmission biases.

In this thesis I present findings from field experiments and naturalistic behavioural sampling conducted with two groups of wild bearded capuchin monkeys inhabiting the *caatinga* (dry savannah). I chose this species as it represents an excellent model for studying socially-biased learning. Also, to my knowledge wild groups of this species have not, as of yet, been subjects of studies of diffusion of a new behaviour within the multifaceted social context in which these monkeys live and learn from each other. This is the first study to conduct a two-action task field experiment with wild groups of capuchin monkeys and the first to apply the analytical methods described above, conjointly, for diffusion data from a neotropical primate species.

CHAPTER 2:

METHODS

The main data collection for this research was carried out over 18 months, between January 2012 and July 2013, on two wild groups of bearded capuchin monkeys (*Sapajus libidinosus*) in the Serra da Capivara National Park – Piau , Northeast Brazil. This main part of the research included naturalistic data collection on social relationships and experiments on social learning. Previously, a pilot study had been conducted with a semi-free group and two semi-captive groups of capuchins (*Sapajus sp.*) at Tiete Ecological Park to test the lift-pull task. After the field study with the wild populations, an asocial control experiment with the lift-pull task, was also carried out with captive capuchins (*Sapajus apella*) at the Living Links in Edinburgh Zoo. This chapter comprises details of the study sites, species, sampling methods, experimental implementations and the some of the data analysis. Further details of methods and analysis, which pertain to specific research questions, will be given in each of the subsequent chapters.

2.1 Study species

Capuchin monkeys are a monophyletic clade (Sub-family: Cebinae) of Neotropical primates with a wide range throughout Central and South America and can be found in habitat types varying from dry savannah to tropical forests, mangroves and flooded forests (Lynch et al, 2012). When compared to their sister taxon, *Saimiri*, capuchin monkeys have an increased body size, semi-prehensile tail, a higher encephalisation quotient, increased manual dexterity and food processing skills, a delayed life history and prolonged longevity (Fragaszy et al, 2013).

Although capuchins monkeys comprise a consistent clade, evidence has gathered showing that there are substantial morphological and genetic differences between two subsections of this clade. Thus, recently the 12 species of capuchin monkeys have been placed within two genera, *Cebus* (gracile or non-tufted capuchins) and *Sapajus* (robust or tufted capuchins). *Sapajus* species differ from *Cebus* in that they have several cranial and postcranial characteristics (such as a sagittal crest, shorter mandibles and larger zygomatic arcs) that allow them to exploit tough foods. Also, they have shorter forelimbs and hands

which might be due to a greater partitioning of time between terrestrial and arboreal lifestyles than seen in *Cebus* species (Lynch et al, 2012).

The genus *Sapajus* consists of 8 species (*S. apella*, *S. cay*, *S. flavius*, *S. libidinosus*, *S. macrocephalus*, *S. nigritus*, *S. robustus* and *S. xanthosternos*) and has a range that extends from extreme northern South America to northern Argentina. There are little, or none, sympatric distributions within *Sapajus* with some species limited to specific biomes and others living in a mosaic of biomes. Within the Amazon Rainforest *S. macrocephalus* (western amazon) and *S. apella* (eastern amazon) can be found, while the other tropical forest dwelling capuchin, *S. nigritus*, inhabits the Atlantic Rainforest. *S. cay* is found in central South America and inhabits the Pantanal grasslands and Chaco with seasonally flooded forests. *S. xanthosternos*, *S. robustus* and *S. flavius* inhabit a mixture of what is left of the Atlantic Rainforest in the north-eastern coast of Brazil, secondary forests and on occasions the dry savannahs (Cerrado and Caatinga). Finally, *S. libidinosus* typically inhabits the xeromorphic forests of the Cerrado and Caatinga (dry savannah-like environment), predominantly, with use of gallery forests and enclaves of moist forest in the Caatinga (brejos de altitude) (Fragaszy et al, 2004; Lynch et al, 2012).

Capuchin groups contain multiple males and females with male/female ratios varying between 0.56 and 1.20 (Fragaszy et al, 2004, includes *Cebus* and *Sapajus* genera). According to the literature, groups of *S. libidinosus* comprise 12 - 27 individuals (Fragaszy et al, 2004). However, some studies have reported much larger sized groups, such as in Serra da Capivara (PF) with up to 45 individuals (Falótico, 2011) and a mangrove group in Maranhão with 31 individuals (Cutrim, 2013).

Neotropical primates typically present either dispersion of both sexes or male philopatry with female dispersion (Strier, 1990). Capuchin monkeys, however, counter the norm and are known for displaying female philopatry, with male dispersion at puberty – similar to most old world monkeys. Dominance hierarchies in capuchins are usually described as partial and as occurring among both males and females, with an alpha-male dominant over all other group members. Sexual maturity is reached at approximately age 7 for males and age 4 for females and female mate choice is biased towards the dominant male (Fragaszy et al, 2004).

2.2 Study sites and focal subjects

2.2.1 Serra da Capivara Nacional Park (SCNP)

The Serra da Capivara National Park (SCNP) is located in the state of Piauí, Northeastern Brazil (coordinates: 08°26'50'' to 08°54'23''S and 42°19'47'' to 42°45'51''W). The climate in the SCNP region is characterized by a high annual average temperature (28° C), with a variation of 12° C to 35° C in the coldest month (June) and 22° C to 48 °C during the hottest months (August-November). Rains are generally of short duration and extremely localized. Irregularity of rainfall is one of the main features of this semi-arid region and the vegetation it sustains (the caatinga).

The average annual rainfall is 689 mm (\pm 200 mm); however, this average can vary quite widely from year to year. During this research (2012/2013) the total rainfall was of 109 mm (below the 1932, year of the catastrophic drought, 250.5 mm) (INMET: <http://www.inmet.gov.br/>). Only 7 days of rain fall were registered on field work days with the monkeys. The rains commonly occur between October through mid-April and early May.

At present at least 9 groups of bearded capuchin monkeys (Jurubeba, Pedra Furada, Bocão, Gato, Baixa Grande, Desfiladeiro, Serra Vermelha, Cerâmica, Casinha da Jurubeba) are known to live within the National Park. Two of these groups have been the focus of previous studies: Jurubeba (JB) (Mannu & Ottoni 2009) and Pedra Furada (PF) (Falotico 2011; Cardoso 2014). The present study involved these two previously studied and non-sympatric groups (Figure 2.1).

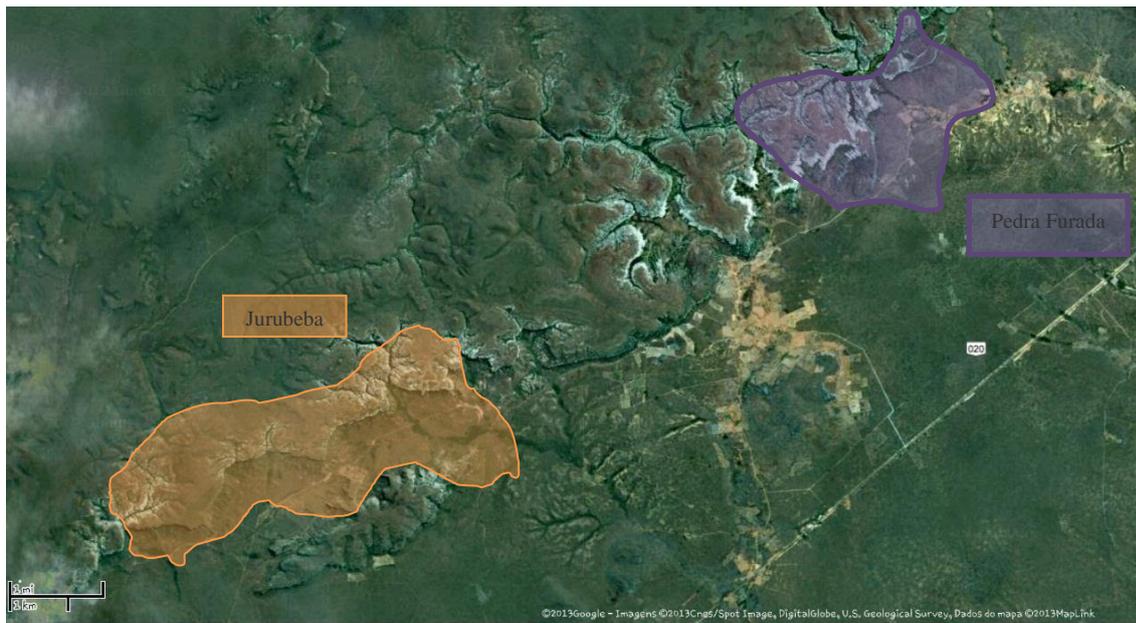


Figure 2.1 – Schematic representation of home ranges for Jurubeba (orange) and Pedra Furada (purple) in the Serra da Capivara National Park.

Jurubeba

The Jurubeba group (JB) was had been habituated in 2004 by M. Mannu, (Mannu & Ottoni, 2009) and hadn't been consistently followed by researchers in the five years prior to the present study. Therefore as of January 2012 we began re-habituating this group, a process that involved offering bananas in the same location every morning. When the monkeys showed up to eat the bananas, we would follow them, trying to get as close as possible to the group and remaining in their presence for as long as possible. The habituation process occurred from January to April 2012, with the invaluable help of F. Reinaldo (field assistant). During this period, locating the monkeys became easier and the duration of time spent with the group gradually increased. Besides the habituation of monkeys to our presence, this increase in observation time was also due to increased knowledge of the natural routes used by this group, allowing prediction of where the monkeys would descend, following their ascent over the largely inaccessible hilltop (serra). In total, the period of habituation and identification of the JB group members took 79 days of fieldwork (55 of which we had contact with the monkeys), totalling an effort of approximately 330 hours.

From May to December 2012 behavioural data were collected with Jurubeba group, on a total of 97 days, involving 451 hours of contact with the group. During the data collection period, the JB group included 51 individuals: 14 adult females, 7 adult males, 7 sub-adult males, 12 juveniles (5 females, 7 males) and 11 infants. Eight of the 11 infants had been born

before the start of data collection (mostly during the habituation period) and three were born in the first two months of data collection (Table 2.1); no deaths or disappearances occurred during this study.

Pedra Furada

There was no need to habituate the Pedra Furada (PF) group since it had been recently studied by R. Cardoso (March to September 2012) and T. Falotico (September 2007 to July 2009). Over the months of January and February 2013, I learnt to identify the Pedra Furada monkeys individually (40.5 hours of fieldwork).

Between February and July 2013 behavioural data were collected with the Pedra Furada group; this involved 69 days of fieldwork and a total of 227 hours of contact with the group. Throughout this period the PF group consisted of 35 individuals: 11 adult females, 7 adult males, no sub-adult males (the three sub-adult males – Cara Preta, Curisco and Blip – present during R. Cardoso's study, the year before, left the group in January and February), 12 juveniles (5 females and 7 males) and 5 infants (Table 2.2).

Table 2.1 Composition of Jurubeba group inhabiting Serra da Capivara National Park. ¥ Dominant male. Date of birth displayed to the infant's name.

AGE GROUP	SEX	NAME	ABBREVIATION	
JURUBEBA N = 51	FEMALE	Acácia	ACA	
		Bianca	BIA	
		Chica	CHI	
		Clarinha	CLA	
		Cristal	CRI	
		Descabelada	DES	
		Gadu	GAD	
		Jane	JAN	
		Noni	NON	
		Maissa	MAI	
		Paçoca	PAC	
		Perninha	PER	
		Sandra	SAN	
		Topetuda	TOP	
ADULT N = 14	MALE	Barba	BAR	
		Bolinha ¥	BOL	
		Elvis	ELV	
		Loirão	LOI	
		Panaca	PAN	
		Penteado	PEN	
		Tirinha	TIR	
SUB-ADULT N = 7	MALE	Cadu	CAD	
		Choquito	CHQ	
		Conde	COD	
		Curioso	CUR	
		Dunga	DUN	
		Mickey	MIC	
		Pelé	PEL	
JUVENILE N = 12	FEMALE	Dado	DAD	
		Costelo	COS	
		Galego	GAL	
		Rose	ROS	
		Olivia	OLI	
	MALE	Boca	BOC	
		Careca	CAR	
		Mini	MIN	
		Orelhudo	ORE	
		Punk	PUN	
INFANT N = 11		Queixinho	QUE	MOTHER
		Skinny	SKI	Bianca
		Biju (05/03/12)	BIJ	Chica
		Chocolate (28/03/12)	CHO	Clarinha
		Cleo (12/04/12)	CLE	Cristal
		Croatá	CRO	Descabelada
		Didi	DID	Gadu
		Giba	GIB	Jota
		Jota	JOT	Maissa
		Manu	MAN	Noni
		Ney	NEY	Sandra
		Saquê	SAQ	Topetuda
		Tomate	TOM	

Table 2.2 – Composition of Pedra Furada group inhabiting Serra da Capivara National Park.
 ¥ Dominant male. Date of birth displayed to the infant’s name.

	AGE GROUP	SEX	NAME	ABBREVIATION			
PEDRA FURADA	N = 35	FEMALE	Alice	Ali			
			Benne	Bnn			
			Canela	Can			
			Encrenqueira	Enq			
			Gorda	Gor			
			Lica	Lic			
			Maçã	Mac			
			Moça	Moc			
			Ninfa	Nif			
			Romã	Rom			
			Vesga	Ves			
ADULT	N = 11	MALE	Assustado	Ass			
			Beißola	Bei			
			Clandestino	Cla			
			Nico	Nic			
			Roger	Rog			
			Torto ¥	Tor			
			Zandor	Zan			
			ADULT	N = 17	FEMALE	Batman	Bat
						Halo	Hal
						Juv6	Juv6
						Narinas	Nar
Juv8	Juv8						
Capacete	Cap						
ADULT	N = 12	MALE				Descabelado	Des
						Limão	Lim
						Padre	Pad
						Voluntário	Vol
						Mala	Mal
			Mola	Mol			
			JUVENILE	N = 5	FEMALE		MOTHER
							Moça
							Lica
							Alice
							Romã
	Ninfa						
INFANT	N = 5	MALE	Mona	Mon			
			Lambido	Lam			
			Andre/a	And			
			Ross/a (22/02/13)	Rss			
			Nambu (28/02/13)	Nam			

2.2.2 Tiete Ecological Park (TEP)

The pilot study, to test the lift-pull task, was run with three groups living in the Tiete Ecological Park, on the outskirts of Sao Paulo city. The main group, studied since 1992, lives in a semi-free condition, in a reforested area of 180,000 square meters with restricted access to the public. At the time of our study the main group consisted of 45 individually recognizable monkeys: 13 adult females, 5 adult males, 1 sub-adult male, 9 juveniles (3

females and 6 males) and 17 infants. The other two groups (Island 1: N=14) and (Island 2: N=17) used for the pilot study were semi-captive groups that lived on isolated fluvial islands. The monkeys at PET were all brought in from illegal trafficking, private owners, circuses and zoos or were born in the park. Consequently, each of the groups consisted of several capuchin species, including some hybrid individuals.

2.2.3 Edinburgh Zoo - Living Links

Edinburgh Zoo houses two mixed-species groups of brown capuchins (*Sapajus apella*) and common squirrel monkeys (*Saimiri sciureus*) in a facility designed, both for public viewing and as a research centre. The enclosures consists of an outdoor and an indoor area, plus a set of testing cubicles where individuals can voluntarily take part in behavioural and cognitive experiments (see Leonardi et al. 2010 for further details).

The testing cubicles were set up such that the monkeys could be isolated and then presented individually with the lift-pull task; thus providing the asocial controls required. Capuchin monkeys from both the East (N = 15) and the West (N = 14) groups were tested individually with the lift-pull task (Table 2.3).

Table 2.3 – Composition of captive capuchins of the East and West groups at the Living Links – Edinburgh Zoo - Scotland.

	Name	Sex	D.O.B		Name	Sex	D.O.B
EAST	Popeye	M	07/08/2001	WEST	Diego	M	22/07/2002
	Junon	F	22/06/2000		Lana	F	02/10/1995
	Kato	M	~ 08-05		Santiago	F	08/01/2002
	Carlos	M	22/07/2006		Sylvania	F	17/08/2003
	Anita	F	14/11/1997		Toka	M	29/12/2004
	Manuel	M	13/01/2004		Figo	M	01/06/2006
	Penelope	F	20/11/2005		Pedra	F	16/02/2008
	Chico	M	25/04/2009		Mekoe	M	23/04/2008
	Rosa	F	20/05/2010		Inti	M	07/09/2009
	Ruben	M	17/06/2010		Rufo	M	21/10/2009
	Sol	F	29/07/2010		Ximo	M	02/04/2010
	Flojo	M	19/06/2011		Torres	M	08/01/2011
	Lindo	F	11/07/2011		Luna	F	02/05/2011
	Willow	F	26/09/2012		Alba	F	18/09/2011
	Nena	F	30/12/2012				

2.3 Experiments

2.3.1 Lift-pull task

Pilot study and final version of apparatus

The pilot study carried out at Tietê Ecological Park had three main objectives: (i) test the materials used to see if the task was sturdy enough to resist the monkeys' destructive behaviours; (ii) evaluate whether there would be some form of monopolisation of the task by certain individuals, such that an individual might naturally become a model for the group; and (iii) test whether the two task solutions, or options, were feasible for the monkeys and of similar difficulty.

Based on the pilot study important modifications to the original two-action task apparatus was made. First, I was able to test the sturdiness of the task and adopt harder acrylic material as the monkeys would otherwise crack open the apparatus using stone tools. A food dispensing mechanism was also added so that a discrete reward was given each time the task was successfully solved. The latter modification guaranteeing that the monkeys would have to repeat the action again and again to be rewarded, not simply hold the door open and empty the box as the first configuration of the apparatus allowed.

The final apparatus for the two-action task consisted of an opaque acrylic box 20 x 30 x 20 cm. Named lift-pull task, after the actions necessary to solve it successfully: the two functional parts of the task were a blue rectangular plate (10 x 8 cm), hinged on the top side, that could be lifted perpendicular to the front of the box, and a green knob (7 x 5 cm) at the end of a protruding stick, that could be pulled away from the front of the box (Figure 2.2). For further details on the lift-pull apparatus, refer to section 4.2.2.

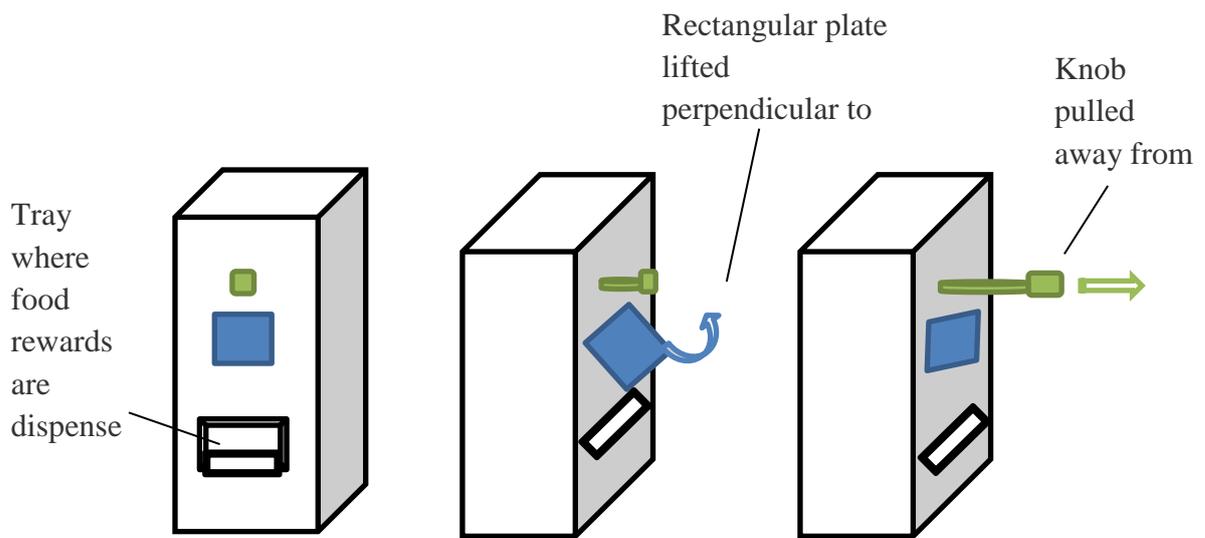


Figure 2.2 Diagram of the lift-pull task: (A) frontal view, (B) side view of lift option to solve the task and (C) side view of pull option to solve the task.

Concerning the monopolisation of the task, the pilot test results were ambiguous. If there was certainty that dominant individuals would initially monopolise the task, one of the two options for solving the task in each of the groups, could be locked; thus introducing one alternative in each group. Such a procedure was done in a similar study with lemurs (Kendal et al 2010). However, during the pilot study, the three groups (one semi-free and two semi-captive) behaved very differently. Capuchins from the main group (semi-free), accustomed to experimental interventions, did not hesitate to touch the task. Manipulating the apparatus in different ways, they also attempted to break open the apparatus using stone tools. Two adult males (Dav and Sus) were the first to approach the task and manipulate it without, however, succeeding in solving it; soon after they gave up. Next, the females and juveniles, who had been observing from a distance, were able to approach the task. Soon after they had access to the task a dominant female (Cis) solved it successfully. At no moment, in the main group, did an individual actually monopolise the apparatus, as there were always other monkeys, mostly juveniles, who would access, and manipulate, the task intermittently. Markedly different to this scenario, on Island-1 the dominant male was the first to have access to the task and he monopolised it throughout the entire experiment. The dominant male finally solved the task and it is possible that, given more time, other group members could have had accessed the apparatus too. Finally, adults on Island-2 were not interested in the lift-pull task at all. Only juveniles approached the task and kept manipulating the task until they finally solved it.

Given these ambiguous results, it was hard to predict what would happen when I conducted the experiment with the wild groups; however monopolisation of the task seemed to be unlikely. Individuals from all three groups were able to solve the task. Both alternatives had the same salience, evaluated by counting *touch square plate* or *touch knob*. The action *lift* (the square plate) was the predominant solution by the main group, possibly due to the group's previous experiences with other apparatus and cages.

Seeding options in an open diffusion approach

With the intention of seeding, one of the two options of solving the lift-pull task correctly in each group, an attempt was made to train one monkey in each group as demonstrators of the options: a demonstrator of *lift* in Jurubeba and one of *pull* in Pedra Furada. Here I report on the process of seeding task options in an open-diffusion approach with the wild groups JB and PF.

In the first group, JB, I was able to lure an adult female, CHI, of intermediate hierarchical position, away from the group. CHI was chosen because she customarily displayed little neophobia, for example, often coming close to and touching the researchers and their equipment or opening the car door. Four captive capuchins were reintroduced into the wild in the region inhabited by the JB group. It is thought that CHI might be one of these monkeys, hence her lack of neophobia.

Over one session - only opportunity I had of temporarily isolating CHI from the group - I performed the action *lift* successfully producing a reward four times. CHI observed my actions on the box attentively all four times and vocalised food upon seeing the reward; she then approached the apparatus and ate the rewards. Before she could manipulate the apparatus herself other monkeys, who had not been within view of the task when I was demonstrating it to CHI, approached the task and the training session had to be terminated. As this was done before CHI could attempt to solve the task we could not know if she had learnt to solve the task correctly. To further the possibility of seeding the option *lift* in JB, I opted for presenting the task to the entire group, initially with only the *lift* option rewarding.

On the first day the task was presented to the entire group with only the *lift* option rewarding, four monkeys interacted with the box before CHI had access to it again. These were two juveniles (ORE and MIN) and two infants (CRO and SAQ). Most of their interactions with the task involved inspecting (looking, sniffing or touching) parts of the box that were not relevant for it to be solved correctly. All four monkeys manipulated the green knob at some point, though they did not perform the action needed to obtain the reward (pull

the knob away from the front of the box); none of them manipulated the blue plate in any way.

The first time CHI approach the task after her “training session”, she briefly inspected it (looking around the back of the task and then sniffing the blue plate). She then solved the task successfully for the first time using the *lift* action on the blue plate, the same action she had seen me demonstrate previously. CHI solved the task 14 times using the option *lift* before being displaced from the task by another monkey. A demonstrator of the action *lift* to solve the task had been successfully seeded in the Jurubeba group.

In the second group, Pedra Furada, it was hard to lure an individual away from the group, as any attempt to do so, led to several monkeys following. PF group inhabit an area frequently visited by tourists and hence the monkeys are more aware of human activities. As I was unable to isolate an individual, I decided to present the lift-pull task to the entire group, initially with only the option *pull* rewarding. After two hours had passed since the task had been offered to the monkeys, the group started leaving the designated experimental area, without having solved the task successfully. As often happened, a few subordinate sub-adult and juvenile males would stay behind for a short time, before moving on with the group. On these occasions, LIM, a juvenile male, stayed behind. Having ascertained that no other monkey was within view of the task, I demonstrated the action *pull* once. Lim was looking attentively at the task as I demonstrated the action and, having seen the food reward, he approached the box. Immediately after my demonstration, Lim solved the task successfully using the *pull* action on the green knob. Lim then solved the task eleven times using the action *pull* before he then left to follow the group; no other individuals saw these demonstrations; I note that LIM, being relatively low in the social hierarchy and a juvenile, was not an ideal choice as a model, although it is representative of the normal pattern of juveniles as the source of innovations. Before this “training” session, some individuals had inspected and/or interacted with the task but only the interactions of two individuals involved manipulations of the functional elements (i.e. green knob and blue plate) of the task. Lim had once manipulated the blue plate and once the green knob however in both cases he did not perform the necessary actions to solve the task. Another juvenile male, Des, had manipulated the blue plate, also without performing the necessary action to obtain the reward.

Training demonstrators in the wild proved to be a difficult endeavour. Although I now had one monkey in each group solving the lift-pull task, each with one of the two options, there was no means to ascertaining that they had learnt and would perform the ‘trained’ variant to standards required for the behaviour to be seeded in the group. To further the goal

of seeding one option in each group, I continued to present the task in an open-diffusion set-up but with only the appropriate option functioning (*lift* for JB and *pull* for PF) and the alternative locked. This experimental setup was maintained until approximately 10% of each group (five subjects in JB; three subjects in PF) had solved the task at least once using the model-trained action. Such was achieved after the first day for JB and the second day for PF. The open diffusion phase then began with the lift-pull task being presented with both options functioning for each group.

Open diffusion

The choice of location where the lift-pull task experiment would be conducted was based on (i) frequency of visits by the monkey groups, (ii) visibility (more open undergrowth) and the (iii) accessibility of the site to the researchers (as it needed to be reached carrying the apparatus, camcorders and food rewards). Accordingly, the experiments were conducted in the vicinity of the troughs, where the monkeys often come to eat corn - placed there by the park staff as part of the management of the peccary (*Tayassu tajacu*) population. In these areas, the monkeys are accustomed to spending time on the ground, and also, to the presence of humans and new objects. See Figures 2.3 and 2.4 for the home range and location of the experimental set-up, for JB and PF groups respectively.

The two-action apparatus was fixed to a tree trunk at ground level. Its front initially covered with a basket by a field assistant (Reinaldo F.) until I could position myself next to the camcorders, approximately 10 meters away. Once the basket was removed, the experiment began (Figure 2.5). Whenever the apparatus had to be refilled with food or adjusted in anyway, it would be covered by the basket so that the researcher could check its operation without risk of demonstrating the task solution to the monkeys.

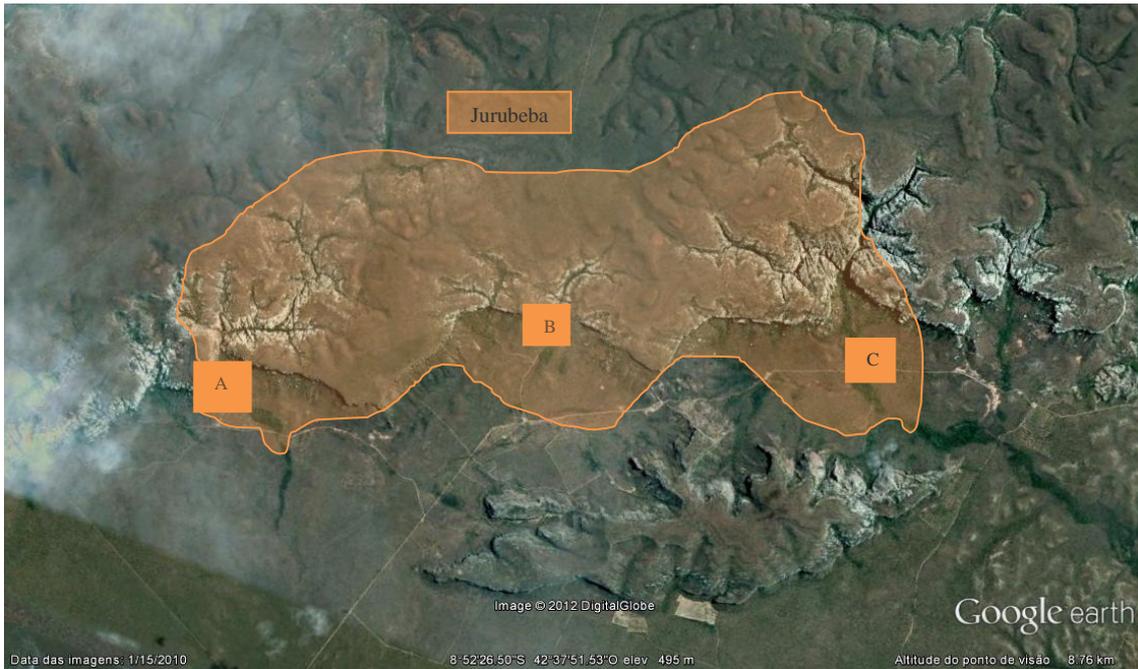


Figure 2.3 Schematic representation of home range for Jurubeba group and the locations where the experiments were conducted. (A) Boqueirão da Baixa Grande, (B) Boqueirão dos Oitenta and (C) Boqueirão do Gato (near Casinha do Isaias).

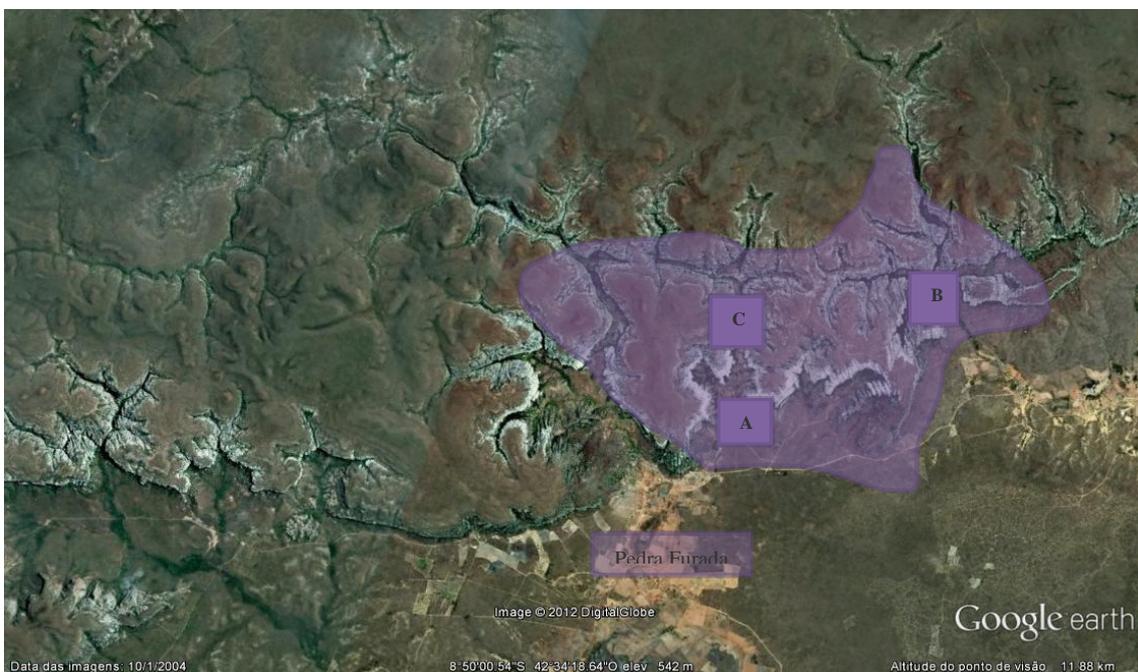


Figure 2.4 Schematic representation of home range for Pedra Furada group and the locations where the experiments were conducted. (A) Sítio do Carlindo, (B) Baixão da Esperança and (C) near cashew trees at the end of the Boqueirão da Pedra Furada.



Figure 2.5 (A) close up on the lift-pull apparatus and (B) the experimental set-up at the Boqueirão dos Oitenta.

For further methodological information on how the open diffusion lift-pull task experiment was conducted, how data was recorded and coded from video refer to section 4.2.2 *Lift-pull task – open-diffusion with trained demonstrators*.

Asocial control – lift-pull task

Asocial control experiments were conducted by applying a replica of the lift-pull experiment, only now with individually isolated capuchin monkeys at the Living Links in Edinburgh zoo. The asocial control data collected give us means to (i) assess how likely it is for the monkeys to individually discover the solution to the lift-pull task and (ii) assess the likelihood of the task being solved using *lift* or using *pull* in the absence of social influences. The latter information can be input in the option-bias analysis), allowing for a test of the power of the analysis (see section 2.5.2. For the methodology on how the asocial experiment was conducted refer to section 4.2.2 *Lift-Pull task - asocial control*.

2.3.2 Tube task

A second problem-solving experiment was conducted with the wild groups (JB and PF). Unlike the lift-pull task which involved introduction of new behaviours, the tube task required the monkeys to applied behaviours customarily used to solve similar problems in their daily activities, now in a new context. Capuchin monkeys at PNSC have been seen

using different techniques (e.g. hand-dipping, tail-dipping and others) to reach water from holes in trees, crevices in rocks amongst others, out-of-reach substrates. We therefore expected them to apply the same behaviours when solving the tube task. The field experiment, however, allowed us to (i) record more instances of such behaviours and (ii) register a greater number of individuals solving this problem, were naturalistic observations might take years to so.

In this experiment, acrylic tubes containing fresh mango pulp (100g per tube) at the bottom- just beyond the reach of an adult male’s arms - were offered to the monkeys of both wild groups and techniques/behaviours used to solve the task successfully (i.e. reach the juice) were registered. For the methodology on how the tube task experiment was conducted refer to section 4.2.2 *Tube task – open diffusion*.

2.3.3 Novel objects

The final experimental intervention to be conducted with the wild groups (JB and PF) was to present the monkeys with novel objects in order to verify whether certain individuals, or classes of individuals, exhibited less neophobia. Data from this experiment was used to inform the Network-based diffusion analysis whether the order of individuals interacting with the lift-pull task and tube-task could be explained simply by neophobia. Each group was presented with three novel objects: a fluffy toy, a football and a sink plunger in a randomised order (Table 2.4) (Figure 2.6). For further details on the methodology of novel object introduction refer to section 4.2.2 *Novel objects – measuring neophobia*.

Table 2.4 Novel objects and order of presentation to each group

Order objects were presented	Pedra Furada	Jurubeba
1 ST	Football	Fluffy toy
2 ND	Fluffy toy	Football
3 RD	Sink plunger	Sink plunger



Figure 2.6 Novel objects and individuals interacting with these objects. (A) Juvenile male (Lim) rolls the ball around, (B) adult female (Gor) pushes the sink plunger over and (C) adult female (Moc) approaching fluffy toy, later she pokes the toys eyes.

2.4 Social context data collection

2.4.1 Behavioural data sampling

With the intent of studying the social context within which wild capuchin monkeys learn, extensive social data was collected by means of Focal, Scan and All Occurrence sampling. Focal samples were 5 minutes-long and at every 60 seconds, I recorded (i) the activity of the focal animal and (ii) any interactions with conspecifics (both affiliative and agonistic) (see Table 2.5 for details). During the Focal sampling I also registered if the focal animal was observing a conspecific (be its engaging in tool-use, foraging, or a social interaction) or looking around, as if for group vigilance (Table 2.5). Furthermore, in order to describe the patterns of association between group members, once every 60 seconds a scan was conducted, recording which other group members were, within a one-meter radius of the focal subject, and those within a ten-minute radius of s/he. Finally, in order to determine behavioural coordination, I noted when the behaviour of the individual(s) within 1 meter of the focal subject matched his/her behaviour.

The order of the individuals to be followed for the Focal sampling was determined semi-randomly. This was done because of the often costly effort to locate an individual among large groups (JB: N=51 and PF: N=35). To determine the sequence of individuals to be sampled, a list of all individuals in the group was generated at random (lottery). At the beginning of each data collection day, the first monkey encountered, of the first five individuals on the list, was sampled. The "sampling window" would then move down and, the first monkey located amongst the next top five individuals listed, was sampled. This procedure was repeated until the entire group had been sampled, and then a new list was created by randomizing all group members again. Focal samples were discarded if focal subject was out of sight for more than 2 minutes.

The Focal method was used as a means of standardizing the observation time between group subjects; allowing for comparisons of the frequency of social interactions. This method also reduces biases that may arise from some monkeys being more accustomed or more conspicuous to the researcher. However, as social interactions - the object of our interest - represent a restricted part of the monkeys' daily activities (approximately 17% of the sampling time - Falotico, 2011) I also conducted All Occurrences sampling of grooming,

social play, co-feeding and agonistic behaviours (Table 2.5). Also, where possible, we recorded ad libitum data on mating and parental care.

Table 2.5 - Description of behaviours displayed by the capuchin monkeys examined in this study and how these were recorded and categorised for analysis.

Activities	
Moving	To be rapidly moving from one location to another.
Resting	To be still, whether standing, sitting or lying, asleep or awake
Foraging	Searching for and/or processing food items. E.g. sifting through dry leaves, breaking branches, digging with their hands and opening fruits without the use of tools.
Feeding	Taking food items to the mouth. Whenever possible the food item being consumed is described.
Tool-use	Any use of stones or wooden sticks as tools. Includes stone for digging up tubers or underground spider borrows, stone to crack open hard/encapsulated food items, stone for breaking dry wood and sticks as probes to access food or push lizards out of crevices. Also includes stone-throwing by females when displaying proceptivity.
Directed attention and observation of conspecifics	
Observing conspecific	Whenever the focal animal was looking towards (head oriented towards) a conspecific(s). We also recorded what they observed: e.g. tools being used, agonistic interactions, food processing.
Affiliative social interactions	
Co-feeding	Coded during Focal follows and All occurrences sampling when individuals were eating and/or drinking while within a meter of each other. A new all occurrence of co-feeding bout was recorded whenever there was a pause of at least 5 minutes following the preceding co-feeding event.
Grooming	When individuals cleaned or straighten a conspecifics' fur using hands or mouth, Coded during Focal follows and All Occurrences sampling. A new grooming bout was recorded whenever there was a pause of at least 5 minutes following the preceding grooming behaviour. A new bout was also considered when groomer and groomed exchanged roles.
Play	Interactions that involved 'races', chasing each other, fighting while displaying relaxed playful facial expressions (loose smile - Fragaszy et al 20014). When possible the types of play were categorised, such as: catch, play fighting, play fighting whilst hanging up-side-down in the vegetation, running roundabout the tree and putting whole fists in playmate's mouth.

Association and subgrouping	
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Proximity	<p>During focal follows the identity of individual(s) within a meter and of individual(s) up to 10 meters from the focal animal, was recorded. Proximity was considered a measure of both association and tolerance depending on the activity in which individuals were involved.</p> <p><i>Proximity as a measure of association:</i> consists of being within 1 meter distance from, the focal animal while it is resting, foraging or socializing. As moving individuals may have little control over who they are close to (e.g., narrow passages and crossings between canopy of the tree or climbing in the mountains), we excluded these focal points from the analysis.</p> <p><i>Proximity as a measure of tolerance:</i> Events in which the focal animal and/or the individual(s) within one meter of each other were eating (i.e. co-feeding events).</p>
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Agonistic displays	
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Threaten	Show teeth, raise hair tuft and adopt typical threat posture (tail raised over head). May include a small movement (lunge) toward the monkey being threatened, which in turn can manifest a submissive grin or move away, but without being chased.
Chasing	The individual being threatened retreats or shows facial expressions and vocalizations of submission, but is still continually harassed and threatened while on the move. Involves quick movements with full body movement by both parties: the threatening and threatened.
Physical assault	Physical contact, in which a monkey pushes, hits or bites a conspecific. The types of aggression as well as injuries incurred were noted.

Gestures of submission and reactions	
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Move away	When threatened and/or chased the target of the agonistic interaction moves away from the threatening individual.
Submissive grin	Facial expression with retracted lips usually produced in response to a threat.
Scream or cry	High-pitched vocalization usually issued in response to a threat and that may, or may not, elicit response from coalition conspecifics.

2.4.2 Social networks

Association networks

Based on the focal scan data I calculated simple ratio association indexes between dyads using SOCPROG (Whitehead, 2009). Simple ratio association indices estimate the proportion of instantaneous points in which individuals were seen together, varying between zero (dyads were never seen together) and one (dyad was always seen together). For each group, association indices were calculated and then used to construct association networks. Entries into the matrix represent the association index between dyads, thus generating undirected (or symmetrical) networks. Three association networks were constructed: *proximity between individuals within a 10 meter radius*, *proximity between individuals within a 1 meter radius* and *co-feeding* (a subset of social proximity when the individuals were consuming food items while within a 1 meter radius of each other). These three levels of social proximity were chosen to portray associations between individuals in three contexts, each requiring a greater degree of tolerance and thus relevant to the question of non-specific or directed social learning. All group members were expected to come within 10 meters of each other at some point in time. So, at this distance, the network represents group membership. Restricting the network to associations within a 1m radius is expected to represent a stronger level of tolerance between individuals. Finally, group members who associate at close range whilst eating, have a level of tolerance that allows for behavioural coordination in both space and time and therefore learning finer details of behaviour, especially with regard to novel foraging information (as pertinent to the observation network, see below).

Interaction networks

Interaction networks were built for social play and grooming, based on matrices containing the total frequency with which the dyads were seen interacting. Social play data is inherently symmetrical as the frequency with which individual A plays with B is the same of individual B playing with A; thus social play matrices were symmetrised using UCINET. Grooming data, on the other hand, is naturally an asymmetrical relationship, with one individual in the role of groomer and the other of groomee. The grooming networks were constructed so that the individual in the column was grooming the individual in the row. Thus, both social play and grooming data generated with cell value pertaining to the

frequency of interactions of each dyad. Play networks were undirected, while grooming networks were directed.

Observation networks

Similar to the interaction networks, the relationship between dyads in the observation networks was quantified by frequency of activity. In contrast, however, here the directionality of the relationship is kept intact, as knowing who observed who is important in determining who is likely to learn from whom. The observation networks were constructed so that the individual in the column was likely to learn from the individual in the row; this follows the recommendations for inputting social networks into the NBDA.

Three observation networks were built based on data scored from the video recordings of the foraging task experiments. For the tube task, a single measure of observation was scored from the video. Every time a monkey solved the task successfully (i.e. reached the juice) all monkeys with their heads facing towards the task, within a ten-meter radius from the task, were recorded as observers. For the lift-pull task experiment, observation events (i.e. heads facing the conspecific successfully solving the task) were registered for two distance measures: overall observations included all *observation events within a ten-meter radius*, and a subset of closer *observations, within a 5 meter radius*. All three observation networks were directed and the cell values depicted the frequency with which the individual in the column saw the individual in the row solving the task successfully.

Node attributes

Attribute data lists properties pertaining to each individual (node). In the present study we used age, sex and dominance rank as properties of nodes in the social network analysis that might portray relevant relationships for directed social learning. Dominance rank of study subjects was determined from the direction and outcome of agonistic and submissive interactions (see appendix A)

2.5 Data Analysis

Each of the two main approaches to studying animal behavioural traditions, presented in the Introduction (group-contrast and diffusion studies), have led to the development of statistical methods to infer social learning based on the assumptions each approach makes. Here I give a brief presentation of the data analysis conducted in my thesis. Further details on the methods for detecting social learning applied to my data will be given in the chapters where these were employed. Also in this section, I describe how the data set was used to construct social networks that would be used in the analysis.

2.5.1 Network-based diffusion analysis

Network based diffusion analysis (henceforth NBDA) was developed as an alternative to diffusion curve analysis, for assessing the likelihood of social learning being responsible for the spread of a novel behaviour. Instead of considering random interactions between individuals within a group it takes into account that individuals vary in the frequency of interactions, or strength of association, with one another. The main input required by NBDA are the order (or time) that individuals in the group acquire a behavioural trait, and a social network that empirically describes the association or interaction patterns of individuals, and therefore the opportunities they have of socially learning from each other.

The original NBDA (Frank & Nunn, 2009) is composed of two agent-based models, one of which assumes that individuals learn probabilistically irrespective of their connections (asocial learning) and the other assumes individuals learn from one another based on how strongly connected they are (social learning model). The agents in each model can exist in two states: (i) naïve (has not, as of yet, learnt the trait) or (ii) skilled (has learned the new trait). The agents learning rates are either considered to be the same for every individual (asocial learning model) or depend on the strength of connection between individuals (social learning model). In more recent versions of NBDA (Hoppit et al, 2010) the agents' learning rate is based solely on individual-level variables (asocial learning model), or on a combination of these individual-level variables and the strength of connections between individuals in the social networks. (social learning and asocial learning).

For both versions the stronger the connection between a naïve and a knowledgeable individual the more likely the information (or new behavioural trait) is to spread between them. Both models (asocial and asocial-and-social) are then fit to the observed diffusion data and maximum likelihood methods are used to determine which model fits better to the diffusion data; AIC value at least 2 units lower indicate a better fit. Social learning is said to have occurred when the model that includes the social model presents a better fit.

Individual-level data

Dominance rank, neophobia and frequency of approaching the task without manipulating it were the individual-level variables, input in the analysis to inform the asocial model. Further details on the calculations and reason for employing these variables can be found in section 4.2.4

Network data

NBDA can use both symmetrical and asymmetrical interaction matrices as inputs for the corresponding social network. The network is entered in the form of a square matrix with the same order of individuals along the rows and the columns. Data were entered into the matrix so that the probability individuals in the columns have of learning, is influenced by their interaction/association with individuals in the rows.

See chapter 3 for a full description of the social networks constructed and section 4.2.2 for the networks used to inform the social models in NBDA.

Diffusion data

The time lapsed from the beginning of the experiment until each individual solved the task for the first time and the order in which they solved the task were input in the *time based diffusion analysis* (TADA) and *order based diffusion analysis* (OADA), respectively. These numbers inform the models when individual went from the naïve to the skilled state. Both models begin with one skilled individual, the remainder of the group being naïve. The final step of the diffusion must be informed in time (max) for the original version of NBDA.

TADA has been shown to have greater power in detecting social learning correctly and is less likely to identify social learning when no social learning is at play (Hoppitt et al, 2011). This greater analytical power is because time data is more sensitive to the acceleration of trait acquisition as it spreads thorough the social group. However, this means that TADA

has to make some assumptions about the curvature of the rate of acquisition. Franz & Nunn's (2009) TADA, for example, assumes an exponential distribution for the rate of social learning. OADA has the advantage of not needing to make such onerous assumptions. Hoppitt et al (2010) argue that when there are "fluctuating variables influencing the rate of acquisition that affects all individuals equally" or when it is believed the diffusion will have a curve shape difficult to model (such as a stepped curve), then OADA is preferable to TADA. An example of a situation where the baseline function is thought to have a shape difficult to model, would be when knowledgeable individuals block naïve individuals' access to the task. By monopolising the task or depleting the resource knowledgeable individuals inhibit naïve individuals from learning to solve the task. In addition, a decrease in the baseline acquisition rate might result from some individuals not acquiring the trait because they adopt scrounging as a strategy instead. A further example of alterations to the baseline rate could occur when knowledgeable subordinate individuals avoid solving the task in the presence of more dominant group members, due to the risk that the food reward might be stolen. All of these examples were possible in our field experiment, which indicates OADA might be better suited for our data.

I opted for running both the TADA and OADA versions and assessing the differences between them.

2.5.2 Option-bias analysis

Option-bias analysis (hence forth OBA) was developed with the aim of inferring social learning of a behaviour based on the behavioural repertoire of individuals at a given moment in time. OBA is based on the assumption that "*when ecological and genetic differences are accounted for, social learning will generate a greater within population homogeneity in the option choices than expected in the absence of social learning*" (Kendal et al, 2009, pg. 2).

In short, OBA is a modification of a chi-square test on a contingency table of options that takes into consideration the non-independence of option choices by the same individual, using randomization procedures. "*If the magnitude of the option-bias calculated from the observed data exceeds that which could be reasonably expected through chance and asocial learning alone (that is, it lies within the upper 5% tail of the bootstrap distribution)*" then "*the null hypothesis, that the observed bias is due to stochastic or asocial learning processes*" can be rejected (Kendal et al 2009, pg. XX) For p-values lower than 0.05, social learning is said to be responsible for the biases in repertoire.

When applying the OBA to my data I used the R function provided by the Laland Lab freeware site (<http://lalandlab.st-andrews.ac.uk/freeware.html>). The script requires entering, for each individual: (i) the frequency of solving the task successfully using option *lift*, (ii) the frequency of total successes (the function calculates the frequency of solving the task successfully using *pull*), and (iii) the group (or subgroup) membership. In this version of OBA the randomization procedure requires there be a higher homogeneity of the variant within groups than between groups, in order to refute the null hypothesis. The latter version of OBA also modifies the original script, enabling individuals who were trained as demonstrators to be taken into account, by constraining them to their original group during the randomization procedure. For the lift-pull task, CHI in JB group, and Lim in PF, were coded as demonstrators and hence restricted to their original group during the randomization process; other individuals were treated as normal participants.

Furthermore, OBA can take into consideration possible biases in the options used due to attributes of the task (such as the asocial likelihood of discovery of each option) based on results from asocial control individuals. Data from the asocial control experiment with individual captive capuchins from Edinburgh Zoo (see 4.2.2 *Lift-pull task -asocial control*), allowed us to estimate the power of our analysis by incorporating the possible asocial bias towards each of the options (*lift* or *pull*).

2.5.3 Social Network Analysis

Some of the issues usually faced by researchers working with small groups of inter-relating (or interconnected) individuals, are the statistical dependencies that result from the repetition of individuals and their relationships in the data set. Social network analysis (SNA) allows us to study these complex relations “*by considering inter-individual dependencies not as an obstacle but as the very subject of investigation*” (Kasper & Voelkl, 2009, p. 344). It remains important, however, to carefully select the social network measures employed in SNA, based on the data set and the questions being addressed. In small cohesive groups, one would expect that at some point in time all individuals will interact with each other at least once. In such cohesive groups it is therefore the strength of the connections (strength of association or frequency of interactions) between dyads that differentiates relationships rather than the presence of a connection alone (Kasper & Voelkl, 2009). Here, I take care to run

SNA parameters that appropriately considered weighted data, rather than those designed for analysing the presence/absence of connections in large networks.

Density, Average Degree (weighted and non-weighted), Components ratio, Clustering Coefficient, Flow betweenness and Assortative mixing were SNA parameters used to quantify the social relationships of the wild groups of capuchin monkeys. For further detail see chapter 3.

In-degree centrality was calculated for each individual as measure expressive of the frequency with which a given individual was the observational target of naïve conspecifics, observing its successful manipulations of the task. This measurement was used in the GLM analysis for identifying transmission biases (see chapter 5).

All SNA parameters and procedures we calculated and conducted using UCINET 6.0 (Borgatti et al, 2013)

2.5.4 Standard inferential statistics

Cohen κ (kappa) scores were calculated using SPSS to determine whether there was significant reliability in inter-observer coding of videos. Generalized linear model analysis and mixed models were conducted, using SPSS 14, to investigate transmission biases. For details on how this analysis was run see chapter 5. Non-permutation statistics were carried out using SPSS version 14.0. All tests were two-tailed with a significance of $p < 0.05$.

CHAPTER 3:

THE SOCIAL CONTEXT OF LEARNING: DIRECTED SOCIAL LEARNING AND SOCIAL NETWORK ANALYSIS

In this chapter, I focus on the opportunities for learning from conspecifics within the social context in which these wild capuchin monkeys live. By integrating social network analysis with the theoretical framework presented by Coussi-Korbel & Fragaszy (1995), I aim to (i) describe behavioural coordination in wild groups of *Sapajus libidinosus* and (ii) gauge how their socio-positive social networks predict the occurrence of non-specific and/or directed social learning in this new world primate.

3.1 Introduction

Coussi-Korbel and Fragaszy's classic 1995 paper developed a conceptual framework relating social learning to the social dynamics within groups. Within this framework, the process of social learning occurs as the result of behavioural coordination between members of a social group in space, in time or in space-and-time. All three forms of behavioural coordination described can facilitate social learning, however, behavioural coordination in both time-and-space enables naïve individuals to learn more than general information, such as timing and location, and acquire more specific information (e.g. food processing techniques), by close observation of the activities of others (see chapter 1 - Introduction for more details).

Within this theoretical framework, a distinction is made between social learning that occurs irrespective of the identity of the active individual, *non-specific social learning*, and social learning that occurs differentially as a function of the identity of the individual (directed social learning) (Coussi-Korbel & Fragaszy, 1995). *Directed social learning* refers to instances in which the information would spread at different rates among subsections of the group (e.g. according to age, sex, status and patterns of association) due to the social dynamics within the group.

Since 1995, the importance of taking the social context into consideration has been a growing argument in the literature on social learning (Kendal et al, 2010). However, advances in delineating how the social context influences social learning have been modest. This is in part, due to the challenges of studying complex social structures in primates. Employing social network analysis to study the intricate social worlds of animals is a possible

way forward. This is because a social network is a relational data set, with properties that permit us to quantify these relationships and investigate how aspects of the relationships describe a group's larger social structure (Croft et al, 2008). Furthermore, by giving a metric description of the social structure of a group, social network analysis provides an important tool for studying the patterns of dissemination of information through a social group (Kasper & Voelkl, 2009). In keeping with the framework of behavioural coordination and directed social learning (presented previously), I focus here on social network measurements that prove useful in describing: (i) social cohesiveness, (ii) patterns of associations and interactions between group members and (iii) the possible pathways through which information might travel³.

Density is a network cohesion measure that gives us a first quantitative description of the group's social structure. It describes how densely connected a network is, by calculating the proportion of the total possible connections between individuals that is actually present in the data. This measure allows us to describe whether the groups form one cohesive unit where all group members eventually come into behavioural coordination with each other at least once. Another network cohesion measure is *Component ratio*, which enables us to detect the extent to which a network (group) consists of a single component or is fragmented into smaller components or isolated nodes (individuals). A single component is present when every member of the group can reach every other member directly or indirectly (via a neighbouring node).

Even when a network presents high density (i.e. all/most individuals are connected to one another) the strength of the connections may vary as a function of varying frequency of interactions or rate of associations between individuals. Graphical representations in the form of sociograms, allows us to visually gauge the variation in the quality of the social relationships of group members. A thicker edge (line connecting individuals) indicates a greater *weighted degree* (tie strength) between dyads, thus describing visually, the patterns of association and frequency of interaction between group members. In addition, the distribution of weighted degree provides a quantitative description of homogeneity or heterogeneity of connections within a group. The social network metrics of cohesion and homogeneity in the distribution of edges (connections) described above are our first indication of the likelihood of non-specific or directed social learning, based on the opportunities these relationships create for group members to learn from each other.

³ For a broader inventory of animal social network measure see Kasper & Voelkl (2009) and Croft et al (2008).

When heterogeneity in the distribution of connections is present, there are two possible suppositions: either the network is composed of several fragmented components (identified by the component ratio) or the single network comprises clusters of more strongly connected individuals within a network, termed cliques. Watts and Strogatz (1998) proposed the *clustering coefficient* in an effort to better understand ‘small world networks’. Human social systems are characterised for being at the same time very compact (short paths connect all individuals) and cliquish (clumped into groups that are more strongly connected within themselves than with others). Nonhuman primate social networks are likely to present similar characteristics. At a network-level, the clustering coefficient measures the density of ties for each node (individual) and then averages this over the entire network. When compared to the group’s density, this metric can help determine whether individuals are clumped up into cliques (Borgatti et al, 2013). Clumped social relationships are less conducive to non-specific social learning, as one would expect, in a cliquish social group, that individuals will be more likely to learn from group members within their clique (i.e. more strongly connected to him/her) than individual in other cliques..

To detect *directed social learning* researchers have to demonstrate that certain individuals are more likely to acquire information from certain other individuals. *Network assortativity* is a SN metric depicting the tendency of individuals (nodes) to connect preferentially with other individuals (nodes) based on their attributes (Croft et al, 2008). If every node is as likely to be connected to every other node, then assortativity is null and conditions more conducive to non-specific social learning. On the other hand, if certain classes of individuals (e.g. age, sex, dominance rank, individuals with higher centrality measures, etc.) tend to be more highly connected with individuals of the same class, then, assortative mixing is said to be occurring. Such assortative mixing can occur within classes (*homophily*), when same classed individuals are more strongly connected amongst themselves, or between classes (*heterophily*), when stronger connections can be found between individuals of different classes. By applying this SN measure, one can easily assess demographic patterns of association/interactions. As an example, assortative mixing can be applied to describe whether grooming behaviour is equally distributed throughout the group or whether it is more frequent between individuals of the same sex. From networks of who observes whom, one can address, for example, whether higher ranking individuals are more often observed by lower ranking individuals or whether younger individuals preferentially observe older individuals as sources of information. Thus, network assortativity is likely to prove a useful tool in describing social relationships conducive of directed social learning.

At the individual-level, *centrality* measures allow us to evaluate how important individuals (nodes) are in the network by quantitatively describing how connected an individual is to other members of its social group. Several measures for centrality are currently available in SNA and it is important to consider which is most suitable for the data being analysed. By describing the roles that individuals play in the structure of the network we can ascertain how they might influence the spread of information. Here I adopt *Flow betweenness* to determine an individual's importance (centrality) in the network, with regards to the transmission of information. Flow betweenness describes the role of an individual (node) in the flow between all other individuals in the network. It takes into consideration the strength of connections of a focal individual with its 'neighbours' (individuals it is connected to) and measures how this affects the maximum flow through the network. Central individuals, as identified by flow betweenness, have a position in the network that is crucial to the flow of information and are, therefore, important 'brokers' in group-wide transmission of information. As well as a measure of individual importance, flow betweenness can be averaged out over all the dyads to give a measure of connectivity for the entire group. The connectivity of a group, as portrayed by the *flow betweenness centralization index* (Borgatti et al 2013), can be compared between groups and across different social networks

As a final point, in the framework presented by Coussi-Korbel & Fragaszy (1995) predictions are made about how different social systems in different species may influence the diffusion of behaviour. According to the model presented, the homogenous relationships between group members in egalitarian species means information can spread efficiently via non-specific social learning, regardless of the behavioural trait being transmitted. In opposition, the heterogeneous relationships between members of despotic societies, means social learning will be directed through the few tolerance pathways available, and directed social learning is to be expected in many cases. Capuchin monkeys have non-linear dominance relationships (Izar et al, 2006), where aggressive interactions are infrequent and tolerance of others is prominent, with a special consideration to younger members of the social group (Fragaszy et al, 2004;); thus they are generally considered to be midway in the egalitarian-despotic spectrum. In intermediate societies both non-specific and directed social learning can occur. Accordingly, we may predict that specific behavioural skills (requiring accurate observation and thus close behavioural coordination in time-and-space) will spread through the restricted pathways of tolerance between subsections of the group, occurring thus, via directed social learning. Other types of information, that do not require a high

degree of behavioural coordination to be acquired, could spread through non-specific social learning and thus homogenously across the group (Coussi-Korbel & Fragaszy, 1995).

Here, I apply social network analysis to Coussi-Korbel & Fragaszy's (1995) theoretical framework. From data collected on two groups of wild bearded capuchin monkeys, I describe the groups' social relationships in the form of association, interaction and observation networks. I consider how the structure of these social networks might inform us about the opportunities for social learning. Finally, I ask whether individuals with differing network positions would vary in their access to information (representative of non-specific/directed social learning), should information be flowing through the social network.

3.2 Methods

3.2.1 Behavioural data sampling

At the time of this research, the study group Jurubeba (henceforth JB), contained 51 individuals, including 14 adult females, 14 adult males, 12 juveniles and 11 infants. The Pedra Furada group (henceforth PF) contained 35 individuals, including 11 adult females, 7 adult males, 12 juveniles and 5 infants (see Table 3.1). My focal subjects were the adults and juveniles of the groups (JB: N=40; PF: N=30), all of which were individually recognized. The groups differ in size and are both larger than the range (12 - 27 individuals) presented as typical for capuchin monkeys (Fragaszy et al 2004, range for several species of capuchin monkeys). Recently, however, Emidio & Ferreira (2012) have described larger groups of capuchins (*S. libidinosus*, N=30; *S. flavius*, N=45), who, like our study groups, inhabit the *caatinga* (dry, savannah-like environment).

Table 3.1 Composition of groups Jurubeba (JB) and Pedra Furada (PF)

	Number of individuals	
	Jurubeba	Pedra Furada
Adult female	14	11
Adult male	14	7
Juvenile female	5	5
Juvenile male	7	7
Infant	11	5
TOTAL	51	35

Behavioural data were collected between May 2012 and June 2013 (full details are given in section 2.2.1). During focal samples I recorded (i) the activity (rest, feed, travel or social interaction) of the focal subject and (ii) the identity of individuals seen in contact, up to one meter and up to a ten meter radius from the focal animal. Finally, in order to determine behavioural coordination, I noted when the behaviour of individual(s) in contact or within 1 meter of the focal subject matched his/her behaviour. All occurrences of social interactions, including affiliative (i.e. grooming, social play, co-feeding), agonistic, and sexual interactions, were also recorded. In total there were 21-34 focal follows per subject in JB (median: 152 min per focal subject), and 69-75 focal follows per subject in PF (median: 363 min per focal subject).

Data regarding observation of conspecifics were obtained from a two-action task experiment (lift-pull task, see chapter 4 for further details) carried out with the two groups. From the video recordings, and accompanying narration of this experiment, I recorded, every time the task was successfully solved (i.e. the food reward was obtained), the identity of the monkey solving the task, as well as the identity and approximate distance of the individuals who were observing (had their heads directed towards the task) the task being solved. The task was solved successfully a total of 8671 times ($N_{JB} = 4591$, $N_{PF} = 4080$), in 92% of which there was at least one conspecific observing. As there was often more than one conspecific observer, a total of 33177 observational events ($N_{JB} = 15566$, $N_{PF} = 17611$) were used to build observation networks of varying distances, representing the differential opportunities to learn the specifics of task solution through observation.

3.2.2 Social Networks

The decision of which social networks are meaningful descriptors for the social context of learning is an important one. Here I opted for studying socio-positive relationships, to portray relationships conducive to social learning. Seven social networks were generated from focal and all occurrence data sampling, for each group, based on three classes of relational data: associations, interactions and observation.

Simple association ratios were calculated (using Socprog) for two spatial scales (within 1 meter and within 10 metres of the focal subject) and for different behavioural

contexts. Specifically, three association networks were generated, each one as a representation of gradually more refined levels of behavioural coordination and tolerance between group members:

- (i) *social proximity within 10 meters*; as a proxy for overall group cohesion and of behavioural coordination in time (which does not require physical proximity)
- (ii) *social proximity within 1 meter*; as a proxy for behavioural coordination in both space and time.
- (iii) *co-feeding*; a subset of the social proximity within 1 meter when both the focal animal and conspecific were both eating; as proxy of higher degree of tolerance during behavioural coordination in space and time.

Association networks were undirected (or symmetrical) and described the rate of association (edges) between individuals (nodes).

The frequency of pair-wise interactions was coded into matrices, so as to characterise other behavioural contexts in which behavioural coordination occurs, namely during:

- (iv) *grooming* and
- (v) *social play* activities.

Interactions networks were undirected (or symmetrical), and graphically represented by the frequency of interactions (edges) between individuals (nodes).

Finally, the last two networks portrayed the frequency with which the individual in the column observed the individual in the row solving the lift-pull task successfully but from different distances:

- (vi) *observation* of a conspecific solving the lift-pull task successfully *within 10 meters, and*
- (vii) *observation* of a conspecific solving the lift-pull task successfully *within 5 meters* distance.

The three types of social networks generated, association, interaction and observation, differ in that (a) the latter two contain frequency values to represent the strength of relationships, whereas the first contains ratios (varying between zero and one); and (b) because the first two are undirected networks while the latter (observation) are directed networks. For further details on how these social network were constructed see section 2.4.2.

3.2.2 Social network analysis and statistical methods

Five network-level metrics and one individual-level metric (flow betweenness) were calculated with the objective of characterising the social relationships between group members and thus the opportunities of social learning:

- (i) *density* to describe group cohesion,
- (ii) *component ratio* to assess fragmentation,
- (iii) clustering coefficient as a measure of how cliquish the SN is
- (iv) *network assortativity* to verify whether social relationships are stronger between certain classes of individuals,
- (v) *flow betweenness* to assess how individual positions in the network, contribute to the maximum possible flow of information through the network
- (vi) *network centralization index* or the average flow betweenness for the entire network, indicative of how fast information can flow through network.

Comparisons were made (a) between the two groups (JB and PF), (b) between the three types of networks (association, interaction and observations) and (c) across the seven networks described in the previous section.

UCINET procedures were used to calculate the network-level and individual-level metrics (Table 3.2) (Borgatti et al 2002, 2013). To statistically compare network metrics (e.g. density, component ratio) across networks, I ran the “compare densities t-test” procedure in UCINET. The bootstrap procedure to compare the densities of two independent networks with the same actors (nodes/individuals), a method analogous to the classical paired sample t-test for estimating the standard error of the differences, was run with 10,000 permutations. For statistical comparisons between types of networks (association, interactions or observation) or between groups the network metrics (calculated using UCINET) were tested for significance using one-way ANOVA with Bonferroni as a post hoc test.

Table 3.2 -Summary of Social Network Analysis measures applied (based on Borgatti et al. 2013)

Network measures	Definition
Average Degree	Average number of connections (edges) in the network.
Average Weighted Degree (or tie strength)	Average strength of connections (edges) in the network.
Density	Proportion of connections (edges) present relative to the total number of possible connections (edges) between nodes. A measure of the network's cohesion.
Component ratio	Another network cohesion measure, it takes into account that networks might be fragmented into components (interconnected individuals) and isolated individuals. Varies in value between 1.0 when every individual (node) is isolated and 0.0 when all individuals (nodes) are part of a single component.
Clustering coefficient	Calculates the sum of tie strengths (weighted degree) of ego-networks (the connections of a single node) and then averages this measure over the whole network. Gives a measure of the extent to which there are areas of high density and low density of connections throughout the network.
Assortative mixing	Measures the extent to which individuals (nodes) of a certain class (sex, age, dominance) associate/interact (connect) more strongly with individuals of the same class (homophily) or with individuals of a different class (heterophily). The E-I index is calculated by subtracting the sum of the strength of ties within classes from the sum of the strength of ties between classes and dividing the result by the total sum of strength of ties. The resulting value can range from 1 to -1. Value 1 means the strongest connections are between members of the same class (i.e. within class assortative mixing). Zero means there is no assortative mixing and strength of connections is similar within and between classes. Value -1 means all edges join members of different classes (i.e. between class assortative mixing).
Flow betweenness	A measure of the contribution of an individual (node) to all maximum flows possible. An individual with high betweenness has a central role in the paths through which information can flow. Flow betweenness can be averaged over all individuals (nodes) to produce a measure of network centralization.

3.3 Results

3.3.1 Focal samples and frequency of behavioural coordination

In most focal samples, 95.6% in JB ($N_{JB}=5267$) and 91.6% in PF ($N_{PF}=7327$), at least one conspecific was present within 10 meters of the focal subject. Social proximity within a 1 meter radius was less common, occurring in 40.8% ($N_{JB}=2248$) of the focal points in JB and in 25.1% ($N_{PF}=2008$) of focal points in PF. In all such instances the behaviour of the conspecific(s), in proximity of the focal, was registered; see Figure 3.1 for the proportion of activities recorded during behavioural coordination in space-and-time for both groups. The third proximity/tolerance measure, co-feeding, was the least frequent form of behavioural coordination in space-and-time, recorded in 6.4% ($N_{JB}=353$) of the focal samples in JB and 4.9% ($N_{PF}=392$) in PF. Finally, the focal animal was observed by conspecific(s) (within 1m) whilst conducting its daily activities in only 0.3% ($N=45$) of the total focal samples. For this reason the observation networks were based on data from a lift-pull task experiment, for which more frequent measures of observation instances could be acquired.

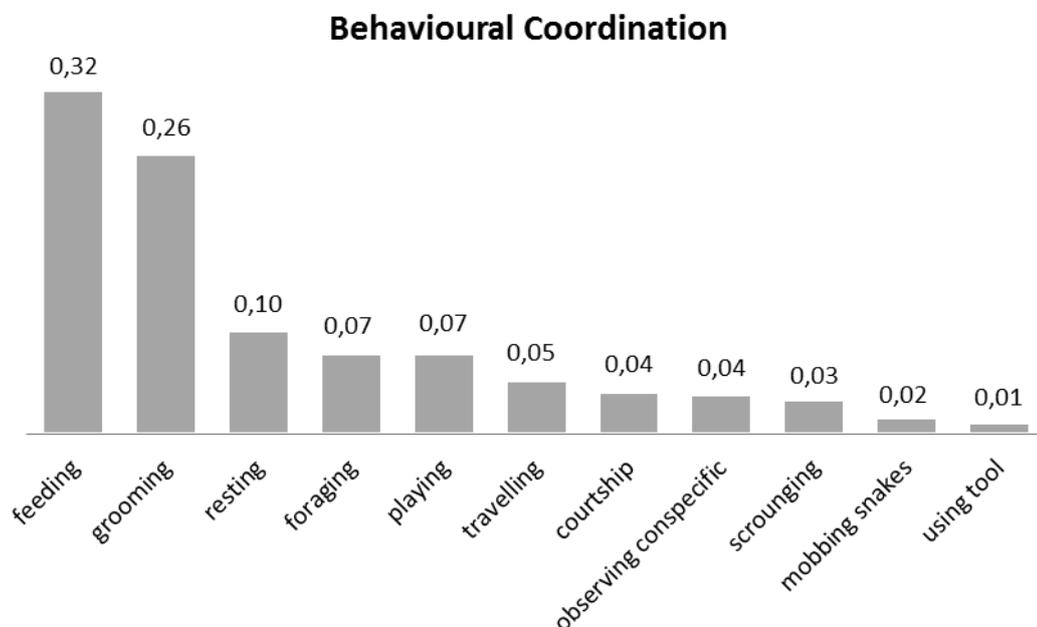


Figure 3.1 Activity of individuals during behavioural coordination within 1 meter, compiled for both groups. Values represent the percent of focal points for each activity.

3.3.2 Graphical representation of networks

Association networks

In both JB and PF, the *social proximity networks for scans up to 10m radius* were fully connected, constituting one single component. Density for both networks reached its highest value (Density = 1), meaning each individual was connected directly to all other group members.

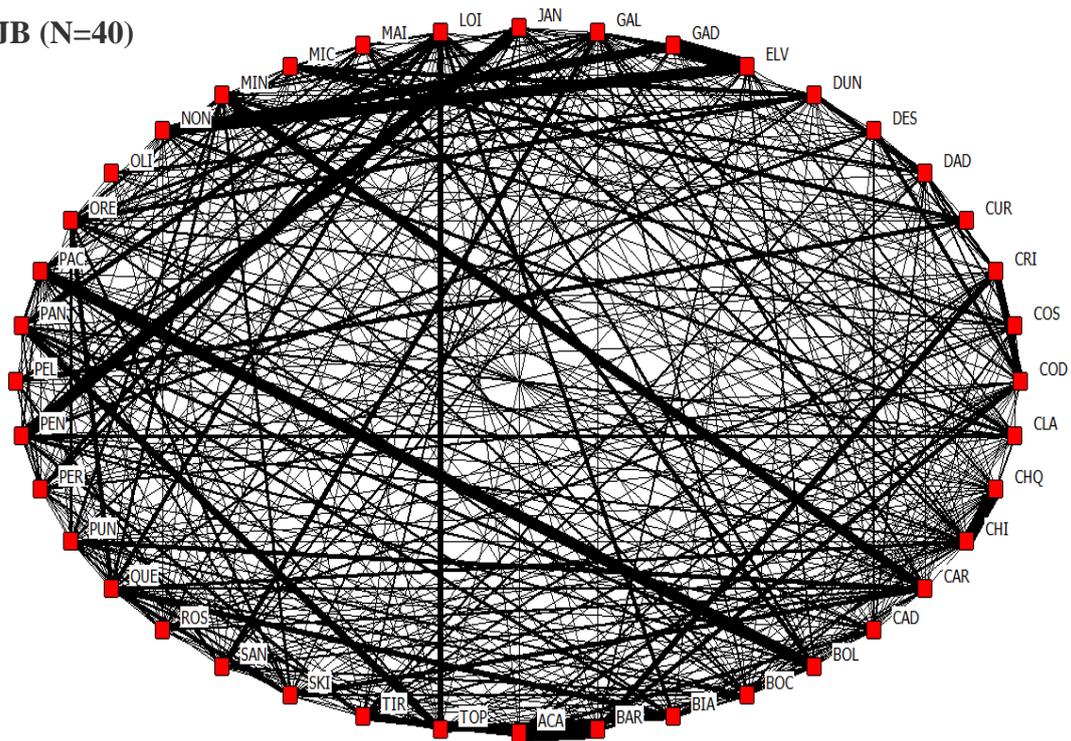
For *social proximity within 1m* the Density of the networks was still high, however, connection possibilities were no longer completely saturated; comprising 56% of all possible connections between nodes (individuals) in JB and 73% of the possible connections in PF (Figure 3.2). The Average Degree indicated that individuals in JB and PF associated on average with 22 (of 40) and 21 (of 35) different group members, respectively, within a 1m distance.

Co-feeding networks had similar densities to that of *social proximity within 1m*: 40% and 73% of the possible connections between dyads were present in JB and PF, respectively (Figure 3.3). On average each individual (node) was connected to 16 group members in JB and 21 in PF.

Each of the three association networks constituted a single component, meaning that all nodes (individuals) could reach every other node, directly or via some other node.

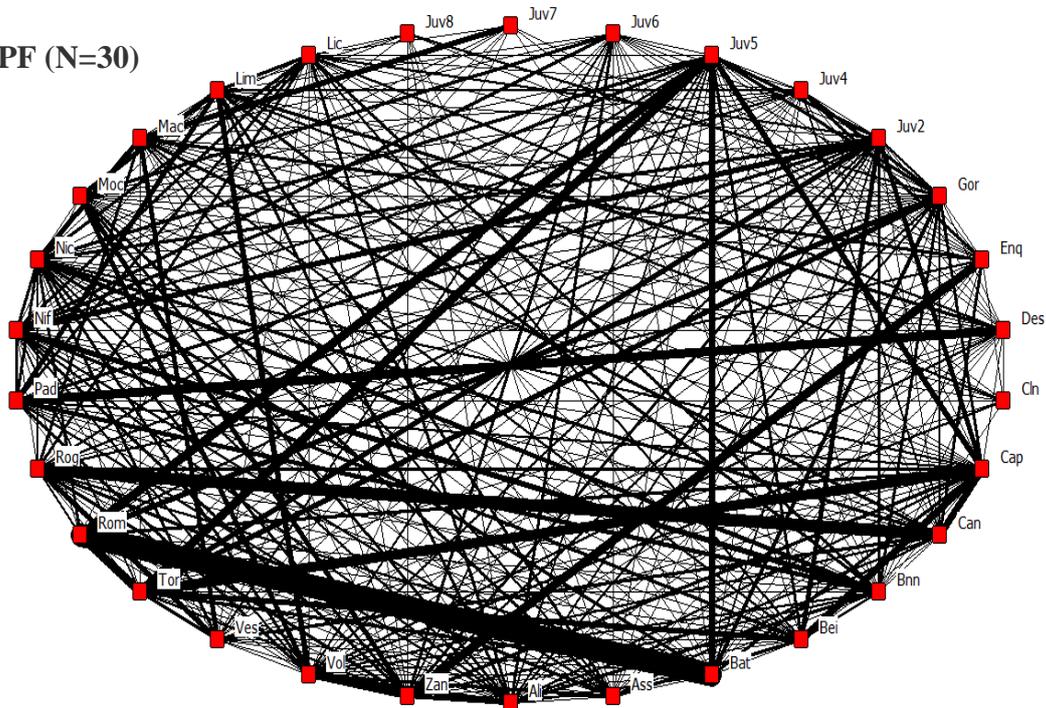
Social Proximity 1m radius

JB (N=40)



Density = 0.56 Average Degree = 22 Components = 1

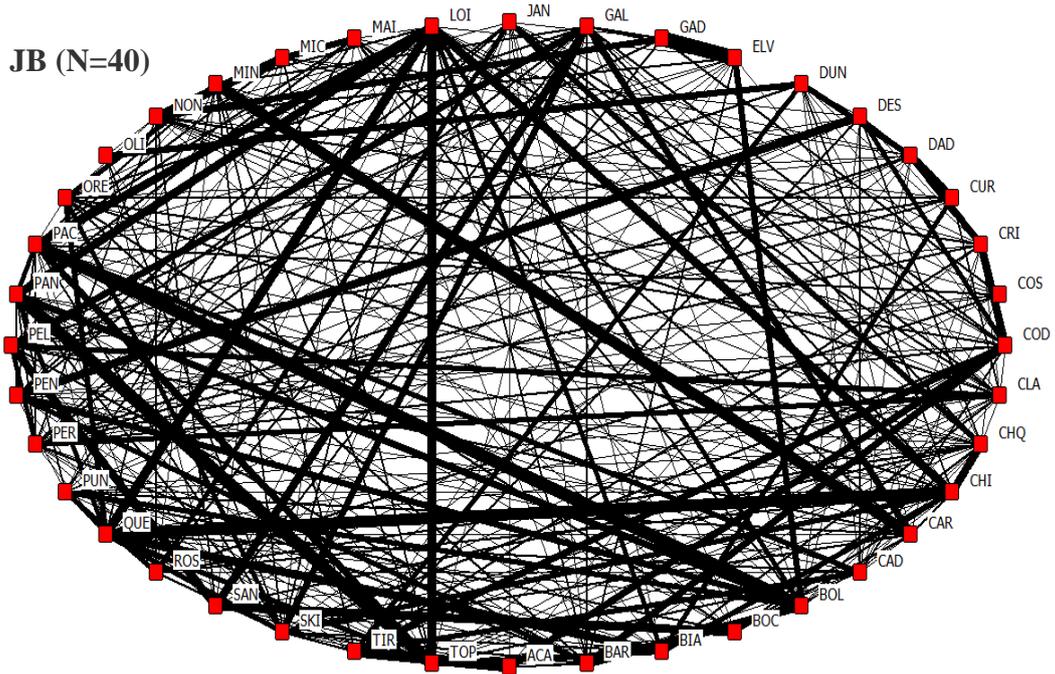
PF (N=30)



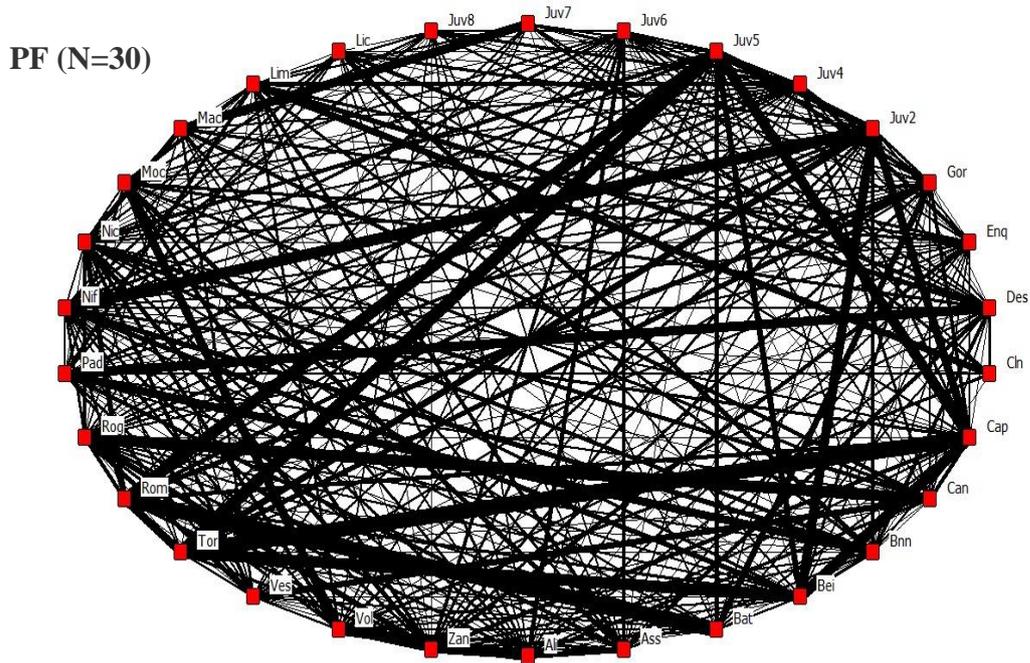
Density = 0.73 Average Degree = 21 Components = 1

Figure 3.2 Graph representation of *social proximity within 1m* networks. Nodes coloured red indicate individuals that are part of the main component. Thickness of edges represents the strength of association.

Co-feeding



Density = 0.40 Average Degree = 16 Components = 1



Density = 0.73 Average Degree = 21 Components = 1

Figure 3.3 Graph representations of *co-feeding* networks. Nodes coloured red indicate individuals who are part of the main component. Thickness of edges represents the strength of association.

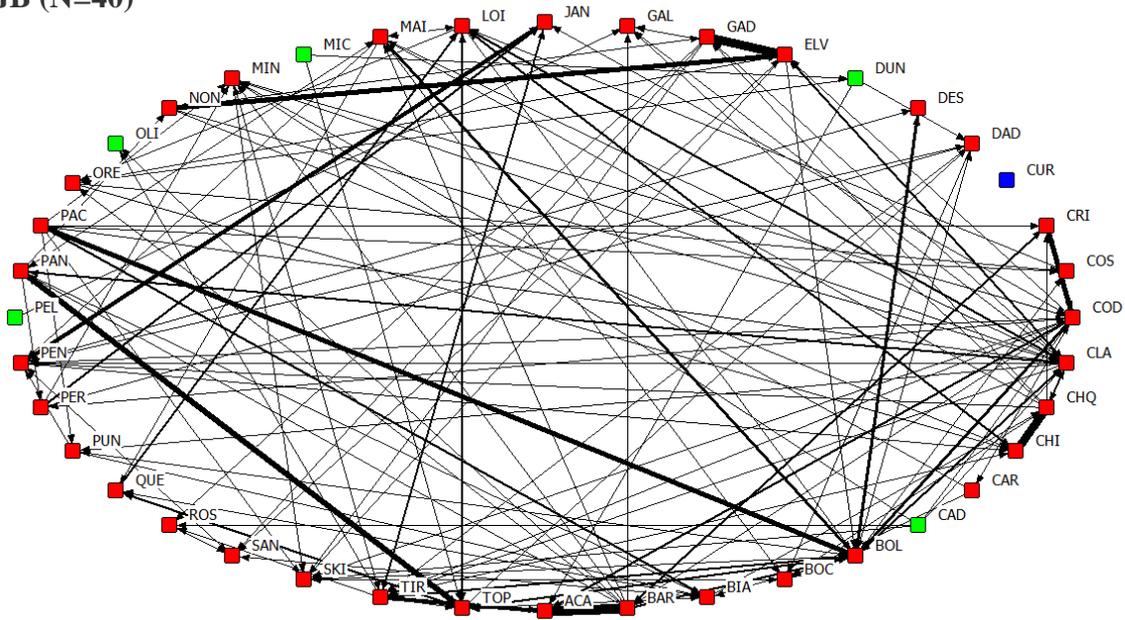
Interaction networks

From focal and all occurrence sampling combined, a total of 1236 grooming events were recorded ($N_{JB} = 626$, $N_{PF} = 610$). *Grooming networks* presented a much lower density, than the association networks above, with only 11% and 13%, of the possible connections present in JB and PF, respectively. From the same sampling efforts, 493 events of social play were recorded ($N_{JB} = 309$, $N_{PF} = 184$). Similar to the grooming networks, *social play networks* comprised low density values: 16% for JB and 17% for PF. Neither *grooming* nor *social play* networks formed single component networks, meaning some individuals (called isolate nodes) were never recorded interacting with other group members (Figures 3.4 and 3.5).

Lower density values and fragmentation of the interaction networks into components may be the result of small sample size due to the rarity of these behaviours. Only 0.8% of focal points in JB and 2.6% of focal points in PF were of grooming activities; and social play was recorded in only 2.4% and 0.3% of focal points in JB and PF, respectively. However, it is also possible that the low density and high fragmentation of the interaction networks is indicative of edges being more frequent between closely affiliated nodes and/or because the type of behaviour is more prominent among certain node classes (e.g. grooming between adults and social play between juveniles). This possibility will be investigated in section 3.3.4 when assortative mixing is detected in some of the networks.

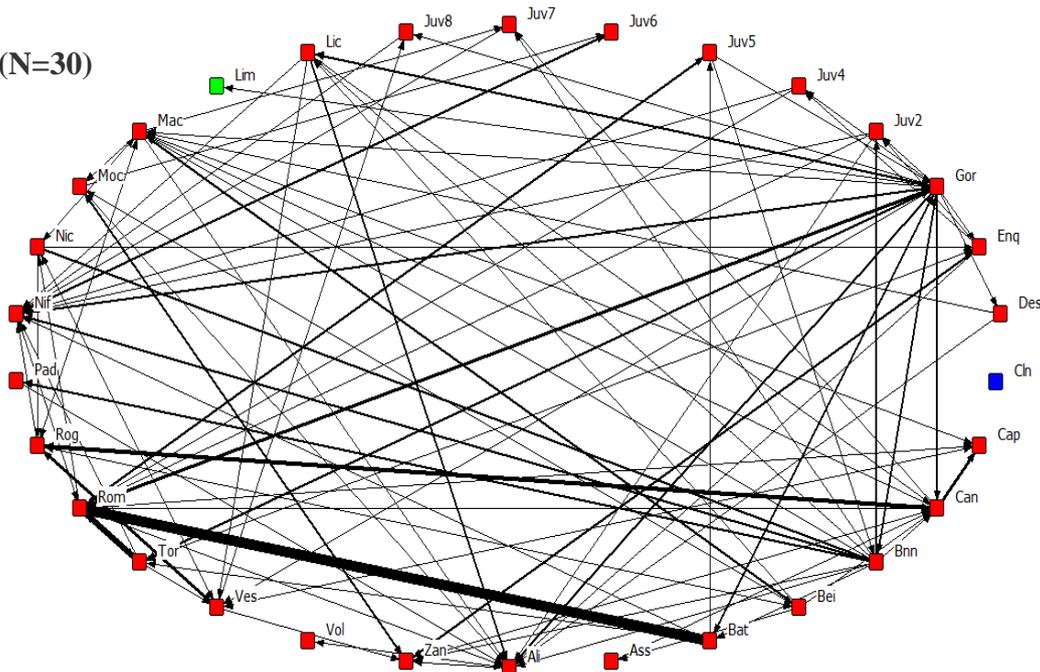
Grooming

JB (N=40)



N = 626 Density = 0.11 Average Degree = 4 Components = 6 Isolates = 1

PF (N=30)

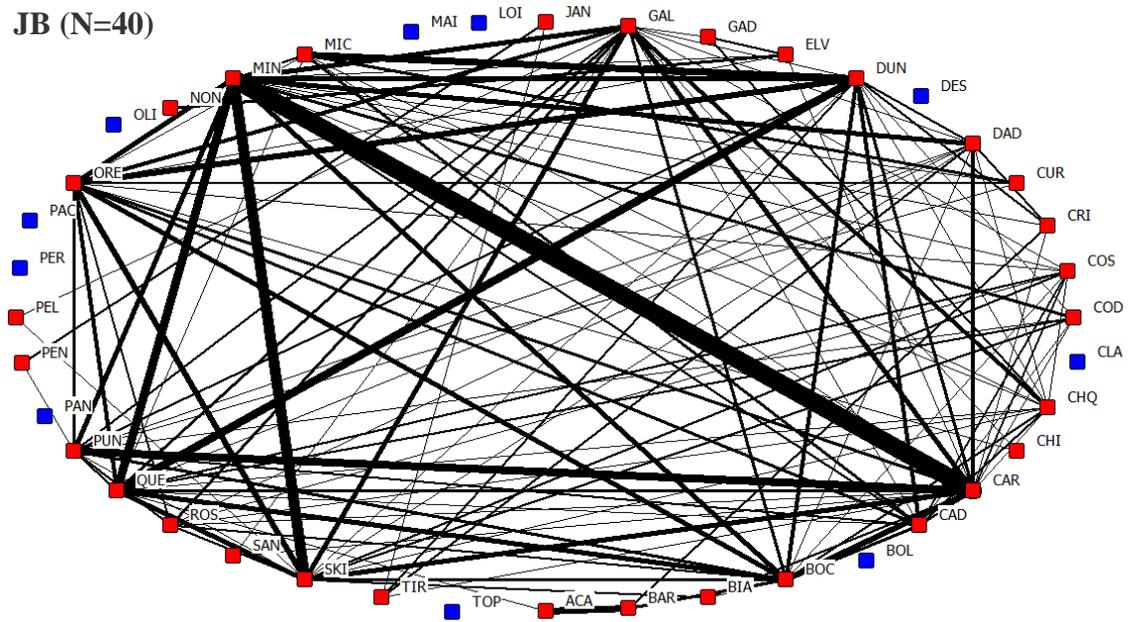


N= 610 Density = 0.13 Average Degree = 4 Components = 2 Isolates = 1

Figure 3.4 Graph representation of *grooming* networks. Nodes coloured red indicate individuals that are part of the main component. Other components in green and isolated individuals in blue. Thickness of edges represents the frequency of interactions.

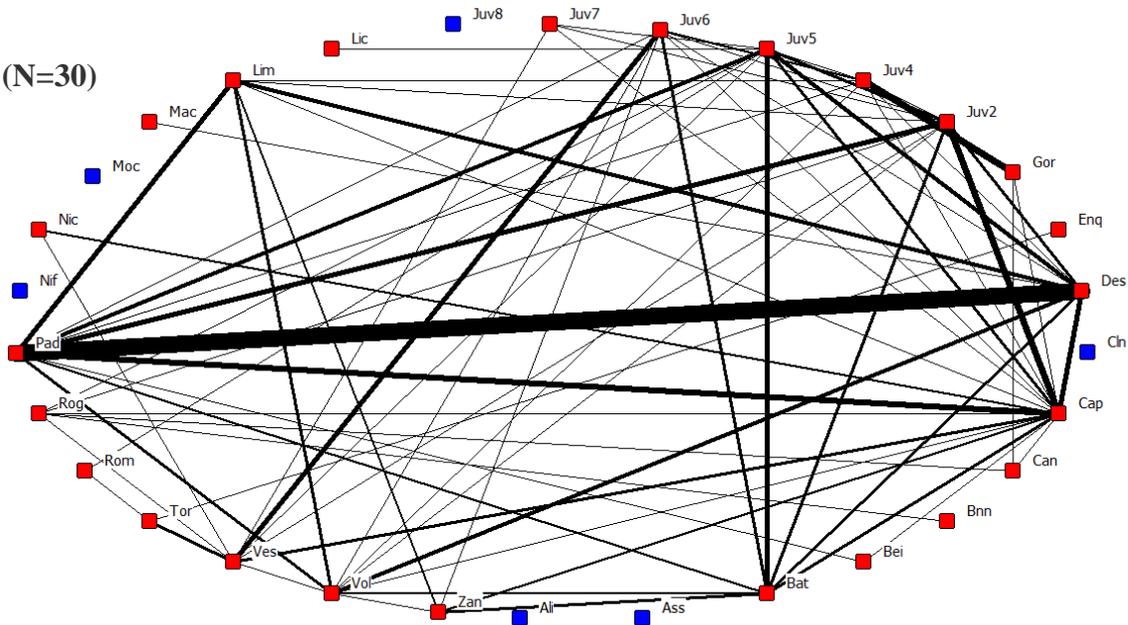
Social Play

JB (N=40)



N = 309 Density = 0.16 Average Degree = 6 Components = 1 Isolates = 10

PF (N=30)



N = 184 Density = 0.17 Average Degree = 5 Components = 1 Isolates = 6

Figure 3.5 Graph representation of *social play* network. Nodes coloured red indicate individuals, part of the main component. Isolated individuals in blue. Thickness of edges represents the frequency of interactions.

Observation networks

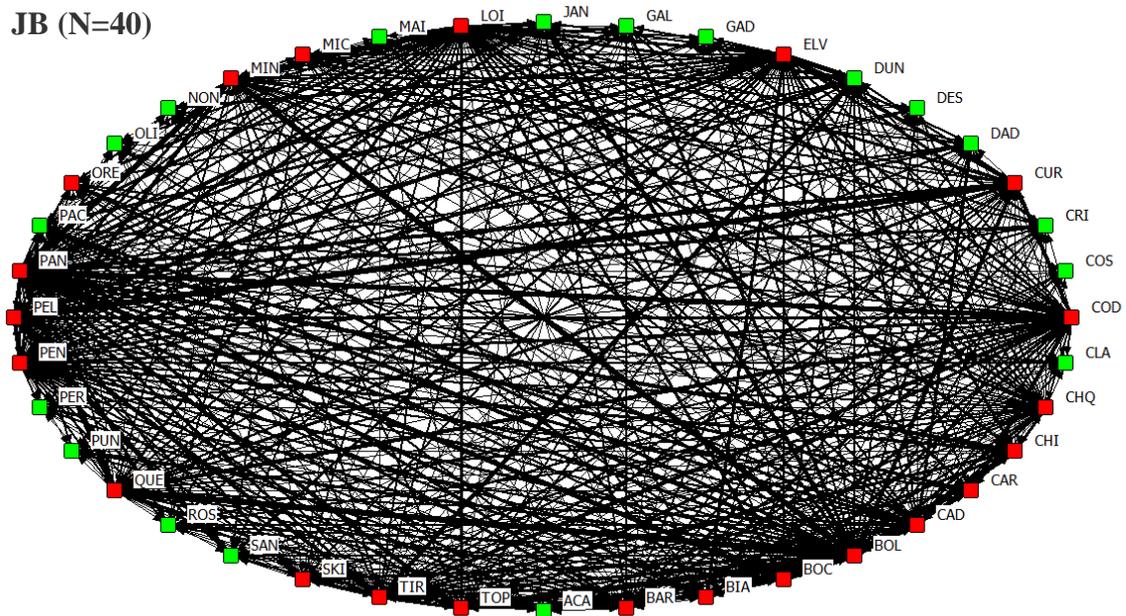
The *observation within 10 meters* network represents all the observational events registered during the lift-pull task experiment, with a total of 23309 observation events ($N_{JB} = 11525$; $N_{PF} = 11784$). The *observation within 5 meter* network is a subset of the observation events when the monkey was able to observe the lift-pull task being solved successfully at close proximity (within 5 meters), with a total of 9892 observation events ($N_{JB} = 4045$; $N_{PF} = 5847$) (Figures 3.6 and 3.7).

The observation networks differed in Density, as expected, with the *observation within 10 meters network* presenting a higher density ($Density_{JB} = 41$; $Density_{PF} = 26$) than the *observation within 5 meter network* ($Density_{JB} = 19$; $Density_{PF} = 15$).

When the directionality of the networks is taken into account, the observation networks show fragmentation into several components. In terms of social learning opportunities, this means that the consistent observation of a novel behaviour performed by a particular group member is restricted to particular others in the group. The greater fragmentation of the observation networks, compared to the other networks described above, is likely due to the directionality of the connections. The distribution of edges in the network is skewed, since many individuals observed the few individuals who solved the task, and the flow reaches ‘dead ends’ thus fragmenting the network into several components. This fragmentation, as a consequence of directionality, may also explain the seemingly unexpected high number of components in the *observation within 10 meter network*. In terms of social learning opportunities, this means that the consistent observation of a novel behaviour performed by a particular individual was restricted to particular others in the group. Each individual had the opportunity to observe within 5m, on average, only 6 to 8 members of the group whilst they were manipulating the task.

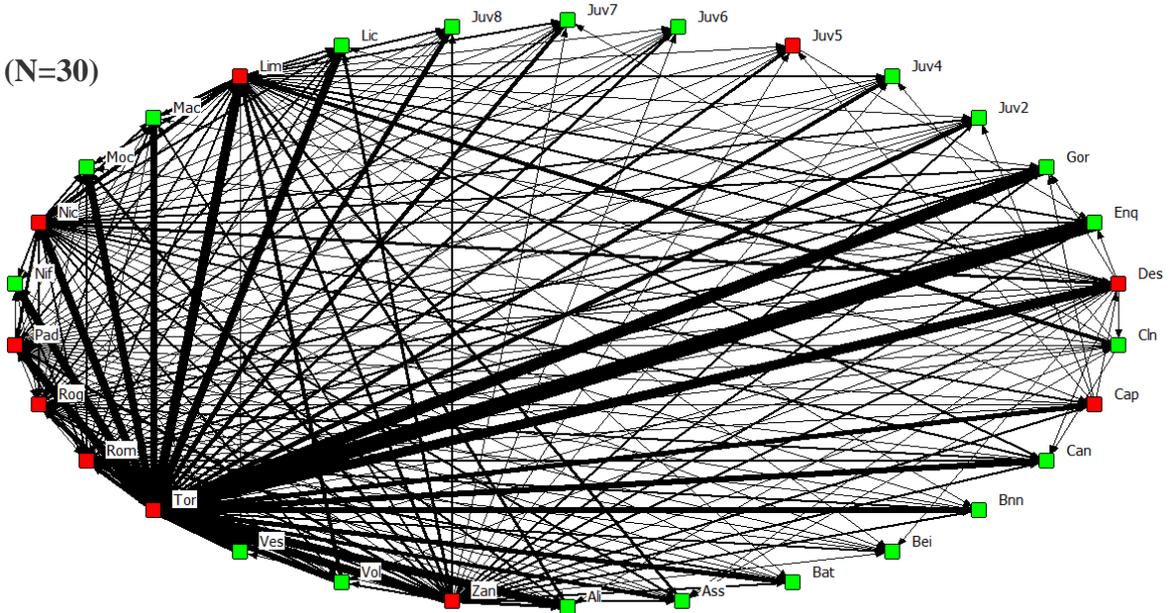
Observation within 10 meters of task

JB (N=40)



N = 11525 Density = 0.41 Average Degree = 16 Components = 19

PF (N=30)

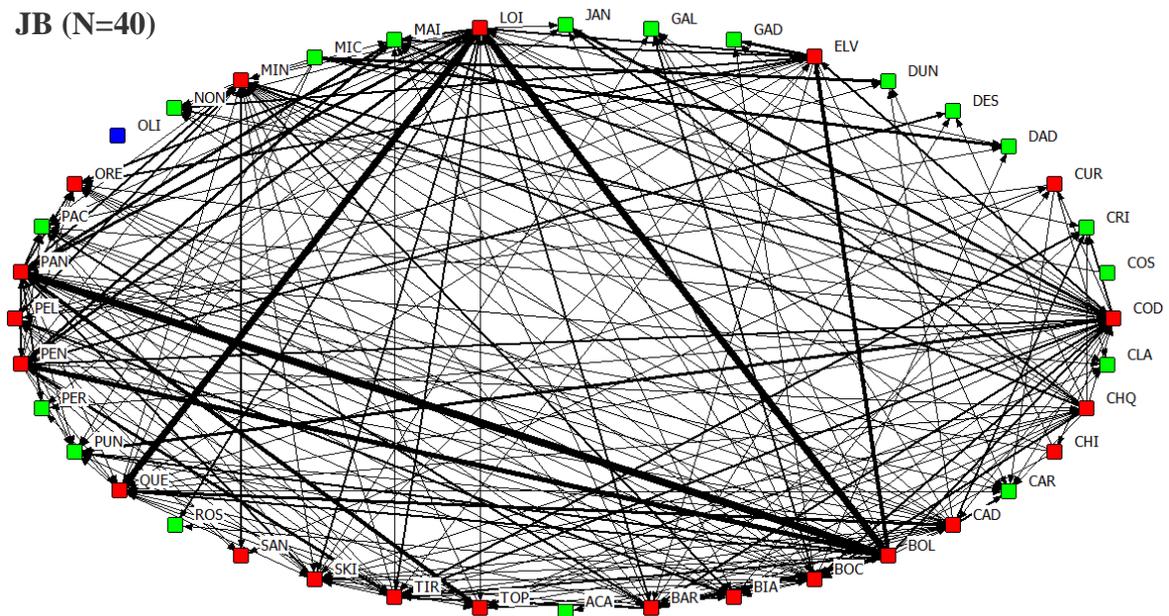


N= 11784 Density = 0.26 Average Degree = 8 Components = 21

Figure 3.6 Graph representation of *observation up to 10 meters* network. Nodes coloured red indicate individuals, part of the main component. In green other smaller components. Thickness of edges represents the frequency of observations.

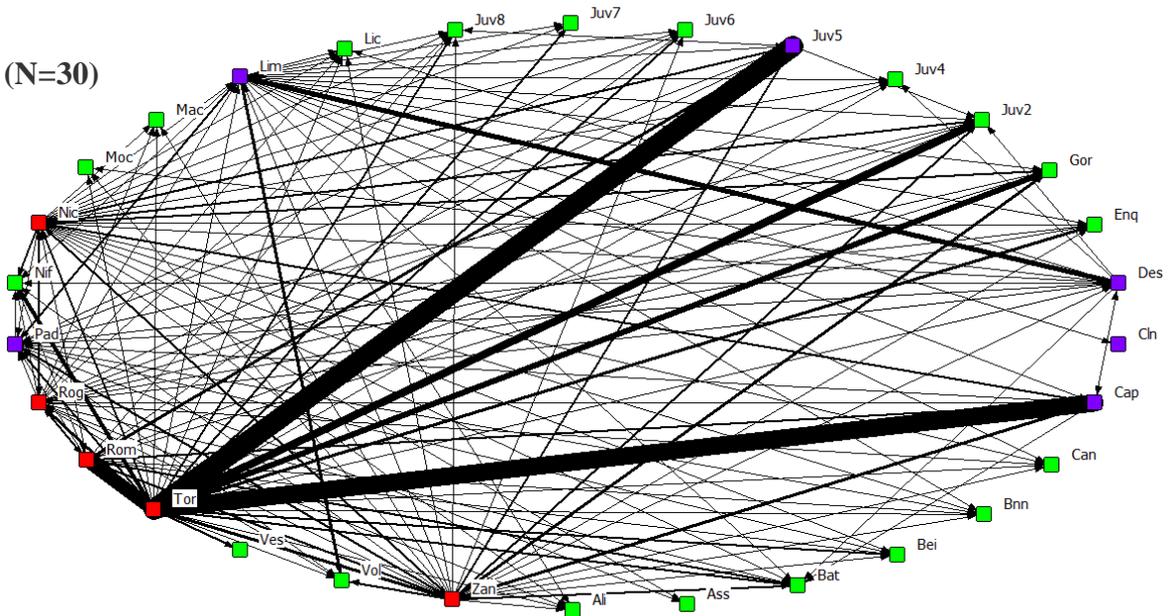
Observation within 5meters of task

JB (N=40)



N = 4045 Density = 0.19 Average Degree = 8 Components = 20 Isolates = 1

PF (N=30)



N= 5847 Density = 0.15 Average Degree = 4 Components = 23

Figure 3.7 Graph representation of *observation within 5 meter* network. Nodes coloured red and purple part of the main components. In green other smaller components. Isolated individuals in blue. Thickness of edges represents the frequency of observations.

3.3.3 Social network analysis: cohesion measures

In this section I compare the group-level network measures across types of networks (association, interaction and observation networks) and across the seven networks described above (Figures 3.2 to 3.7).

Data was collapsed across groups as there were no statistical difference between JB and PF groups concerning the average cohesion measures across all seven networks and for any of the group-level network measures (one-way ANOVA: *density*: $F(1,12) = 0.066$, $p=0.802$; *component ratio*: $F(1,12) = 0.201$, $p=0.662$; *clustering coefficient*: $F(1,12) = 0.687$, $p=0.423$; *flow betweenness centralization index*: $F(1,12) = 0.802$, $p=0.388$).

Density and component ratio

A significant difference was found in the mean Density values between the three types of social networks (one-way ANOVA: $F(2,11) = 18.508$, $p<0.0001$). Bonferroni post hoc tests indicated that association networks (mean density=0.737) showed significantly higher mean Density than interaction networks (mean density=0.115) ($p<0.001$), and observation networks (mean density =0.254; $p=0.003$), while interaction and observation networks did not differ from each other (Figure 3.8). Component ratios were significantly different between all types of networks (one-way ANOVA: $F(2,11) = 25.916$, $p<0.001$). The component ratio was zero for all association networks, indicating that each of these networks had a single component and no fragmentation. Observation networks (mean components=0.599) presented more fragmentation into components (i.e. higher component ratios), than interaction networks (mean components=0.277; Bonferroni, $p=0.014$) and association networks (mean components=1.00; $p<0.001$). Interaction networks were also significantly more fragmented than association networks ($p=0.020$). The component ratio was zero for all association networks, indicating that each of these networks has a single component and no fragmentation (Figure 3.8)

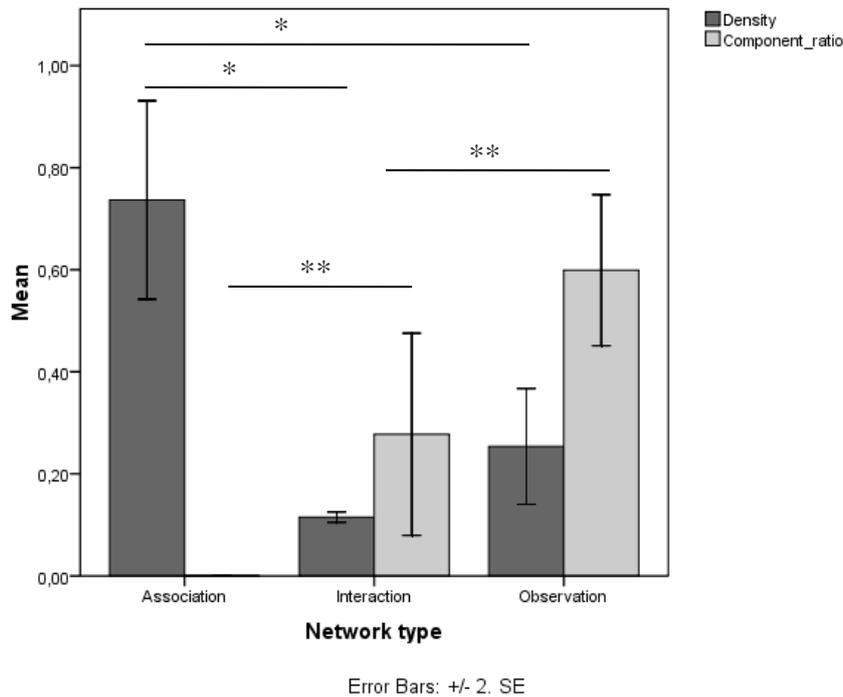


Figure 3.8 Comparison of network metrics Density and Component ratio, between the three types of networks: Association, Interaction and Observation. * significant differences in Density between network types. ** significant differences in Component ratio between network types.

Significant differences were found in Density values between the seven social networks here studied (one-way ANOVA: $F(6,7) = 19.023, p=0.001$). There was no significant difference in Density between the association networks: *social proximity within 10 meters* and *social proximity within 1 meter* (0.36 ± 0.11 ; $p=0.278$), *social proximity within 10 meters* and *co-feeding* networks (0.44 ± 0.11 ; $p=0.104$), *social proximity within 1 meter* and *co-feeding* networks (0.08 ± 0.11 ; $p=1.000$); as detected by the post hoc test (Bonferroni). Nor was there a significant difference between the interaction networks: *social play* and *grooming* (mean difference = 0.01 ± 0.11 ; $p=1.000$); or between the observation networks (mean difference = 0.16 ± 0.11 ; $p=1.000$).

The *Social proximity within 10 meters* network had significantly higher Density when compared to each of the interaction networks: *grooming* (mean difference = 0.88 ± 0.11 ; $p=0.002$) and *social play* (mean difference = 0.89 ± 0.11 ; $p=0.001$); and each of the observation networks: *observation within 10m* (mean difference = 0.53 ± 0.11 ; $p=0.038$) and *observation within 5m* (mean difference = 0.54 ± 0.11 ; $p=0.034$). No other difference in Density value was significant for the remaining networks (Figure 3.9).

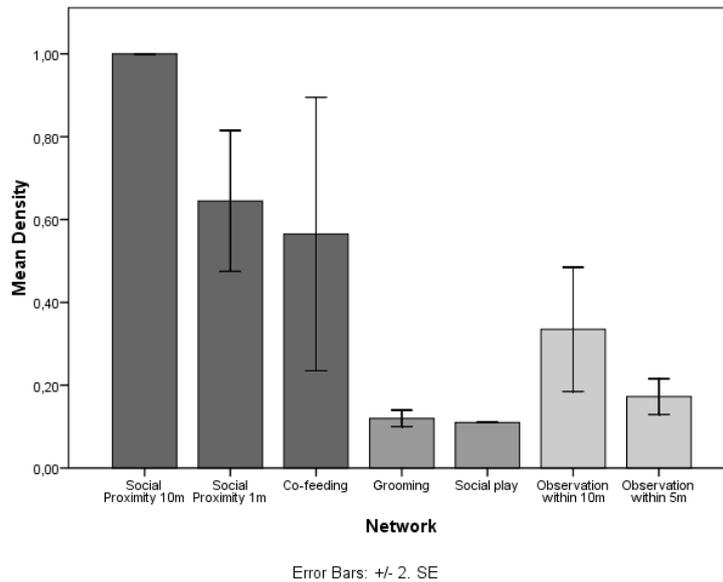


Figure 3.9 Comparison of network metric Density between different networks.

The network densities described for proximity and co-feeding networks in the present study are within the range of network densities presented by Kasper & Voelkl (2009) who studied such metrics in similar socio-positive networks across 70 primates groups (range = 0.49 - 0.93). The median values of network densities described here were however lower (JB: =30; PF=50) than the median density found for primates in general (median density = 0.75).

Network fragmentation (which correlates with density to some extent) was high for the low density networks, such as, the observation networks. Accordingly, component ratio (which describes fragmentation in networks) differed significantly between networks (one-way ANOVA: $F(6,7) = 16.544$, $p = 0.001$). Observation networks had significantly higher component ratios when compared to each of the association networks *social proximity within 10 meters* (mean difference = 0.57 ± 0.10 ; $p=0.014$), *social proximity within 10 meters* (0.57 ± 0.10 ; $p=0.014$) and *co-feeding* (0.57 ± 0.10 ; $p=0.014$); and when compared to *grooming* (0.47 ± 0.10 ; $p=0.047$) but not to social play (0.13 ± 0.10 ; $p=1.000$) which were also fragmented networks (Figure 3.10).

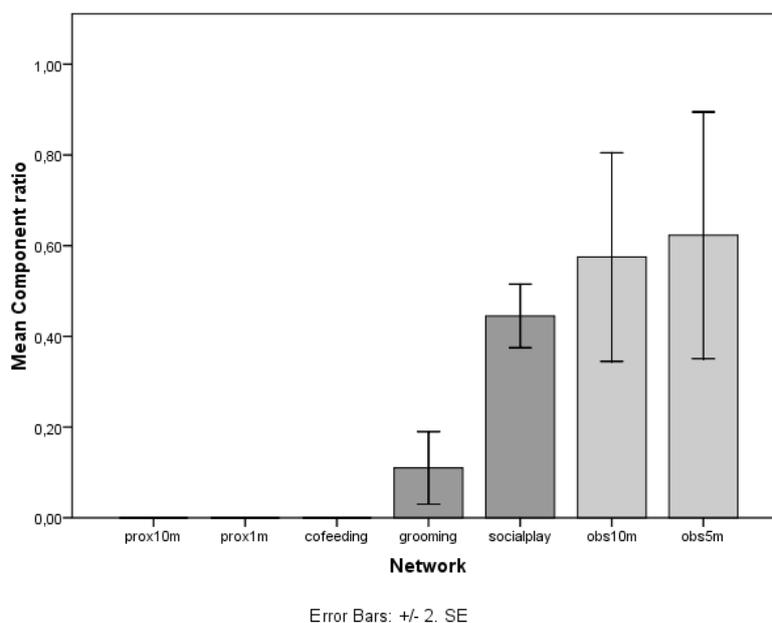


Figure 3.10 Comparison of network metric Component ration between different networks.

Clustering coefficient

The clustering coefficient measures whether there are areas of high and low densities of connections in the network. This allows us to determine whether the networks are made up of cliques (tightly connected groups of individuals). There was no significant difference in clustering coefficient between the three types of networks (association, interaction and observation) (one-way ANOVA: $F(2,11) = 2.322, p=0.144$).

When comparing each network, a significant difference in clustering coefficient was found (one-way ANOVA: $F(6,7) = 5.978, p=0.017$). Bonferroni post hoc tests revealed that network of *observation within 10 meters* had a significantly higher clustering coefficient than the *grooming* network (mean difference = $14.7 \pm 3.11; p=0.045$) and a non-significant tendency in the same direction when compared to *social play* ($14.1 \pm 3.11; p=0.057$). No other differences were deemed significant (Figure 3.11). In all networks analysed the clustering coefficient was larger than the network densities, indicating that some individuals in the network were more strongly connected with each other than with others; this shall be explored in further detail when I look at assortativity in the follow section.

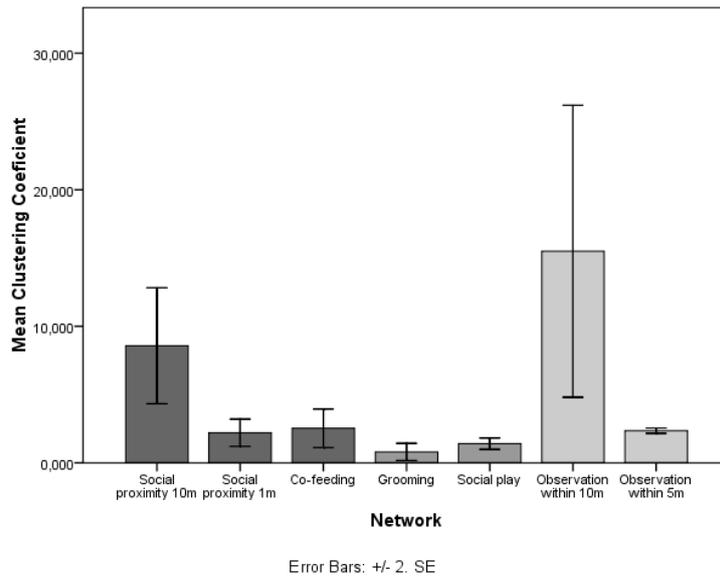
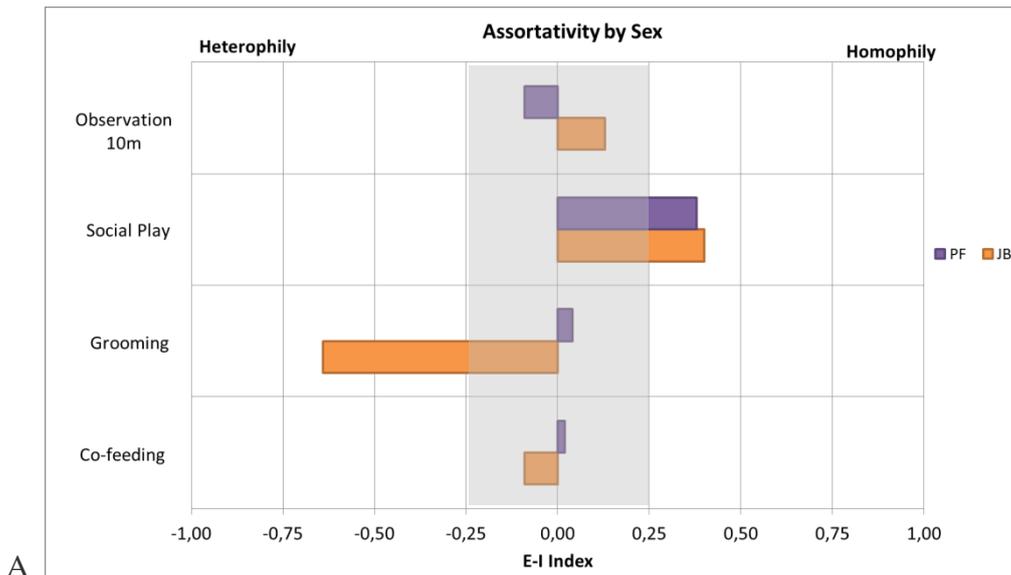


Figure 3.11 Mean Clustering coefficient for each of the social networks.

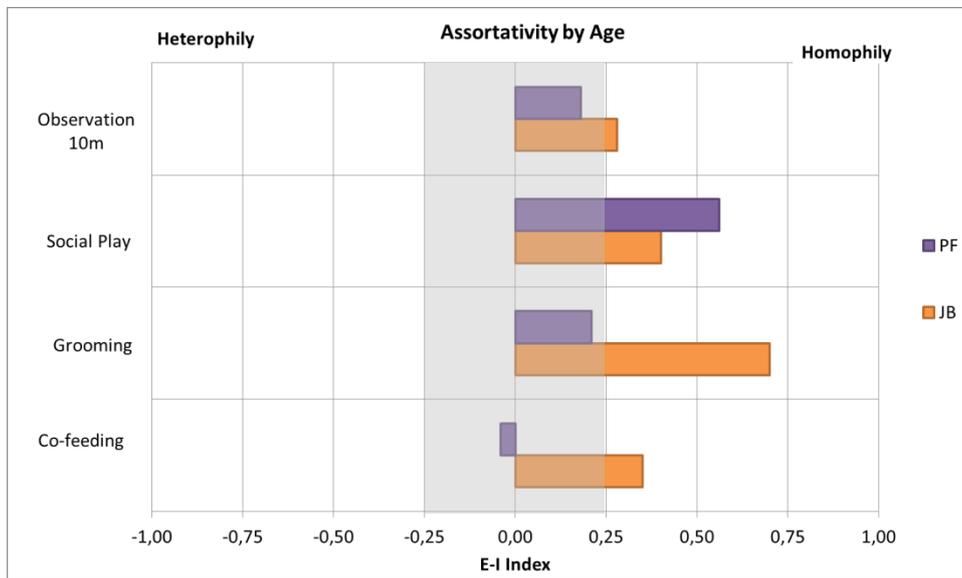
3.3.4 Assortative mixing

The social network measures presented above detected heterogeneity in how group members associate, interact and observe each other. Do individuals of certain classes (age, sex, dominance rank) interact preferentially with others of the same class? In order to answer this question, I calculated assortativity (Ucinet: E-I index) for sex, age and dominance rank of the different social networks, as a means to detect whether nodes (individuals) of a given class connect preferentially with nodes of the same class (homophily) or with nodes of different classes (heterophily) (Figure 3.12). Given that an E-I index of 0 equates to equal distribution of connections between individuals, here I decided to investigate further the cases where at least 25% of the connections were between individuals of different classes (-0.25) or within individuals of the same class (+0.25).

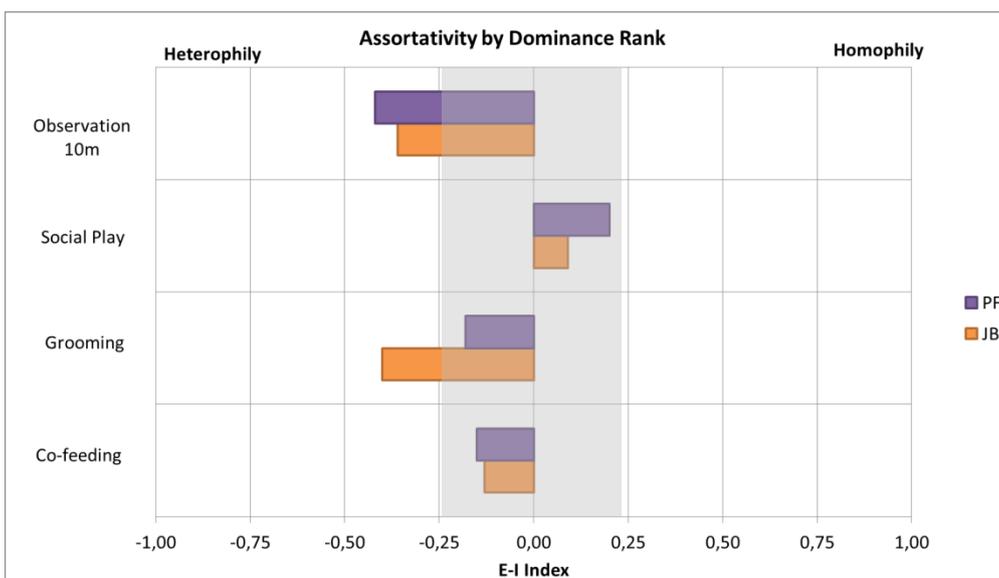
JB group's grooming network showed heterophily with regards to sex ($E-I \text{ Index}_{\text{Sex}} = -0.64$), indicating that grooming was more frequently performed between the sexes. Most grooming interactions were of males grooming females, followed by females grooming males (Figure 3.13A). JB's grooming network also exhibited homophily of age classes ($E-I \text{ Index}_{\text{Age}} = 0.70$), with more frequent grooming bouts between adults (Figure 3.13 B). Grooming also presented heterophily with regards to dominance ranks ($\text{Index}_{\text{Dominance}} = -0.40$) with grooming between high-ranking and mid-ranking individuals most common (Figure 3.13 C). In contrast, the grooming network of PF group showed no assortative mixing ($E-I \text{ Index}_{\text{Sex}} = 0.04$; $E-I \text{ Index}_{\text{Age}} = 0.21$; $E-I \text{ Index}_{\text{Dominance}} = -0.18$).



A

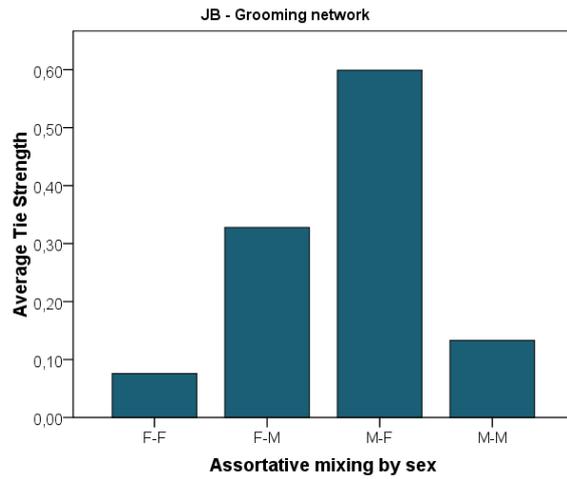


B

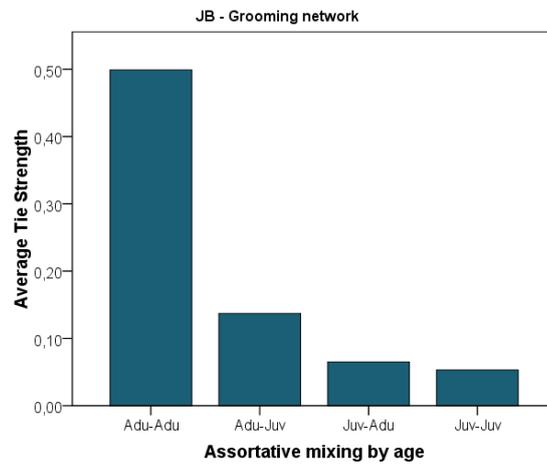


C

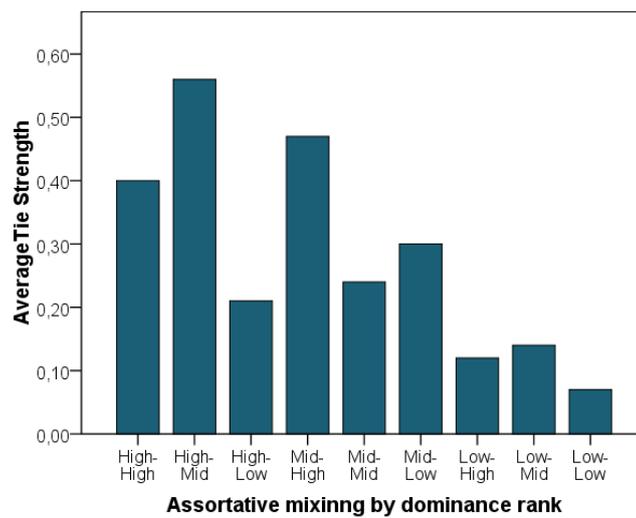
Figure 3.12 Assortativity by (A) sex, (B) age and (C) dominance rank in social networks for each group, Jurubeba (in orange) and Pedra Furada (in purple)



A



B



C

Figure 3.13 Assortative mixing between classes of individuals, by average tie strength, for grooming network in Jurubeba group. Groomer-groomee (e.g. M-F: indicates male grooms female).

Social Play networks in both JB and PF showed homophily of sex classes (JB: E-I $\text{Index}_{\text{Sex}} = 0.40$; PF: E-I $\text{Index}_{\text{Sex}} = 0.38$), indicating that social play was more frequent amongst same sexed individuals, in this case amongst males (Figure 3.14 A and B). The same network showed homophily of age groups in both groups (JB: E-I $\text{Index}_{\text{Age}} = 0.40$; PF: E-I $\text{Index}_{\text{Age}} = 0.56$), with juveniles playing with juveniles most frequently (Figure 3.14 C and D). No assortative mixing was found for Social Play networks with regards to dominance rank (JB: E-I $\text{Index}_{\text{Dominance}} = 0.09$; PF: E-I $\text{Index}_{\text{Dominance}} = 0.20$).

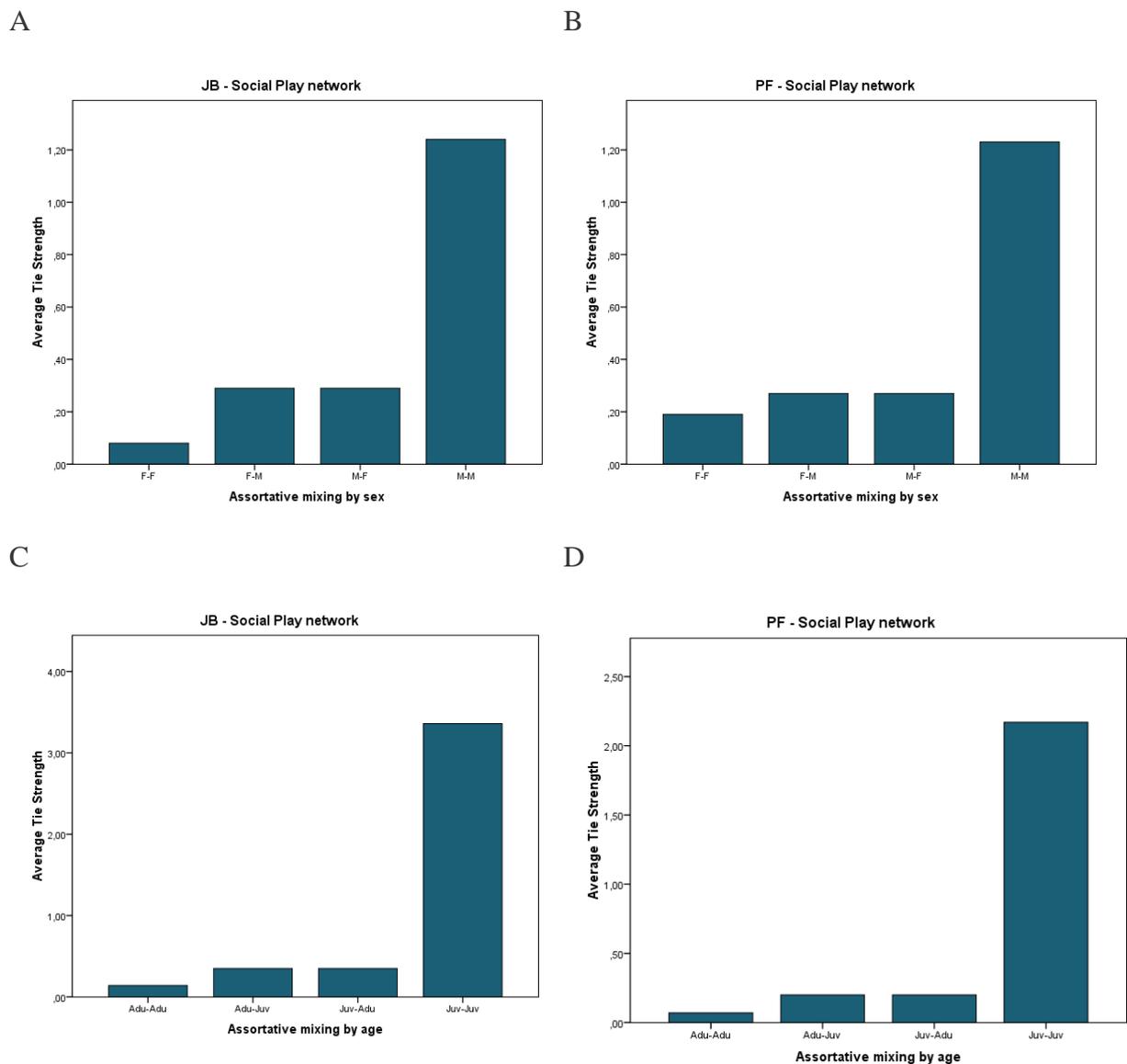
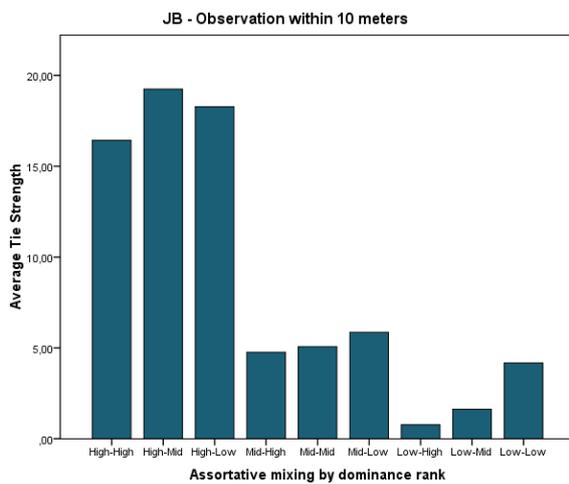


Figure 3.14 Assortative mixing by sex (A; B) and age (C; D). Average tie strength for social play networks in Jurubeba (A; C) and Pedra Furada (B; D).

Observation of conspecifics

Observation within 10 meter networks in both JB and PF showed heterophily of dominance ranks (JB: E-I Index_{Dominance} = -0.36; PF: E-I Index_{Dominance} = -0.42), indicating that observation was more frequent amongst individuals of different social ranks. In Jurubeba high-ranking individuals were more frequently the target of observation by conspecifics, regardless of the rank of the observer (Figure 3.15 A). In PF, however, mid-ranking individuals were more frequently targeted by conspecific observers, also regardless of the observer's rank (Figure 3.15 B). The contrasting results may be explained by the fact that for the lift-pull task experiment, the trained model in JB was a mid-ranking female, and the behaviour was quickly acquired by dominant individuals in the group, who thereafter monopolised the task. In Pedra Furada however, the monkey trained as a model was a subordinate male, and the behaviour spread mostly from him to mid-ranking individuals, before being acquired by high-ranking individuals. As the *opportunities* for social learning, only, are considered in this chapter the data are not normalised according to the frequency of successful manipulations performed by individuals (see chapter 5 for this analysis). Here the monopolisation of the task by high-rankers (JB) and mid-rankers (PF) is the important consideration.

A



B

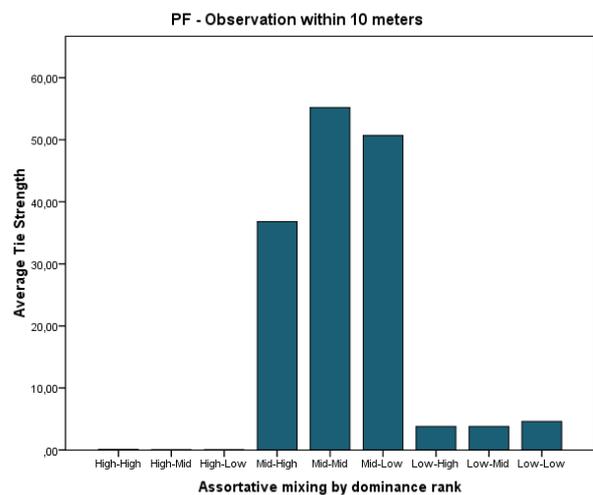


Figure 3.15 Assortative mixing by dominance rank. Average tie strength for observation within 10 meters networks in Jurubeba (A) and Pedra Furada (B).

3.3.5 Flow betweenness and network centralization index

Flow betweenness is a measure of a node's prominence in the flow of information through a network (Freeman 1991). The *flow betweenness centralization index* is a network-level measure calculated by averaging out the node-level measure, *flow betweenness*, for the entire network. Here I calculate it to determine whether, as a whole, the network flow was concentrated along paths including more central nodes (individuals).

A significant difference was found between the three types of social networks (one-way ANOVA: $F(2,11) = 8.403$, $p = 0.006$), with interaction networks presenting significantly higher *flow betweenness centralization indices* than association networks (mean difference = 0.11 ± 0.03 ; $p = 0.006$), as identified by a Bonferroni post hoc test. Comparing the networks separately, a significant difference in *flow betweenness centralization index* was also found ANOVA: $F(6,7) = 9.699$, $p = 0.004$). Grooming networks had a higher *flow betweenness centralization index* when compared to each of the association networks *social proximity within 10 meters* (mean difference = 0.19 ± 0.03 ; $p = 0.007$), *social proximity within 1 meter* (0.17 ± 0.03 ; $p = 0.013$) and *co-feeding* (0.17 ± 0.03 ; $p = 0.012$); and a tendency in the same direction when compared to *observation within 10m* (0.13 ± 0.03 ; $p = 0.057$) (Figure 3.16).

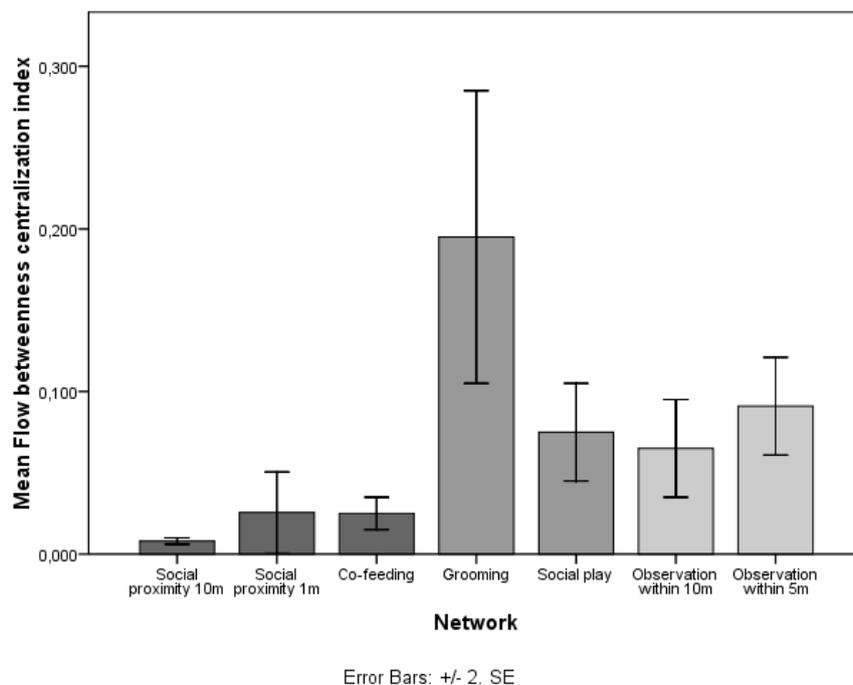


Figure 3.16 Flow betweenness centralization index each of the social networks.

Flow betweenness allows us to identify the key individuals in the networks in terms of flow. The more central an individual's position in terms of network flow the higher its flow betweenness. Plotting the distribution of flow betweenness for individuals allows a description of how group members vary in their roles as connecting paths through which information may flow (Figure 3.17). For co-feeding networks, group members presented similar flow betweenness; for the remaining networks the clearly skewed distribution of flow betweenness indicates that some individuals had very central roles in network flow compared to others.

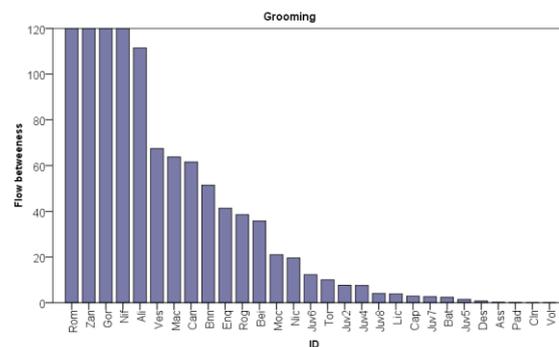
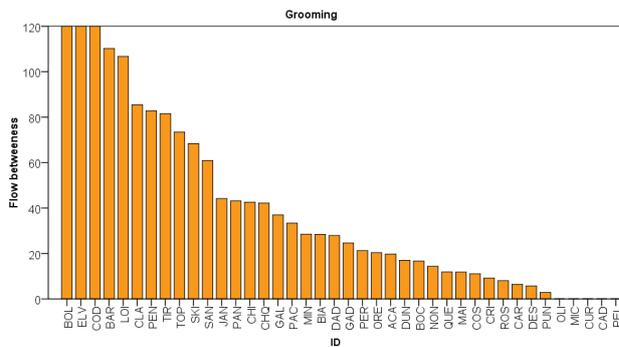
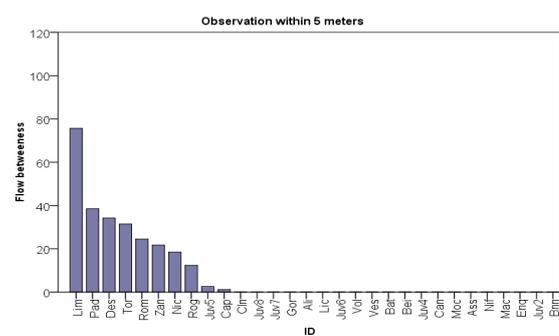
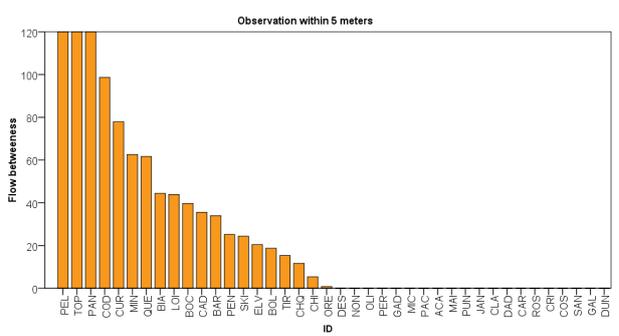
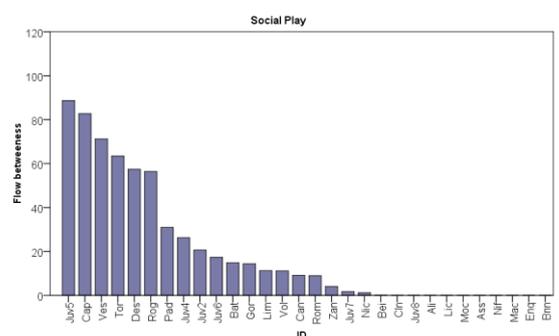
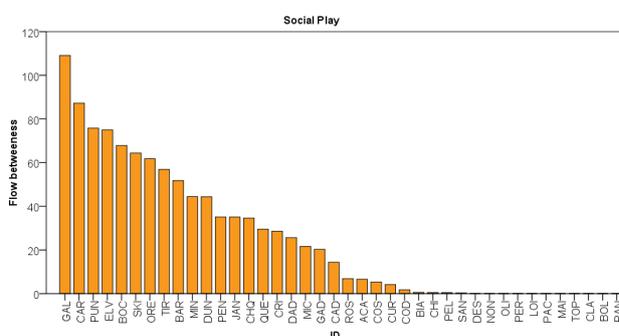
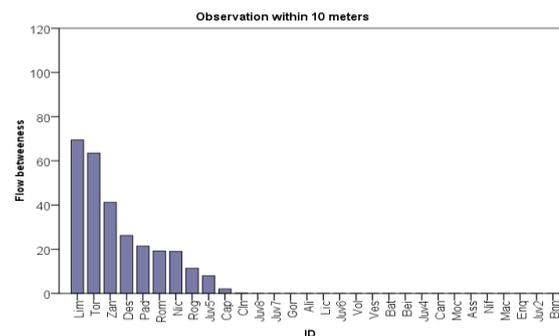
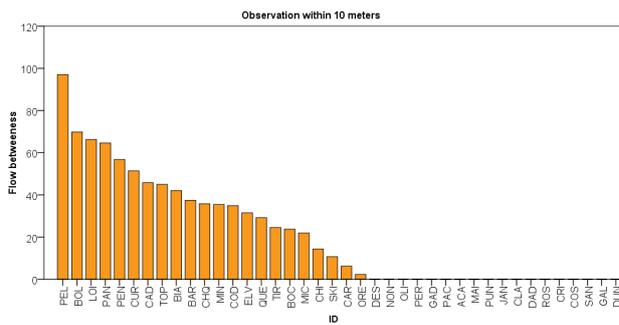
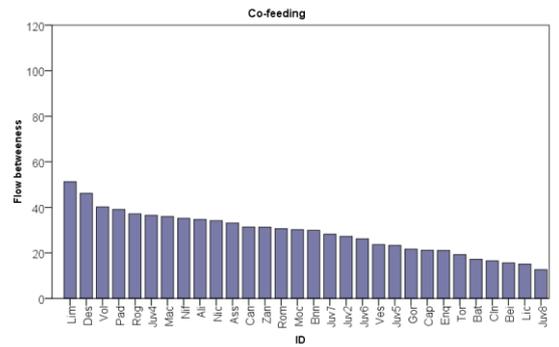
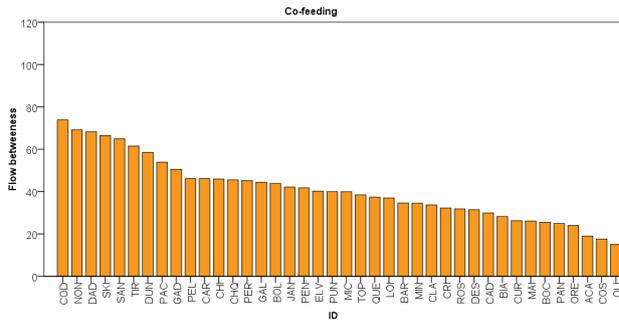


Figure 3.17 Flow betweenness of each individual for the several networks: on the left, Jurubeba group (in orange); on the right Pedra Furada group (in purple).

By calculating an average *flow betweenness* across all seven networks it is clear that overall some individuals hold potentially key positions in the potential social transmission of information (Figure 3.18). In Jurubeba the dominant male (BOL), and in Pedra Furada the dominant female (Rom), hold the most central position in terms of network flow. The varied distribution of flow betweenness shows that group members vary greatly in the likelihood of information reaching them.

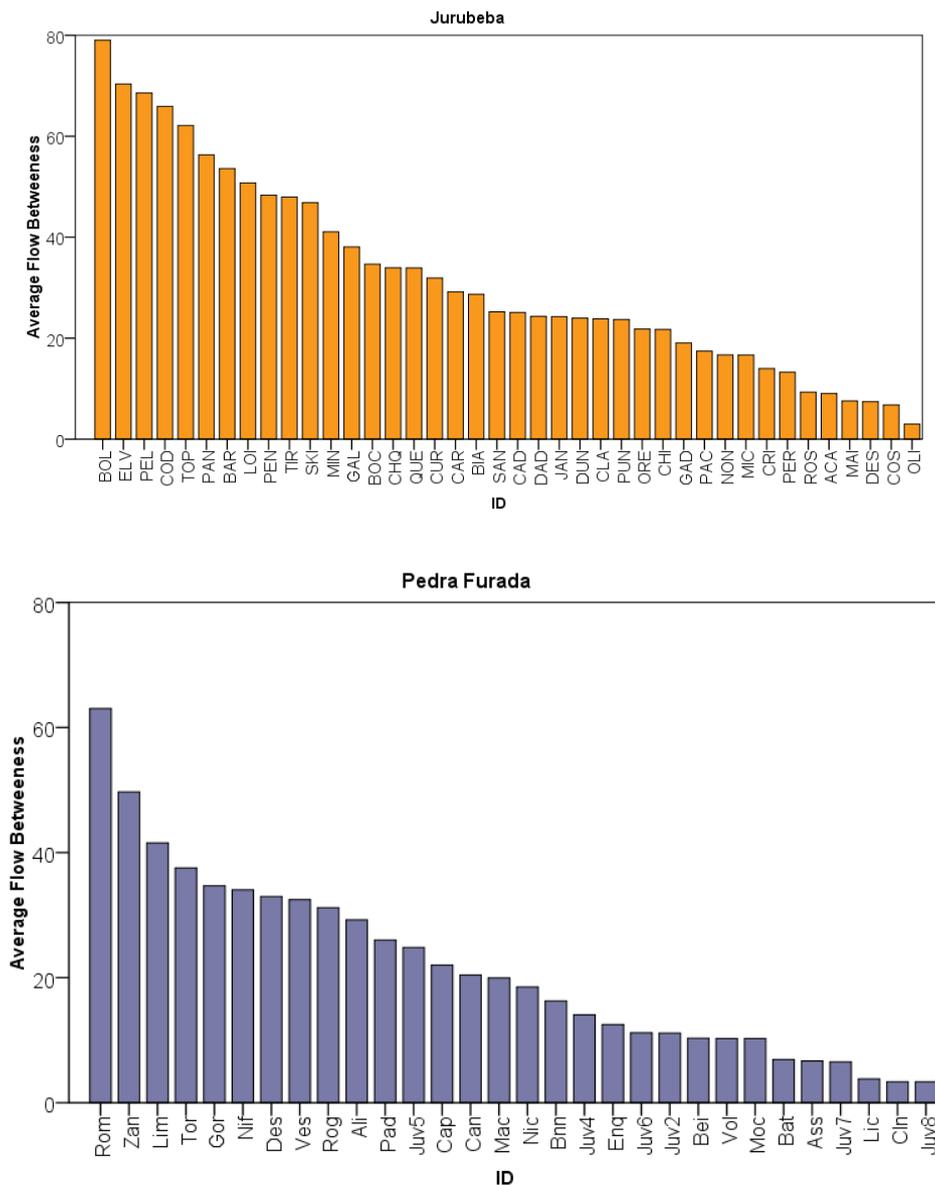


Figure 3. 18 Average Flow Betweenness from co-feeding, grooming, social play, and observation networks for each member of the groups, Jurubeba and Pedra Furada.

3.4 Discussion

Frequent behavioural coordination in space and time was recorded for group members during daily activities; representing between one fourth (PF) to half (JB) of the sampled time. Group differences, with JB presenting higher ratios of behavioural coordination in space and time than PF, might be due to JB having been sampled during the dry season and PF during the rainy season. During the dry season, lack of foliage means the monkeys might be exposed to higher predation risks, leading to more frequent behavioural coordination. Also, the dry season, with reduced and more clumped food resources, can result in pressure towards greater tolerance and behavioural coordination in time and space. Further data are necessary to address these hypotheses. Nonetheless, the frequent behavioural coordination in time and space indicate that ample opportunities for social learning were present in both the groups studied.

Cohesion network metrics differed substantially between association networks (social proximity at different distances and co-feeding) and interaction networks (grooming and social play). Association networks were saturated, that is, individuals were highly interconnected and the network composed of a single component. In contrast, interaction networks had sparser, more asymmetric connections between individuals and were often fragmented into components. Denser (i.e. more interconnected) networks would be conducive to non-specific social learning where information can be transmitted through many pathways, independent of the identity of the individuals. Fragmented and/or asymmetrical networks are more conducive to directed social learning in that specific pathways for the transmission of social information are present. These findings are in line with that predicted, according to the framework of Coussi-Korbel & Fragaszy (1995) for capuchin monkeys who hold an intermediary position in the egalitarian-despotic spectrum and thus are expected to have relationships conducive of both non-specific and directed social learning.

Observation networks, similar to interactions, were also sparse and fragmented, as well as highly asymmetric. This was due to the directionality that results from few models (individuals) being observed frequently by many naïve individuals. The network portraying total frequency of observations (irrespective of the distance from which observation occurred) presented high clustering coefficients in both groups. This finding indicates that the opportunities individuals had of observing conspecifics foraging on a clumped resource (the lift-pull task) were restricted to a few other group members. On average, each naïve

individual observed only one third of the available that models, indicating that they were probably restricted to observing those within the same clique only).

Previous studies of animal social networks show that social networks become less dense as group size increases (meerkats: Drewe & Perkins, 2015; primates: Kasper & Voelkl, 2009). The results here presented do not corroborate these findings, despite quite a pronounced difference in group size, both groups presented similar Density values across networks. The same studies describe a simultaneous increase in network clustering, with increase in group size, indicating that individuals interact more locally within cliques, rather than trying to maintain interactions with all group members (Drewe & Perkins, 2015). Again, despite group size variations, the groups here studied did not differ in terms of clustering coefficient. It is important to call attention to the fact that here I am comparing two groups only and, therefore, have little grounds to ascertain relevant differences. Nonetheless, it is noteworthy that the two groups showed great similarity in overall network metrics, in spite of differences in group size and in total frequency of behavioural coordination. Even though both groups showed similar network-level measures, on occasions the internal patterns of interactions were quite distinct.

Several networks presented some form of assortative mixing; indicating that often, there were more interactions or stronger association within individuals of the same class or between individuals of different classes. Grooming relationships presented strong assortative mixing in JB group, however little assortative mixing in PF. More importantly, the assortativity in the two groups were opposing. Grooming relationships in PF followed that commonly described as typical of capuchin monkeys, i.e. with a tendency for homophily between adult females, the philopatric sex. The literature (reviewed in Fragaszy et al, 2004) indicates that adult females are the more active groomers and are more likely to direct their grooming to other adult females in wild groups of several species of *Cebus* and *Sapajus*. JB group, however, deviated from this pattern with males more actively grooming females (and vice versa as opposed to the typical homophily). This may be a consequence of the presence of many large adult males besides from the alpha-male (BOL). Males more frequently groom the same females that follow them during their proceptivity (courting behaviour) (Coelho et al 2013). Here is an example of how dynamic the social relationships in a group might be and thus the importance of collecting data that will depict meaningful social networks, based on the behaviour spreading and on the social dynamics of the group at the time of the diffusion.

Social play networks also showed strong assortative mixing, and in this case relationships were similar for both groups. Homophily was present for sex and age-group with a

predominance of interactions between juvenile males. The highly fragmented social play networks are indicative that novel behavioural traits acquired in such social contexts would be unlikely to reach the entire group. This echoes what Susan Perry described for white-faced capuchins (*Cebus capuchinus*) and their ritualised games (e.g. eye poking game, Perry et al, 2003). These behaviours required high degrees of behavioural coordination in space and time, a pre-existing close relationship during play activities, and exhibited restricted diffusion.

Grooming relationships presented the highest indices of flow betweenness centralization index; meaning that information flowing through these networks would likely be directed through pathways that join central individuals in that network. This finding is especially interesting because it resonates with the findings of the next chapter, where NBDA detected social learning of the lift-pull task based on grooming networks. In the general discussion, I argue further why grooming might be a particularly good network for portraying the social context in which the monkeys learn to solve a foraging task, despite this, a priori seeming counter intuitive.

Besides social opportunities to learn, as described previously, one might look in further detail at which individuals are differentially attended to by conspecifics, while they are performing certain behaviours. Data on observation events during a two-action task experiment, presents us with the chance to look at this motivation to attend to certain models. Amongst the possible observational targets (as indicated by connections present) some are chosen preferentially (as indicated by strength of connections), a fact clearly portrayed by the skew present in the distribution of flow betweenness. This skew means that some individuals are positioned within the observation network, in a way, that information flowing through it would more likely flow through these individuals. Thus, individuals (nodes) with high betweenness centrality play a crucial role in the spread of information. In the groups studied, dominant individuals, particularly the dominant male, were found to be more central than other group members in both the socio-positive networks (e.g. co-feeding, grooming and social play) and in the observation networks. Observation networks, on the other hand, displayed assortative mixing based on dominance ranks. Thus, dominant individuals monopolise the rewarding task and by doing so generate social tensions around it, modifying the landscape of tolerance, and consequentially the social learning opportunities. In such scenarios the pathways (i.e. the opportunities) of social learning are directed along the strongest of tolerant relationships. This constitutes a form of directed social learning (Coussi-Korbel & Fragaszy, 1995), where information passes through subsections of the group, here subsections that even within a limited tolerance space still allow for transmission to occur.

In this chapter I have described the opportunities monkeys have of learning from group members and of how the social context can bias these learning opportunities. In the following chapter I apply NBDA to a field experiment in order to detect whether the social context (described in the form of a social network) influences the spread of a novel trait between group members. Thus, in the next chapter I test whether novel information diffuses through the groups following pathways through the networks analysed in this chapter. As NBDA takes into consideration the strength of connections in a social network when determining the likelihood that information will spread from one individual to the next, it is essentially detecting whether identity-specific directed social learning is occurring.

CHAPTER 4:

IDENTIFYING SOCIAL LEARNING IN WILD BEARDED CAPUCHIN MONKEYS (SAPAJUS LIBIDINOSUS): AN OPEN DIFFUSION EXPERIMENT WITH TWO FORAGING TASKS

In the previous chapter, I described the opportunities for learning in the social context in which these wild capuchin monkeys live, by integrating social network analysis and the directed social learning framework. In this chapter, I combine social learning field experiments and methodologies, developed for identifying social learning in naturalistic contexts, with the intent of empirically identifying social learning in the wild capuchin monkeys (*Sapajus libidinosus*) here studied.

4.1 Introduction

Behavioural traditions are behaviours shared by members of a social group and acquired by new practitioners through socially aided learning (Fragaszy & Perry, 2003). The existence of behavioural traditions in non-human animals has been, in the last decade, the subject of intense debate (Fragaszy & Perry, 2003, Laland & Janik, 2006, Laland & Galef, 2009). One means of identifying behavioural traditions is the group contrast approach (also known as comparative or ethnographic approach), which documents how behavioural repertoires differ between social groups (eg. Whiten et al., 1999; Ottoni & Izar, 2008). If the variation in repertoire cannot be attributed to intrinsic genetic characteristics of each population or individual interaction history of animals with their own environment, then, by exclusion, the behaviour in question is deemed to be spreading by social learning and therefore constituting a behavioural tradition (Galef, 1976).

The group-contrast approach has been strongly criticized by authors who argue that it is logically impossible to prove in absolute terms the absence of ecological or genetic factors (Fragaszy & Perry, 2003, Laland & Janik, 2006, Laland et al, 2009). Furthermore, the group contrast approach is subject to (i) false negatives by denying the cultural nature of a behaviour because it is present in several or all populations and (ii) false positives, when it identifies a behaviour as cultural due to group differences, even if these differences are not the result observed result of social learning (Fragaszy & Perry, 2003). Nevertheless, the group-contrast approach is an important tool for identifying putative behavioural traditions van Schaik, however consensus seems to have been reached by researchers that, to be definitively classified as a behavioural tradition, naïve individuals must be seen to acquire the

novel behaviour through social learning (Fragaszy & Perry, 2003, Laland & Galef, 2009). Social learning is here defined as “learning that is facilitated by observation of or interaction with other individuals or its products” (Hoppitt & Laland 2013, p. 4; Heyes 1994).

Another approach to studying behavioural traditions has been to study the spread of a new behavioural trait among group members (Huffman, 1996).). Examples of this approach are the now classic studies of innovation and diffusion of new behaviours in Japanese macaques (*Macaca fuscata*) (e.g. potato washing, separating wheat from sand and stone-handling; Huffman, 1984, 1996; Huffman; Quiatt, 1986; Itani; Nishimura, 1973). Although many of these innovations occurred as a consequence of human provisioning, they constitute an interesting opportunity to study the origin of a behavioural innovation and describe the network of individuals in which the new behaviour spreads.

Recording the inception and diffusion of a novel behavioural trait in the wild, however, depends on opportunistic observations. Field experiments can therefore provide a means to study social learning and the establishment of behavioural traditions (Kendal et al, 2010, Reader & Biro, 2010). The experimental introduction of a novel behaviour (or of a behaviour conducted in a novel context) allows us to observe the (i) inception of a novel behaviour, (ii) its appearance in other group members and (iii) whether social learning underlies the diffusion of the behaviour. In addition, the experimental set-up allows us to register all occasions of the transmission of information between individuals, since it only occurs when the researchers provide the means to produce the novel behaviour (Hoppitt & Laland, 2013). Finally, by working with wild groups we are able to study social learning within the complex ecological and social context in which it occurs (Coussi-Korbel & Fragaszy, 1995).

Two-action task experiments have been conducted with captive capuchin monkeys showing that these monkeys are capable of social learning and that such capabilities can lead to the establishment of behavioral traditions (Custance et al.,1999; Dindo et al., 2009; Crast et al., 2010). If, on the one hand, studies with captive groups have the advantage of controlling the experimental variables, on the other hand, studying wild populations has the advantage of working with the complex ecological and social contexts in which social learning actually occurs. Coussi-Korbel and Fragaszy (1995) call attention to how the social learning field has been dominated by studies focused on social learning mechanisms in highly controlled settings, usually involving dyads in isolated cubicles. These authors questioned the ecological validity of the dyadic model-observer set-up, since in the natural environment social learning takes place within a structured social context. They advocate the need to give due attention to

the specific social context in which a particular social animal lives, as this reflects the propensity that a given animal will have to learn from group members.

The use of experimental approaches such as the two-action task with wild populations is very recent in the study of social learning with wild primates (van de Waal et al 2010; Kendal et al, 2010b; Schnoell & Fichtel, 2012). The main scientific challenge posed by these studies - and that this thesis addresses - is how to identify social learning in a naturalistic context based on data collected from the diffusion of a new behaviour. New data analysis methodologies (Franz & Nunn, 2009; Hoppitt & Laland, 2011; Kendal et al, 2009) are proving to be a promising development in identifying social learning in wild primate populations.

Network Based Diffusion Analysis (henceforth NBDA), as proposed by Franz & Nunn (2009), is able to identify the occurrence of social learning by assessing which of two agent-based models best explains the spread of a novel behaviour. The first model assumes that individuals learn probabilistically irrespective of their connections to others (asocial learning). While the second model assumes individuals learn using a combination of asocial learning and also from one another based on how strongly connected they are (social learning). Both models are fit to the observed diffusion data and then maximum likelihood methods (AIC and Akaike weights) are used to determine which model is most representative of the observed diffusion data (Akaike, 1998).

NBDA “makes use of the fact that socially learned traits will spread more quickly between animals that have strong connections in a social network” (pg 1830, Franz & Nunn, 2009). Therefore, in line with the argument made previously, regarding the need to take into account the complex social context in which learning occurs (Coussi-Korbel & Frigaszy, 1995), this analysis takes into account that individuals vary in the frequency of interactions, or strength of association, with one another.

In the current literature, NBDA has been used in the study of social learning of several wild animal populations: starlings (*Sturnus vulgaris*; Hoppitt et al, 2010, Boogert et al 2014), ring-tailed lemurs (*Lemur catta*; Kendal et al, 2010), red-fronted lemurs (*Eulemur rufifrons*; Schnoell & Fichtel, 2012), songbirds (Family: Paridae; Aplin et al, 2012), humpback whales (*Megaptera novaeangliae*; Allen et al., 2013), three-spined sticklebacks (*Gasterosteus aculeatus*; Webster et al, 2013) and chimpanzees (*Pan troglodytes*; Hobaiter et al, 2014). Most of these studies detected social learning using NBDA, while in some (ring-tailed lemurs and red-fronted lemurs) the analysis was incapable of finding a significant fit for either of the models (asocial or social learning).

Option-bias analysis (henceforth OBA) is another methodology aimed at identifying social learning in wild groups (Kendal et al, 2009). Social transmission has been defined as “cases of social learning that result in increased homogeneity of behaviour of interactants that extends beyond the period of their interaction” (Hoppitt & Laland, 2013; Galef, 1976). OBA is based on this commonly held premise that social learning will generate greater within population homogeneity in the frequency of behavioural variants, than would be expected by chance (Kendal et al, 2009).

It is not always the case that researchers can observe and track the spread of a naturally occurring novel behaviour among group members. Repertoire-based methods allow us to infer and quantify social transmission of a behaviour based on a “snap shot” of the group at a given point in time. Thus, option-bias analysis (OBA) is a method proving to be an important analytical tool in detecting behavioural traditions based on group behavioural repertoires.

OBA has been applied in studies of social learning of both captive and wild animals: callitrichid monkeys (*Callitrichidae*; Kendal et al 2009), chimpanzees (Huffman et al 2010, Kendal et al 2015), wild ring-tailed lemurs (Kendal et al 2010), lemurs (*Varecia variegata* and *Varecia rubra*; Dean et al 2011), red-fronted lemurs (Schnoell & Fichtel, 2012) and wild meerkats (*Suricata suricatta*; Hoppitt et al, 2012). Most of the studies listed above identified social learning using OBA. Exceptions being Dean et al (2011)’s study of captive lemurs and Hoppitt et al (2012) study of wild meerkats; despite these studies having found evidence of social learning from applying other methodologies.

Capuchin monkeys have been the subject of several cognitive studies; including studies of social learning abilities (see Fragaszy et al, 2004 for a review). Furthermore, group differences reported for wild populations could be indicative of behavioural traditions (Ottoni & Izar 2008, Mendes et al 2015) in capuchin monkeys, although empirically not as of yet demonstrated. Studies with captive groups of capuchin monkeys have shown that these new-world monkeys are cable of social learning (Custance et al, 1999, Dindo et al, 2009, Crast et al, 2010). However, these studies were conducted within controlled experimental set-ups and captive populations which might not be representative of the natural social context in which learning occurs. Here I aim to bridge this gap by applying new methods designed specifically for studying social learning in a social context. For such we conducted field experiments with wild capuchin monkeys in an attempt to verify the occurrence of social learning based on the patterns of spread of two new behavioural traits and on the final distribution of traits in the

group repertoire. To our knowledge, this is the first such study of social learning to be conducted with wild capuchin monkeys.

4.2 Methods

4.2.1 Study site and subjects

This study was conducted at the Serra da Capivara National Park (PNSC) in Piauí – North-eastern Brazil. Data collection occurred between May 2012 and June 2013, with two non-sympatric groups of bearded capuchin monkeys (*Sapajus libidinosus*). We studied 86 individuals living in two habituated groups: JB (N=51) and PF (N=35) (for more details see chapter 2 - Methods).

Sapajus libidinosus at SCPN live in multimale–multifemale groups of 30 to 51 individuals with a 1:1 sex ratio, female philopatry, and male dispersal. They exhibited non-linear hierarchies. However, hierarchy ranks can be partially identified amongst females and among males separately, with a clearly identifiable alpha male (see Appendix A). Like other capuchin monkeys, *S. libidinosus* is believed to hold an intermediary position in the egalitarian-despotic spectrum of primate societies, with infants and juveniles being highly tolerated by all group members (Fragaszy et al, 2004, Coussi-Korbel & Fragaszy, 1995).

4.2.2 Experimental set-up and procedures

Two extractive foraging experiments were conducted with the JB and PF groups, the lift-pull task and the tube task. The first task could be solved one of two ways, *lift* or *pull*, following the two-action task paradigm. The second, consisted of a tube containing juice that was just beyond arms reach, and could be obtained by any means the monkeys chose to use. A novel object experiment was also conducted in order to verify individual's neophobia levels.

Lift-pull task – open-diffusion with trained demonstrators

The Lift-Pull task consisted of a matte white acrylic box 20(w) x 30(h) x 20(d) cm. The two functional parts of the task were a blue rectangular plate (10 x 8 cm), that could be lifted perpendicular to the front of the box, and a green knob (7 x 5 cm) at the end of a protruding rod, that could be pulled away from the front of the box. Both actions (Table 4.1), when successfully executed, triggered an internal mechanism that released a batch of food rewards into a tray below (Figure 4.1). The functioning part of the box, rectangular plate or green knob, would then return to its initial position by a system of internal springs. The internal mechanism would automatically pre-position another batch of food rewards, ready for the next trial (manipulation by a monkey). This meant the researcher did not have to re-bait the box at every trial, and interference with the natural dynamic of monkeys interacting with the task was kept to a minimum. Both actions for solving the task (*lift* and *pull*) resulted in the same quantity and quality of food rewards (a mixture of corn, peanuts and raisins).

Table 4.1 Definitions of actions on extractive foraging apparatus.

Task	Action	Definition
<i>Lift-pull task</i>	Lift	To move the blue rectangular plate perpendicularly to the front of the box until the food dispensing mechanism is actioned
	Pull	To move the knob (attached to the tip of a protruding rod) away from the front of the apparatus until the food dispensing mechanism is actioned
<i>Tube task</i>	Tail dipping	To place the tail in the tube, letting the fur absorb the juice, then retrieving it and liking or sucking the juice off the fur.
	Stick tool as probe	To prepare a stick probe, or use on of the available probes (prepared by other monkeys) to dip into the tube. The stick probe is then retrieved from inside the tube and juice is licked off the wet tip.
	Stone tool as hammer	To use a stone as a hammer to hit against the sides of the tube. Juice is then spilt on the sides of the tube (which can be reached with their hands, or squirted out the top of the tube and then licked from the sides.

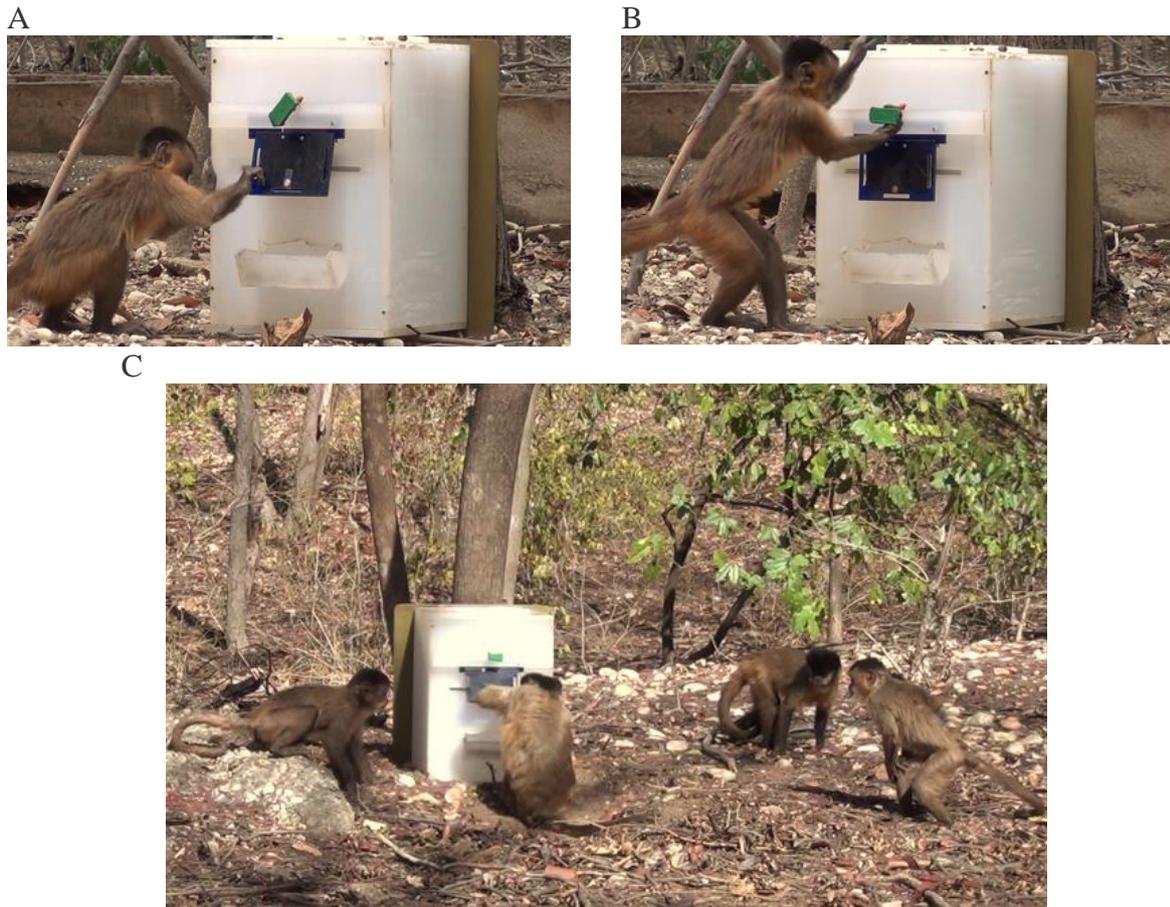


Figure 4.1 – The Lift-Pull task set up with JB group. A juvenile male solving the task by (A) option *lift* and (B) option *pull*. Food reward slides down a shaft into the tray at the bottom of the task. (C) within a 5-meter radius of box, an adult male (LOI) solves the task using *lift*. At the moment the food reward was released three other monkeys (an adult female, TOP, and two juvenile males, QUE and MIN) were observing.

The few two-action task studies carried out with wild primates so far (e.g. Kendal et al, 2010; Schnoell & Fichtel, 2012; Gunhold et al, 2014), have relied on dominant individuals monopolising the task, learning the seeded behaviour and having conspecifics watch them performing the seeded alternative. A pilot study conducted with semi-free capuchin monkeys, at Tiete Park, Sao Paulo, however, indicated it would be unlikely that an individual capuchin would monopolise the task. I therefore attempted to seed each group with a trained demonstrator. To do so, I attracted a monkey away from its social group and trained it out of sight of other group members. In JB group a mid-ranking adult female (CHI), received a single training session out of sight of group members, encompassing 4 full demonstrations of

the action *lift*. When the open diffusion phase started, CHI was the first to solve the task and she did so by using the option *lift*. Thus, it is likely that she learnt to solve the task, from my demonstrations. In PF, a mid-ranking juvenile male (Lim) received a single demonstration of the alternative form of solving the task *pull*, after the rest of the group had departed. Immediately after this single demonstration, Lim approached the box and solved the task using the same technique he saw me demonstrating.

To further the goal of seeding one option in each group (*lift* for JB and *pull* for PF), the task was initially presented, to the entire group, with the appropriate option functioning and the alternative locked. This experimental setup was maintained until approximately 10% of each group (five subjects in JB; three subjects in PF) had solved the task at least once using the seeded action. Such was achieved after the first day for JB and the second day for PF. The open diffusion phase then began with the lift-pull task being presented to each group with both options functioning.

The open diffusion experiment ran for a total of 14 days for each group. However, as the monkeys would, on occasion, go days without passing through the experimental setup area, the open diffusion occurred over a total of 38 field days with JB group (September-October 2012) and 21 days with PF group (March - April 2013). The lift-pull task was offered for as long as the group remained in the experimental area or until they had consumed the established limit of two kilograms of food rewards per day. On average, Jurubeba group spent 90 minutes around the apparatus, when they encountered it, before setting off on their daily routes; this resulted in a total of 19 hours and 20 minutes of experimentation. Pedra Furada group spent, on average, 120 minutes per experimental day around the apparatus, with a total of 29 hours and 15 minutes of experimentation.

To accurately record the activities at the task and the opportunities the monkeys had of observing conspecifics solving the task, the lift-pull experiment was concurrently filmed with two video cameras: the first was zoomed in on the box to clearly register the manipulations of the task (Figure 4.1 A and B), whilst the second filmed the task and a five-meter radius around it (Figure 4.1 C). Furthermore, I narrated to the video camera the identity of all monkeys within a ten-meter radius of the box and whether these individuals had their heads oriented towards the box when a demonstration occurred, to provide an indicator of the opportunities of observing the task being solved.

Videos were coded independently by two researchers (myself and M. Miguel). We registered (i) which individuals solved the task, (ii) latency from the beginning of the experiment until each successful task solution (iii) which of the two options (*lift* or *pull*) was

used, and finally, (iv) the identity of the monkey(s) who observed the task being solved by a conspecific and (v) from what distance they observed the task being solved (Table 4.1).

The data pertaining to who used *lift* or *pull* to solve the task and who observed this were input into the OBA and NBDA respectively. We used the data to build observation networks (Figure 4.5) where the edges' (connecting lines) thickness represents the frequency with which a monkey (node) observed another monkey (node) solving the task. The observation networks at different distances were used to inform the social model of the NBDA in an attempt to verify whether observational learning (requiring close proximity) was occurring.

Lift-Pull task - asocial control

Data upon response to the lift-pull task by control individuals only able to use asocial learning, was carried out between December 2013 and February 2014, with captive capuchins in Edinburgh Zoo. The monkeys were tested with an identical replica of the functioning front of the lift-pull apparatus used with the wild population. Once more, they could solve it using the same two actions: either lifting the blue plate or pulling the green knob. The task was presented to both captive groups of capuchin monkeys at the Living Links: East (N = 15) and West (N = 14). The monkeys were tested individually as a means to determine if either of the two actions for solving the lift-pull task was more likely to be individually discovered than the other. If a bias is identified, then the relative probability of discovering each technique may be included in the subsequent Option-bias analysis.

Each individual was voluntarily isolated with the lift-pull task for a total of 5 minutes or until he/she solved it 10 times, whichever ever happened first. Each monkey was given 3 such trials on separate days. The monkeys came into the isolated cubicles voluntarily and were allowed to leave when they decided to; in two cases (a female with an infant and a juvenile) indicated a desire to leave the isolation cubicle and the trial was terminated before 5 minutes. The monkeys were rewarded every 30s with raisins for remaining in isolation in the experimental cubicle and with a full peanut (preferred reward) each time they solved the task.

The interaction of each monkey with the apparatus was filmed and, from the video, I coded (i) whether the individual solved the task and, if so, (ii) which action (*lift* or *pull*) was used and (iii) the frequency with which they solved the task using each of the two actions.

Tube task – open diffusion

The tube task, consisted of a 54cm-long tube (11cm in diameter) with fresh mango pulp (100g per tube) at the bottom - just beyond the reach of an adult male's arms (Figure 4.2). On the first day, a single tube was fixed to a tree in the experimental area and the monkeys were allowed to solve the task (drink juice from the tube), however they chose to do so. The experiment ran until 300g of mango pulp had been consumed. On the following two days, three identical tubes were placed in the experimental area, 10 meters apart, roughly on the vertices of an equilateral triangle. This was done to prevent monopolisation of the task by dominant individuals, enabling more group members to interact with the task. The same protocol was carried out with both groups.

Each tube was filmed by a researcher (myself and two field assistants, B. Rawlings and C. Corat) who also narrated to the camera the identity of the monkeys with their head orientated towards the task whilst it was being solved, and who were beyond the range of video recordings. The experiment ran for approximately 500 minutes in total over 6 days: JB: 255 minutes and PF: 249 minutes. From video recordings I. Smith, following inter-observer reliability training and scoring with myself, coded: (i) the identity of the monkey solving the task successfully, (ii) the techniques used to access the mango pulp. Three behaviours were predominantly used to solve the tube task (i) tail-dipping, (ii) using sticks as probes and (iii) using stones hammers to bang on the tube. From video recordings (images and narrations) the identity of individuals observing the tube task being solved from within 10 meters distance, was recorded (Table 4.1, Figure 4.2).

Novel objects – measuring neophobia

Both groups of wild capuchins were presented with three novel objects: a fluffy toy, a football and a sink plunger in a randomised order. Each object was presented to the group five times throughout the day in 5 minute-long trials, with no less than 15 minutes between presentations. The objects were placed in different locations within the area the monkeys were using that day. The experiment was filmed from the moment the object was placed in the chosen location until it was removed. From the videos, I. Smith, following inter-observer reliability training and scoring, coded (i) the identity of the monkeys, (ii) their latency to come within 1 meter of the novel object (approach the object), (iii) their latency to physically touch the novel object (with the hands or nose) and (iv) the frequency and duration of interactions with each object. Data from this experiment were used to determine to which extent the order of individuals interacting with the foraging tasks (lift-pull task and tube-task)

could be explained simply by neophobia (see Appendix B for further details on the novel object experiment).



Figure 4.2 Tube task experiment with the Pedra Furada group: (A) adult male (Nic) trying to reach the mango pulp with his hands, without success, (B) adult female (Ali), with infant on her back, using tail-dipping technique, successfully, (C) dominant male (Tor) using a stick probe to solve the task successfully while being observed by conspecifics.

Inter-observer reliability

Videos from the lift-pull experiment were coded by two independent researchers: all footage of PF group was coded by M. Miguel and all footage of JB group was coded by me. To test for reliability we each ‘blind’ coded 2 hours (approximately 10% of the total footage time) of each other’s videos. Very good inter-observer reliability was found, according to Cohen κ scores, for the identity of the monkey manipulating the task (0.90), the action being performed on the task (0.92), and which conspecifics were observing (head directed towards task) the manipulations (0.82).

Videos of the tube task and novel object experiments were coded exclusively by I. Smith. Extensive inter-observer training was carried out, at the beginning and during coding, to confirm that I. Smith was correctly identifying the monkeys and coding their behaviours consistently.

4.2.3 Behavioural observations

Focal and All Occurrences sampling was conducted outside the experimental sessions, in order to determine social dynamics between group members and to characterize the dominance relationships between individuals. Each focal sample was 5 minutes long, with records taken of monkeys in proximity every minute. Subjects were sampled in a randomized order (for further details refer to section 3.2.1).

Data from the Focal and All Occurrences sampling were used to construct social networks, namely social proximity, co-feeding, grooming and social play, (for further details on how the social networks were constructed refer to section 3.2.2). The social networks represent opportunities one monkey has of learning from another and were used for the Network-based diffusion analysis, where the connections represent possible routes for the diffusion of information pertaining to extraction of rewards from the foraging apparatus (lift-pull task and tube task).

4.2.4 Statistical methods

Standard inferential statistics

To examine whether observations of specific manipulations (such as lift or pull) might be predictive of the manipulation options later performed by the observer, I conducted a linear mixed model analysis of these variables using SPSS 14. A significant fit between the response variable (proportion of lift manipulations performed) and the main predictor (proportion of lift manipulations observed) would be indicative that observational learning was occurring. The monkeys who were trained (N=2) and those who solved the lift-pull task during the seeding phase, when only one option was available (N=5), were excluded from this analysis.

Option-bias analysis

The option-bias analysis (OBA) is based on the assumption that social learning will generate greater within group homogeneity of behaviour than would be expected by chance or asocial learning alone (Kendal et al, 2009). Here I applied the randomization version of OBA to the data (R function provided by the Laland Lab freeware site: <http://lalandlab.st-andrews.ac.uk/freeware.html>). In this version the null hypothesis is that individuals in the same group are no more likely to use the same option than those in different groups. Thus, to generate a null distribution, a randomised procedure is conducted, where the assignment of individuals to groups is arbitrary to the option used for solving the task. If a higher homogeneity of the option is actually observed within groups than between groups, the null hypothesis can be refuted and social learning is said to be responsible for the variation in group repertoires.

OBA takes into consideration the non-independence of option choices by the same individual, using randomization procedures (Kendal et al, 2009). Trained demonstrators are accounted for by constraining them to their original group during the randomization procedure. Furthermore, possible biases in the options due to attributes of the task (such as the asocial likelihood of discovery of each option) can be accounted for by inputting variables from the asocial control individuals.

The novelty of the lift-pull task means it is unlikely the wild capuchin monkeys would show propensities towards using one action over the other. Still, affordances of the task, such as one of the actions being easier to discover or more salient to the observer, might result in an option-bias that would be unrelated to social learning. To address this matter was asocial

control data was collected with captive capuchins at Edinburgh zoo. The underlying bias for the use of *lift* versus the use of *pull* options was calculated from the asocial control data and input into the analysis. The method uses the underlying biases in option use from the asocial control when conducting power analysis and assessing estimates of Type 1 error.

Network-based diffusion analysis

Network-based diffusion analysis is based on the underlying assumption that socially transmitted behaviors should spread at a higher rate between individuals who are more strongly connected i.e. associate and/or interact more frequently (Franz & Nunn, 2009). NBDA requires two sets of data: (i) a list of when each individual acquired the novel trait and (ii) a social network that informs the strength of connection between group members. The first set of data, when individuals acquired the trait, is used for calculating the rate of diffusion and is input into the analysis as the time, or order, of acquisition of the trait. These two forms of quantifying the diffusion are named *time of acquisition diffusion analysis* (TADA) and *order of acquisition diffusion analysis* (OADA). I opted for running both TADA and OADA from Hoppitt and collaborators (2010) in its version 2.1). Both analyses take into consideration that asocial factors might affect the rate of diffusion alongside social factors. Therefore one model is purely of asocial factors, that is the social parameter is set to zero ($s=0$), and the other model is of *social and asocial learning*, where the rate of diffusion is a function between the asocial factors and the strength of the connections between individuals according to the social network data (social parameter s). Social transmission is said to have occurred when the model that includes s presents a better fit (having an AIC value at least 2 units lower) than a model where $s=0$. To inform the social model, the second set of data required by the NBDA, three observation networks were used: (i) the *total* observation network portrayed all the observations of the lift-pull task being solved from within 10 meters of the apparatus, (ii) observation network including only observations by conspecifics *within 5 meters* of the task being solved and (iii) observation network including only observations by conspecifics *more than 5 meters* from the task. The strength of connections (edges) between group members represents the frequency with which the monkeys were registered observing each other's successful activities at the task (for further details on the observation networks see sections 3.2.2 and 3.3.2 of previous chapter).

Five individual-level parameters were used to inform the asocial model. This was done to ascertain whether the rate of diffusion of the trait was a consequence of the social

opportunities of learning and not an artefact of individual-level variations. For example, dominance hierarchy is a factor likely to influence the rate of diffusion. The monopolisation of the task by dominant individuals, as well as the avoidance knowledgeable subordinate individual's may have of solving the task in the presence of dominant individuals, can slow down the rate of diffusion, which could, in turn, lead to the erroneous identification of social learning. To avoid this type I error, two dominance ranks, I&SI rank (Vries, 1998) and high, mid or low-rank (see appendix A for how these were calculated), were used to inform the asocial model.

Difference in neophobia between individuals is another variable that can alter the rate of diffusion of a novel trait. If, at the beginning of the diffusion, the trait spreads faster between less neophobic individuals, with a subsequent reduction in the speed of diffusion occurring due to gradually more neophobic individuals acquiring the trait, again an erroneous identification of social learning could occur. To control for this, two variables depicting neophobia were input in the analysis to inform the asocial model. These variables were: the level of avoidance of and interaction with novel objects (neophobia1) and the latency to touch novel objects (neophobia2) (for further details on how these variables were calculated see appendix B). The final individual-level variable input into the asocial learning model was the frequency with which individuals were registered within 10m of the apparatus but did not attend to (and thus approach) the task, even though it was not being manipulated by any conspecifics. This variable indicates variation in the likelihood with which individuals approach the lift-pull task, be it due to monopolisation, neophobia or other unknown factors.

If the diffusion of the trait is best explained by the individual-level variables described above, one could argue that asocial learning factors were responsible for the diffusion rate described. However if a model based on a combination of these asocial influences, and the opportunities to observe conspecifics solving the task (or an alternative social network), is a better fit to the diffusion data, than there is reason to suggest that social learning is occurring. Both TADA and OADA versions of the NBDA resulted in similar results. As TADA can have more statistical power than OADA (Hoppit & Laland, 2010), here, I only present the results for TADA (see Appendix C for details of findings with OADA).

4.3 Results

4.3.1 Lift-pull task

Open diffusion with wild groups

The diffusion pattern of the novel trait (solving the lift-pull task) in the wild groups of capuchins, can be seen by plotting the cumulative number of knowledgeable individuals in the group over time (Figure 4.3).

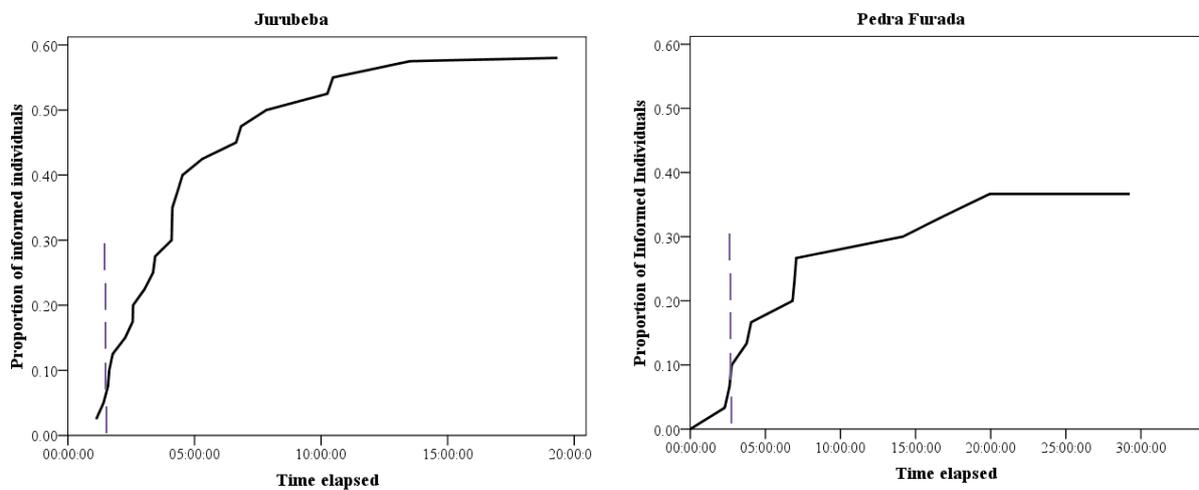


Figure 4.3 Proportion of informed individuals over time elapsed of experimentation for Jurubeba (N=40) and Pedra Furada (N=30). Dotted line indicates when open diffusion began.

By the end of the open diffusion experiment the lift-pull task had been solved a total of 4591 times in the JB group and 4080 times in the PF group. For both groups, there was a clear bias towards solving the task using the lift action: JB 93.8% of successful actions and in PF, 87.3% of successful actions were *lift* (Figure 4.4).

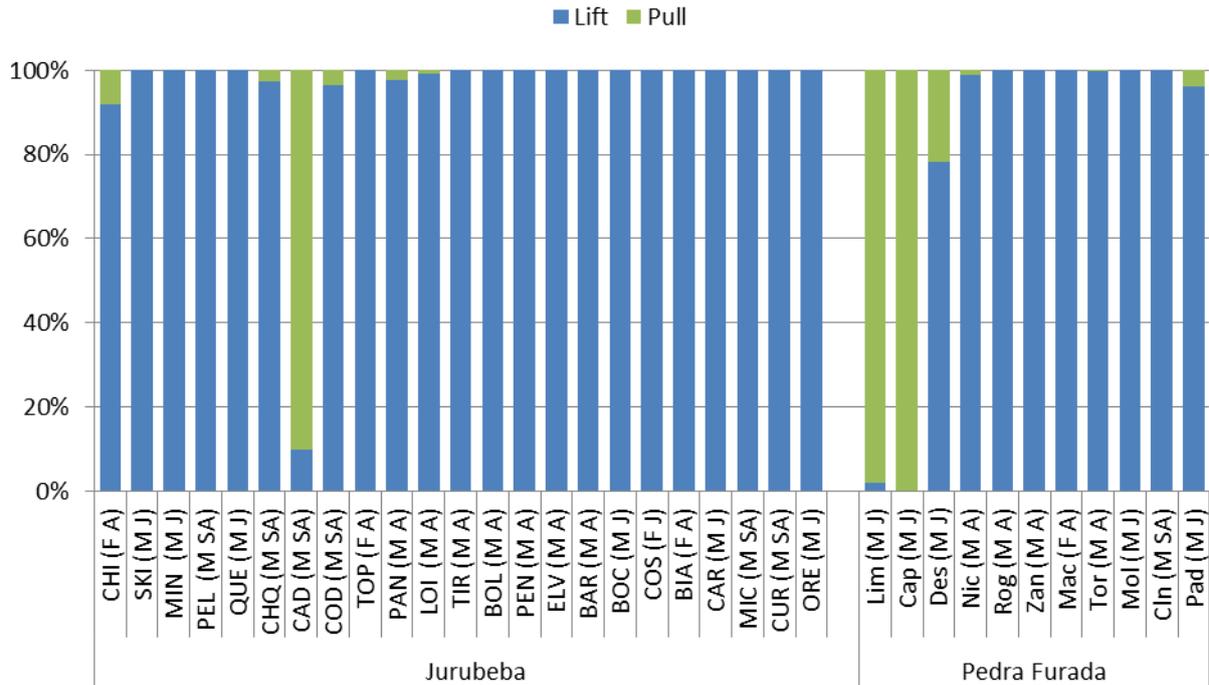


Figure 4.4 Percentage of options used to solve the lift-pull task, per individual, for both wild groups.

Asocial controls

Of the 14 asocial learning control individuals, 7 were unable to solve the task after being given 4 trials each. This result indicates that the task is fairly difficult and therefore social learning might be required for it to become a group-wide behaviour. Of the 7 control individuals that solved the two action task, 4 showed a preference for lift (lift:pull = 20:0, 20:0, 7:0, 28:2), 1 showed a preference for pull (lift:pull = 6:12) and 2 had no clear preference (lift:pull = 15:15, 9:11). An overall bias of 2.6 times ($N_{\text{total lift}}=105/ N_{\text{total pull}}=40$) higher likelihood of solving the task using lift than pull was thus found in the asocial control. This bias was input as an underlying bias in the OBA.

For a more accurate measure of the power to detect social learning, an estimate of the probability of asocial learning causing repeated use of one option over the other was calculated. The strength of association (α) causing return to the same option was calculated as, the proportion of individuals that solved the task the first and second time using the same option (6/7) minus the proportion of individuals that changed the option used on their second solve (1/7). The default value for α (0.5) was therefore exchanged for 0.7, which represents

the likelihood of using the same option a second time, as found in the asocial control experiment.

Option-bias Analysis

Option-bias analysis found no evidence of social learning based on the final repertoire of the lift-pull task in JB and PF groups, regardless of the randomisation technique used (option bias: $\chi^2=5792.3144$, $p=0.820$; GLM=107.3478, $p=0.821$; LLM=107.3478, $p=0.825$) (Figure 4.5). This lack of evidence for social learning of options was despite the fact that power, with an underlying bias for use of *lift* over *pull* of 2.6 to 1 and $\alpha=0.5$, was high (power=0.98) and the power considering the uncertainty of α having been set at 0.7 (7/6 used the same action in their first and second solutions) also being high (power=0.98).

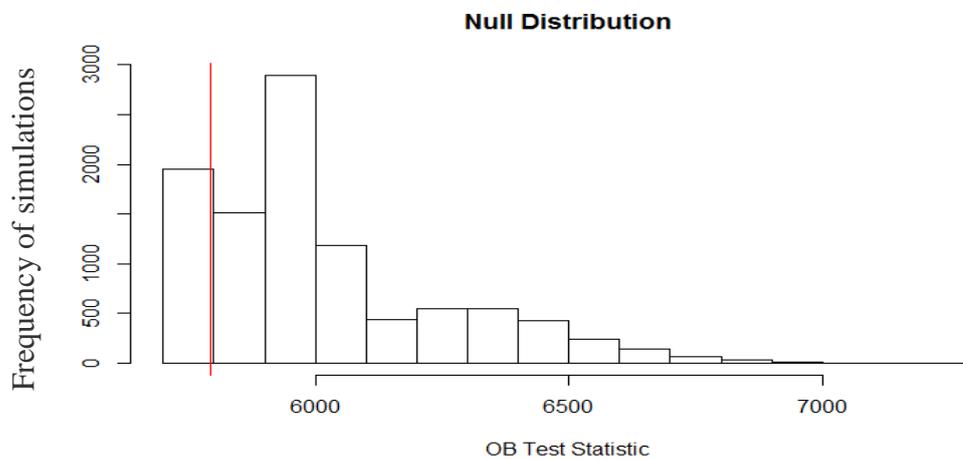
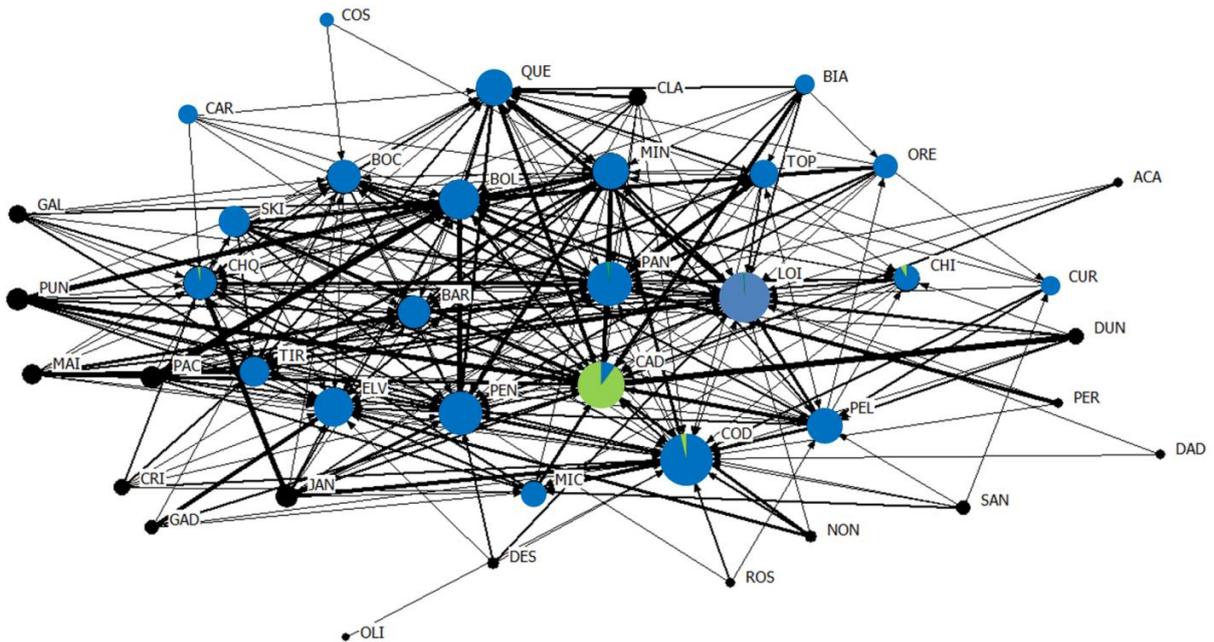


Figure 4.5 Results of the Option-bias analysis for the lift-pull task experiment. Red line indicates the observed chi-square metric value which does not fall within the upper tail of the null distributions of the chi-square values, created by the randomised simulations.

Network-based Diffusion Analysis: observation networks

The NBDA presented strong support for social learning by observation in the lift-pull task. When the social model was informed by a network portraying *observation events within 5 meters* of the apparatus, NBDA found a better fit for the social-and-asocial model, over the purely asocial model, in both JB and PF groups. However, when the social model was informed by a network based on *observation events above 5 meters* distance from the apparatus, NBDA did not find a significantly better fit of one model over the other, for either group. (Table 4.2, Figure 4.6).

A



B

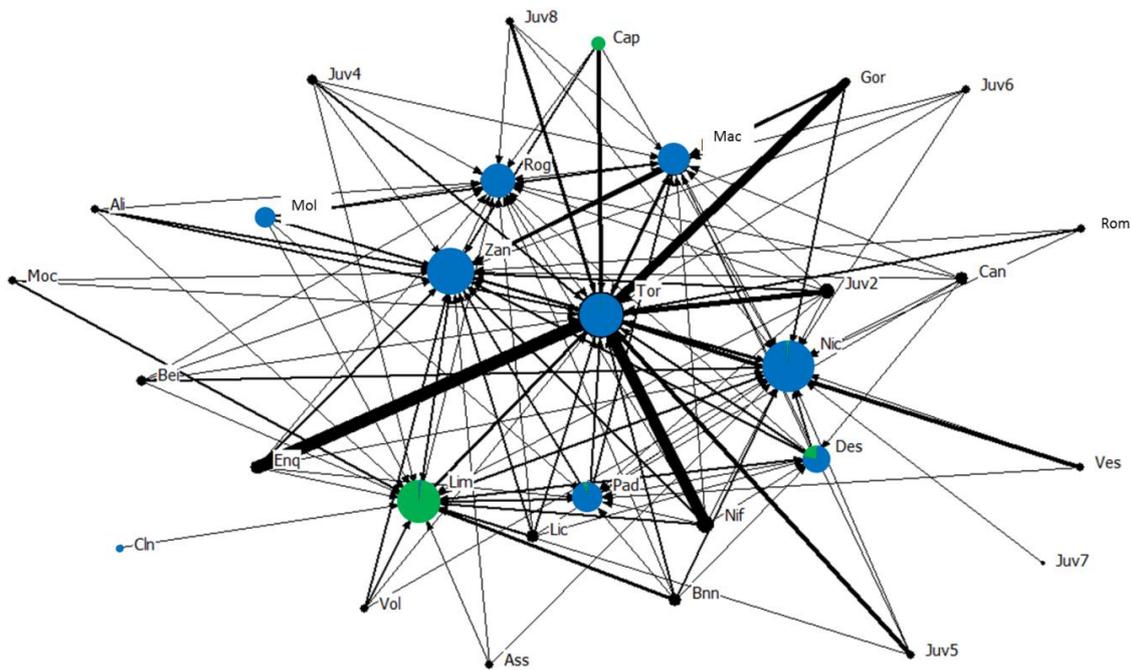


Figure 4.6 Observation networks within 5 meters. Edge thickness is proportional to the frequency of observation. Node size is proportional to the degree (number of arriving (observed) and leaving (observing) from node) Pie chart on nodes represents proportion of options used to solve the task successfully: blue for lift and green for pull options. In black are monkeys that never solved the task successfully. Panel A for Jurubeba group and panel B for Pedra Furada group.

Furthermore, the social-and-asocial model better explained the diffusion data (90% for JB and 74% for PF) when observation occurred at shorter distances (0-5 meters), as is evident from the higher Akaike weights (Table 4.3). The more modest model fit for PF group is likely due to the smaller social network involved in the diffusion. This result not only indicates strong support for socially biased learning, but suggests that observing from close-up yields better chances of learning to solve the task, indicative of observational learning.

Table 4.2 Results for Time of acquisition diffusion analysis (TADA). Observation networks for data on observation of manipulations of the lift-pull task by conspecifics, at different distances from task.

	Observation Network	Purely asocial model		Social and asocial model	
		AIC	Akaike	AIC	Akaike
Jurubeba (N=23)	Total (0 – 10m)	151.49	0.22	148.93*	0.78
	0 - 5 m	151.49	0.10	147.10*	0.90
	5 -10 m	151.49	0.32	149.95	0.68
Pedra Furada (N=11)	Total (0 – 10m)	54.15	0.328	52.72	0.67
	0 - 5 m	54.15	0.26	52.05*	0.74
	5 -10 m	54.15	0.62	55.15	0.38

* indicates a better fit of one model over the other (AIC difference of at least 2 points).

Akaike shows percentage of the diffusion data described by the models.

Network-based Diffusion Analysis: social networks

NBDA also presented strong evidence for social learning in the lift-pull task when the social model was informed by grooming interactions; the social-and-asocial model explained 95.9% of the diffusion data for JB and 80.8% for PF. In contrast, NBDA found no evidence for social learning in the lift-pull task when the social model was informed by play interactions; the purely asocial model explaining 73.1% of the diffusion data for both JB and PF groups.

For PF, NBDA could not find a better fit for either social-and-asocial or purely asocial models when the social learning model was informed by association networks (social proximity and co-feeding relationships). Again this may be attributed to a lack of power due to the small number of individuals involved in this group. However, for JB, when association networks were informing the social model, NBDA found evidence for social learning, with

the social-and-asocial model explaining 93.8% of the diffusion data for social proximity and 97% of the diffusion data for co-feeding (Table 4.3).

Table 4.3 Results for Time of acquisition diffusion analysis (TADA) of solving the lift-pull task with the social model informed by social networks (proximity, co-feeding, play and grooming)

		Purely asocial model		Social and asocial model	
		AIC	Akaike	AIC	Akaike
Jurubeba (N=23)	Social proximity	151.49	0.062	146.06*	0.938
	Co-feeding	151.49	0.030	144.51*	0.970
	Play	151.49*	0.731	153.49	0.269
	Grooming	151.49	0.041	145.18*	0.959
Pedra Furada (N=11)	Social proximity	54.15	0.595	54.92	0.405
	Co-feeding	54.15	0.563	54.66	0.437
	Play	54.15*	0.731	56.15	0.269
	Grooming	54.15	0.192	51.28*	0.808

* indicates a better fit of one model over the other (AIC difference of at least 2 points). Akaike shows percentage of the diffusion data described by the models.

4.3.2 Tube task

The experiment ran for approximately 250 minutes for each group. During this time, 15 monkeys in JB (38% of the group) and 10 monkeys in PF (29% of the group) solved the task successfully at least once. The three most common techniques used to reach the juice were tail-dipping, using a stick probe and using a stone hammer tool.

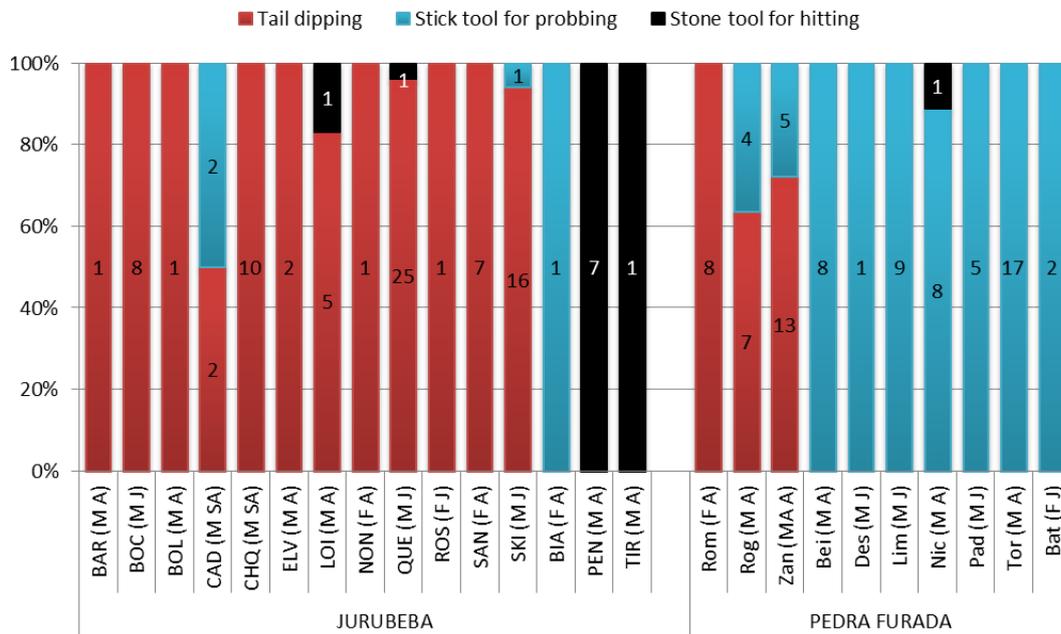
In total the tube task was solved successfully 181 times (N_{JB} =93, N_{PF} =88). The groups differed in the techniques/options used to solve the tube task, with tail-dipping being favoured in JB and stick probing in PF (Figure 4.7 A).

Option-bias Analysis

The option-bias analysis found significant evidence in favour of social learning for the options (*tail-dipping*, *stone hammer* and *stick probe*) used to solve the tube task, regardless of the randomisation technique used ($\chi^2=169.4963$, $p=0.002$; LLM=91.275, $p=0.002$, GLM was not run as it can only be used for two options) JB group presented a preference for using the

tail dipping technique to solve the tube task, while PF used stick probing preferably to solve the task (Figure 4.7 B).

A



B

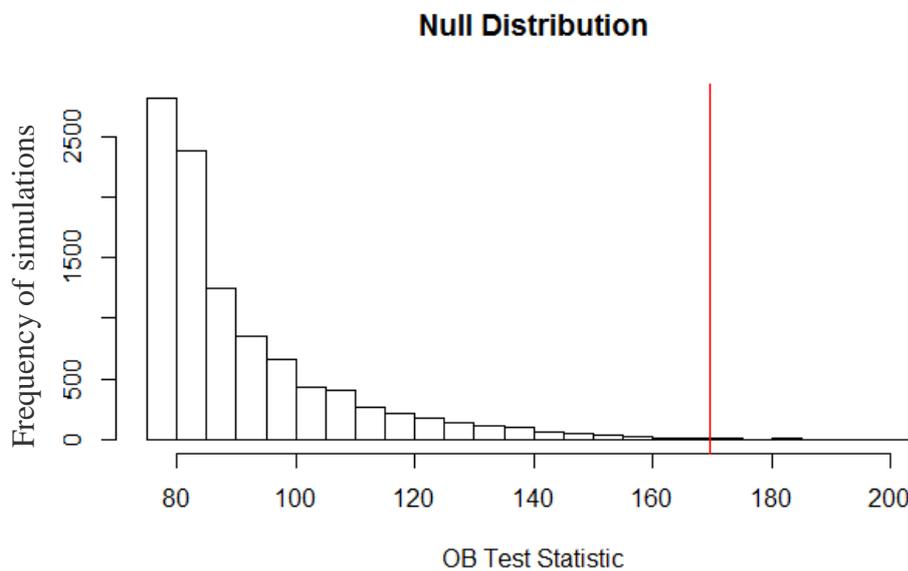


Figure 4.7 Results of the Option-bias analysis for the tube task experiment. Panel A depicts the observed percentages of options used to solve the tube task, per individual, for both wild groups. Panel B shows that the observed chi-square metric value (red line) falls within the upper tail of the null distributions of the chi-square values created by the randomised simulations. Thus the null hypothesis is rejected and evidence of social learning present.

Network-based Diffusion Analysis: observation networks

When the social models were informed by observation networks, NBDA presented support for social learning of the tube task in JB group; however, the agent-based model could not find a better fit for either the social-and-asocial learning model or the purely asocial learning model for PF group (Table 4.4). In JB, the social-and-asocial model explained 79% of the diffusion data.

Table 4.4 Results for Time of acquisition diffusion analysis (TADA). Observation networks for data on observation of manipulations of the tube task by conspecifics.

	Observation Network	Purely asocial model		Social and asocial model	
		AIC	Akaike	AIC	Akaike
Jurubeba					
(N=16)	Total	100.52	0.21	97.85*	0.79
Pedra Furada					
(N=11)	(0 – 10m)	61.47	0.39	60.54	0.62

* indicates a better fit of one model over the other (AIC difference of at least 2 points). Akaike shows percentage of the diffusion data described by the models.

Network-based Diffusion Analysis: social networks

The NBDA for the tube task showed similar results to that found for the lift-pull task. For JB group, when the social model was informed by social proximity, co-feeding or grooming relationships, strong evidence in favour of social learning was found; 85%, 64% and 90% of the diffusion data was explained, respectively (Table 4.5). When the social parameter was informed by play interactions, NBDA found the purely asocial learning model to be a better fit for the diffusion data. All the results for NBDA of the tube task in the JB group were similar to that found for the previous experiment (lift-pull task). Results for the PF group were not as clear. When the social parameter was informed by co-feeding relationships, the social-and-asocial learning model had a better bit to the diffusion data, explaining 86% of the latter. For the remainder of the social networks (social proximity, play and grooming), NBDA could not find a better fit for either social-and-asocial or purely

asocial models (Table 4.5). This differs from the lift-pull task in PF, where social-learning was detected for social models based on grooming relationships but not co-feeding.

Table 4.5 Results for Time of acquisition diffusion analysis (TADA) of solving the tube task with the social model informed by social networks (proximity, co-feeding, play and grooming)

	Social Networks	Purely asocial model		Social and asocial model	
		AIC	Akaike	AIC	Akaike
Jurubeba (N=16)	Social proximity	100.52	0.15	97.02*	0.85
	Co-feeding	100.52	0.36	99.36*	0.64
	Play	100.52*	0.70	102.20	0.30
	Grooming	100.52	0.10	96.03*	0.90
Pedra Furada (N=11)	Social proximity	61.47	0.29	59.69	0.71
	Co-feeding	61.47	0.14	57.93*	0.86
	Play	61.47	0.60	62.25	0.40
	Grooming	61.47	0.37	61.47	0.63

* indicates a better fit of one model over the other (AIC difference of at least 2 points). Akaike shows percentage of the diffusion data described by the models.

4.4 Discussion

Drawing on the available literature, to our knowledge, this is the first study to report direct evidence for social learning in wild capuchin monkeys. Furthermore, given the recent reclassification of capuchin species (see section 2.1) this study is also the first to present evidence for social learning in *Sapajus libidinosus*. The field experiments conducted with the wild groups, together with the asocial controls in captivity, have allowed me to integrate different methodological approaches, in order to empirically demonstrate wild capuchin monkey's social learning abilities. By running open diffusion experiments in the wild, I was able to study the diffusion of novel behavioural traits in the natural social context these capuchin monkeys live in.

Repertoire-based approach

In the tube task experiment, the repertoire based method (i.e. option-bias analysis) statistically identified differences between groups in the techniques used. The repertoire of both groups contained the three techniques (tail dipping, stick probe tool and stone tool) however, a clear predominance was found for tail dipping in JB and stick probe tool-use in PF. This bias could be the result of PF having been recently subjected to a task where they had to use sticks for probing honey (Cardoso, 2014), whereas Jurubeba had never been subjected to any field experiments. I am therefore unable to exclude the possibility that the group differences found for the tube task are not due to previous individual experience with a foraging task, or other un-assessed ecological differences.

The lift-pull task involved the introduction of new behaviours (or behavioural sequences typical to the species now applied in a new context) to the wild populations; thus previous individual experience could be excluded. The repertoire-based method (OBA) did not yield positive results for social learning for the lift-pull task, despite robust evidence of social learning having been found in the diffusion approach. This result was expected in the case of the lift-pull task, as the diffusion of the behaviours did not result in the generation of two clear alternative traditions (*lift* and *pull*); *lift* was the predominant technique used to solve the task by individuals in both groups. OBA requires that there be a strong within-group homogeneity when compared to the between-group homogeneity. As our experiments resulted in a high between-group homogeneity the OBA could not detect social learning.

OBA is subject to many of the same problems faced by the group-contrast approach, such as requiring there to be clear group differences or requiring ecological and genetic variations between groups to be accounted for. However, it is an improvement on the group-contrast approach as it allows us to quantitatively evaluate the group differences in homogeneity and test statistically the likelihood of us finding the repertoire bias registered. Furthermore, as a repertoire-based method, OBA is more readily applicable to studying wild populations where registering the inception of a new behavioural trait, its diffusion and establishment as a behavioural tradition would be highly unlikely outside an experimental context.

Diffusion approach

The diffusion approach found strong evidence of social transmission of information along the network pathways. Network based diffusion analysis with social models informed by frequency of observation between conspecifics produced evidence that capuchin monkeys are capable of acquiring new behaviours by observational learning. Indeed, this appeared to be the predominant learning process rather than merely stimulus/local enhancement/social facilitation as there was no evidence for social learning using observation networks of 5-10 metres from the task. The results from NBDA informed by observation networks, alert us to the need to give due attention to the distances of observation. For the lift-pull task observations network at any distance were informative enough for NBDA to find a better fit for one of the models for the JB group, however, for PF, only observations made at a shorter distance produced significant opportunities to learn socially. In the tube-task experiment, a single general measure of observation of conspecifics solving the task within a ten-meter radius was coded. Again, NBDA could not find a better fit for either model based on the observation network for, PF group, although the social learning model was favoured for JB. A more refined measure of observation within shorter distances (as done for the lift-pull task) might have yielded a positive result for observational learning of the tube task for both groups. Finally, the finding that social models informed by observations within shorter distances better described the diffusion pattern of the novel behaviour than social models based on observations from a larger distance, points to an important role of tolerance in the dissemination of knowledge through the group.

Often, when studying wild populations, researchers are able to register the gradual appearance of a new behavioural trait, tracing its apparent diffusion among group members. However, registering all (or most) opportunities animals have of observing the new behaviour is more problematic. In this scenario (e.g. regarding a spontaneous/natural innovation), applying NBDA with social models informed by social relationships (associations or interactions) between group members can prove to be a valid means of identifying social learning in the wild. Overall, our results for the lift-pull task show that, where the social model was informed by interaction networks (grooming and play), NBDA was able to clearly discern between the two agent-based models, whether finding a better fit for the social-and-asocial model or for the purely asocial model. Association networks, on the other hand, presented mixed results for the different groups. This could be because of different social learning dynamics being present in each group or issues of power due to differing network

sizes and magnitude of diffusion through the group. Alternatively, it might be the result of association networks presenting more homogenous relationships than interaction networks. As described in the previous chapter (section 3.3.2), the association networks were fully connected, that is, every individual associated with every other individual in the group; although with different rates of association between dyads. In a larger group, such as JB, a greater variation in the rate of association between dyads was present (i.e. individuals tended to associated with some group members more often than with others). Therefore, in the larger group, a finer differentiation of information paths can be made, through which the novel information might have diffused. In a smaller group, such as PF, the social model might not have been able to discern between more and less relevant pathways for diffusion of information, given the more equal distribution of connection strengths between group members, when compared to the larger group. We thus emphasize the importance of considering different social networks, and more refined measures of tolerance and learning opportunities, when attempting to identify social learning in wild populations.

Clear model fits were found for all socio-positive networks (whether indicating social or asocial learning) for the Jurubeba group. For Pedra Furada, however, NBDA did not have the strength to identify a better fit for all the models run, possibly due to a more restricted diffusion (11 out of 35 individuals) compared to JB (23 out of 40 individuals) or due to smaller social networks informing the model. Overall, the findings regarding socio-positive relationships, produced positive identification of social learning of the lift-pull task in both groups, when the social model was informed by grooming networks. Grooming networks presented particularly high flow betweenness centralities, which indicate that clear pathways, through which information can flow, are present. Together, these findings point towards directed social learning being responsible for the diffusion of the lift-pull task. In the general discussion I compare the findings here describes with that of the current literature on identifying social learning in the wild, by employing the same analytical methodologies.

The combined results of NBDA and OBA indicates that there was either (i) in both groups, social learning enabled the spread of the same information (*lift*), generating an option bias in the same direction or (ii) some simpler form of social learning was occurring, where learning to solve the task was irrespective of the specific action/option performed. Currently we are unable to tease apart these two possibilities.

Contextual variables, such as the characteristics of the demonstrators and/or observers, could also be biasing social learning, and consequentially influencing the final

distribution of the behavioural trait. In the following chapter, I investigate transmission biases (also known as transmission biases), such as conformity and the varying influence of different demonstrators (model-based biases), in an attempt to further the understanding of how transmission bias affects the establishment of and patterns of new behavioural traditions.

CHAPTER 5:

**TRANSMISSION BIASES IN WILD BEARDED
CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*)**

In the previous chapters I looked at the opportunities for social learning (chapter 3) and the preferential attendance to certain models in order to determine social learning using NBDA (chapter 4). In this chapter, I turn my attention to the transmission biases during social learning in order to investigate whether these opportunities and attendances translate into what is learned (here indicated by the lift/pull behaviour performed by observers). Here I examine two frequency-dependent transmission biases, namely *copy the majority*, and *copy the variant that is increasing in frequency* and four model-based transmission biases, related to the *age-, sex-, dominance- and success* of the individuals copied, that might have been in play during the lift-pull task experiment.

5.1 Introduction

The last two decades have seen great advances in the study of social learning, in part due to the efforts to identify it as the basis of behavioural traditions. Integrating the different approaches to social learning, such as the proximal (psychological, ecological) and the ultimate (functional) has helped to establish a strong field of study, with important implications for the understanding of cultural evolution (Galef, 2004; Lonsdorf & Bonnie, 2010; Shettleworth, 2010). In turn, the discipline of Cultural Evolution spans a broad range of areas, such as biology, psychology and anthropology, and is concerned with the modelling of cultural change, often mathematically (Hoppitt & Laland, 2013; Mesoudi et al, 2004, 2006; Richerson & Boyd, 2005). Such modelling of the frequency and spread of cultural practices in populations, showed that cultural variation was not a random process, but governed by generalizable rules. In the case of cultural inheritance, unlike genetics, transmission biases seem to be the rule rather than the exception (Avital & Jablonka, 2000).

Among these learning rules or heuristics, there is often the assumption that social learning is intrinsically adaptive, as copying would be easier, safer and/or less time consuming than learning something on one's own (Hoppitt & Laland, 2013). Studies on the evolution of social learning, however, have shown that an equilibrium between learning from others and individually sampling the environment must be established, and that this equilibrium depends on how frequently the environment changes (Boyd & Richerson, 1995).

Boyd and Richerson (1995) confirmed Roger's (1989) claim that social learning was not always adaptive and demonstrated, through mathematical models, that social learning is expected to be customary in environments with intermediate rates of environmental change. In such environments, change is not too frequent that individuals would be better off sampling environmental conditions themselves nor so slow that genetic adaptation would suffice. Concomitantly, the environment is not so stable that a fixed behavioural variant could be copied without concerns as to environmental conditions. For an extensive review on studies that have addressed the matter of trade-offs in the adaptive use of social and asocial learning in non-human animals see Kendal et al 2005.

Cultural evolutionists have described forces that specify when an individual should learn from a conspecific, and from which conspecifics (or classes of conspecifics) they should learn from. Among the cultural evolutionary forces listed by Richerson & Boyd (2005), are the biased transmission which the authors then sub-divide into *content-based (or direct) biases*, *frequency-based biases* and *model-based-biases*. Rendell et al (2011) expanded on the latter adding *state-based biases*, which describe the transmission biases based on the state of the individual copying, e.g. copy if uncertain and copy if dissatisfied. The content-based (or direct) biases refer to scenarios in which an individual copies a given variant because the variant itself will provide an adaptive advantage, e.g. copy greater pay-off. In this chapter, I address *frequency-based biases* and *model-based-biases*. Both behavioural variants (*lift* and *pull*) yielded the same amount and quality of reward therefore content biases would not be expected.

Frequency-based biases occur when a behavioural variant is adopted based on its commonness or rarity in the population and includes strategies such as copy the majority (conformist bias), copy a rare behaviour (anti-conformist bias) or copy variants that are increasing in frequency. Model-based biases occur when a behavioural variant is adopted based on the observable attributes of the individuals exhibiting the trait; this includes sex-based, age-based, success-based (e.g. copy most successful individual), dominance-based and kin-based biases, amongst others (Richerson & Boyd, 2005; Rendell et al, 2011). Alternatively, these transmission biases have been termed social learning strategies (Laland, 2004); here I used transmission bias and social learning strategies interchangeably.

Many studies, upon identifying social learning have subsequently sought to address transmission biases, however, few of these studies were developed specifically to address transmission biases. Recent claims of findings consistent with social learning strategies in nonhuman primates include: *copy the most successful* (e.g. capuchin monkeys: Ottoni et al,

2005, Coelho et al, 2015) , *copy philopatric sex* (e.g. vervet monkeys: van de Waal et al, 2010) , *copy older individuals* (e.g. chimpanzees: Horner et al, 2010), *copy dominant individuals* (e.g. chimpanzees: Horner et al 2010; Kendal et al 2014), *copy most frequent behavioural variant* Perry (2009) and *copy the majority* (Whiten et al, 2005, Dindo et al, 2009). (see Rendell, Fogarty et al, 2011 for review).

Although conformist bias and conformism are well-defined concepts within a long tradition of cultural evolution and psychology, respectively, and both require a majority of group members to influence the behaviour of the minority (van Leeuwen & Haun, 2013), other researchers have on occasion applied the term quite loosely. Some authors, for example, use conformity in the social psychology sense of overriding personal information to copy what others are doing. This is the case of Whiten et al (2005), who in a study on social learning in chimpanzees, described conformity as “a powerful tendency to discount personal experience in favour of adopting perceived community norms” (p. 738). Perry (2009) in a paper on food processing techniques in white-faced capuchins adopted the following definition of conformism: “*the tendency for individuals to preferentially exhibit (i) the behavioural alternatives they witness most frequently in their peers or to exhibit the behaviours that are performed by peers (ii) who are considered most prestigious or successful, or (iii) those peers with whom they have the highest quality social relationships*” (pg. 561). The latter definition of “conformity” can thus be divided, at least, into three distinct learning strategies as identified by the numerations above: (i) frequency-dependent bias, (ii) success-bias or prestige bias and (iii) unbiased transmission.

In the literature of social learning, in non-human primates in particular, “conformity” is often called upon as the process generating group homogeneity (e.g. Whiten et al, 2005, Perry 2009, Dindo et al, 2009). This is not surprising, given that most social learning studies in primates are, to some extent, interested in identifying behavioural traditions, and therefore, in processes that generate within-group homogeneity and between-group diversity. The processes listed in the definition by Perry (2009), above, essentially describe ways in which with-group homogeneity might become predominant and therefore result in cultural diversity. As argued by van Leeuwen & Haun (2013), however, it is important to maintain definitional uniformity and thus here I adopt the definition of conformist bias according to Richerson & Boyd (2005), i.e. copy the behavioural variant used by the majority of individuals.

By conducting experiments with groups of wild primates, one is able to establish whether social learning is in fact occurring and then move on to identifying the types of social learning strategies at play, whilst maintaining the ecological validity not found in

laboratory experiments. Experimental designs with multiple demonstrators/models and observers (i.e. open diffusion) have been scarce, but are important as they allow us to investigate biases in who is attended to and copied (e.g. copy older, copy dominant, copy successful individuals). Furthermore, open-diffusion studies, such as the ones here conducted, are conducive to registering multiple transmission events, which in turn allows us to address population-level properties such as frequency-dependent biases (e.g. copy the majority, copy variant increasing in the populations) (Hoppitt & Laland, 2013).

Here I analyse data from a social learning field experiment conducted with wild capuchin monkeys in an attempt to better describe the transmission biases that might be occurring. First, I address whether individuals preferentially exhibit the behavioural alternatives they witness most frequently. This is a frequency dependent bias, whereby individuals copy variants that are increasing in frequency in the population. I then examine whether the monkeys solve the lift-pull task by preferentially using the behavioural variant they saw a greater number of conspecifics using. This transmission bias, namely copy the majority (where the ‘greater number of individuals’ represents a majority), is the most broadly accepted definition of a conformist bias (Boyd & Richerson, 1985; van Leeuwen et al, 2013; Hoppitt & Laland, 2013). After assessing these frequency-dependent biases, I turn my attention to model-based SLS, specifically age-, sex-, dominance- and success-based biases in the choice of observational targets during the field experiment.

5.2 Methods

Data on solving the lift-pull task and conspecifics observing the tasks being solved were scored from the video recordings of this experimental set-up. For further details regarding the experiment and coding of behaviour, refer to sections 4.2.2 and 4.3.1. Here I analyse together data for both groups, to increase the sample size and therefore the power of the analysis conducted.

5.2.1 Observation records and first successful manipulations

On occasions, a naïve individual (i.e. one who had not yet solved the lift-pull task) would have seen from within 5 meters both actions (*lift* and *pull*) being used to solve the lift-pull task being by both actions. In these cases I ask whether, when that individual eventually solved the task, did it perform the same action as:

- a. the first successful action it observed being done? A primacy effect.
- b. the most recent successful action it observed? A recency effect.

5.2.2 Frequency dependent social learning strategies

To investigate the two frequency-dependent transmission biases I pose two distinct questions: Did individuals solve the lift-pull task successfully using the same actions as:

- i. the most frequent successful action s/he observed? A frequency effect. Or,
- ii. the most frequently favoured action, across individuals? A conformity effect.

Only monkeys who solved the task during the open diffusion stage (when both options were functional) were included in this analysis (N=26, data for both groups combined).

To assess the frequency effect I calculated the proportion of the lift action observed and proportions of lift action performed, per individual. This allows us to evaluate whether the actions an individual observed being used to solve the task predicted the actions s/he then performed when solving the task. The proportions were calculated as follows:

- (a) *Proportion of actions observed*: calculated for each individual by dividing the frequency of observing the task being solved using the action *lift* by the total frequency of observing the task being solved (with both *lift* and *pull* actions).
- (b) *Proportion of actions performed*: calculated for each individual by dividing the frequency with which each individual solved the task using *lift* by the total frequency each individual solved the task (using *lift* and using *pull*).

Similar to Perry's (2009) analysis of foraging techniques in capuchins, I here apply a General Linear Model to test whether individuals are copying the variants in the proportion these are observed. Accordingly, the GLM tested whether the response variable, *proportion of actions performed*, could be predicted by the predictor variable, *proportion of actions observed*. The model included possible effects of sex and age as factors predicting the performed manipulations, as well as a combination of these factors with the main predictor variable (observed manipulations). An offset value (*total frequency of observation* by each individual) was included in the model to control for the effect of any very active observers.

To investigate a conformity effect (*sensu* Boyd & Richerson, 1985) I calculated, for each monkey, the proportion of individuals s/he observed using *lift* predominantly. Here I define predominant use of an action when it was used more the 75% of the times the individual solved the task successfully (see Figure 5.1). This proportion was calculated by

dividing the total number of individuals s/he observed using lift predominantly by the total number of individual s/he observed solving the lift-pull task, irrespective of action used.

The *proportion of individuals observed performing lift predominantly* was our predictor variable. The binary response variable being zero when the subject *performed lift predominantly* and one when the subject *performed pull predominantly*. The model included sex and age as possible predicting factors, as well as interaction between these factors and the main predictor variable (*proportion of individuals observed performing lift predominantly*). An offset value (*total number of different individuals observed*) was included in the model to control for the effect of varying numbers of models available to the observer.

By running these two analyses, I hope to tease out the differences between the two types of frequency-dependent SLS described above.

5.2.3 Model-based social learning strategies

Four variables were considered as possible factors/covariates in the GLM analysis conducted to test for model-based biases: sex, age, dominance and success at solving the lift-pull task of the models. Sex and age-group was known for all experimental subjects (see chapter 2 - Methods) and dominance rank was determined for the months during and around the time the lift-pull task experiment was conducted with each group (see appendix A for further details on dominance rank). With the intent of estimating the success of individuals in solving the lift-pull task, I calculated a success ratio for the experimental subjects during the open-diffusion phase of the experiment. The success ratio was calculated, for each individual, by dividing the frequency of successful manipulations by the total frequency of manipulations of functional parts of the apparatus (successful manipulations + unsuccessful manipulations) (see supplementary material in appendix E for more details).

The observation records used in this analysis, portrayed the frequency with which naïve observers (i.e. observers who had not as of yet solved the task successfully) saw the lift-pull task being solved successfully (and by whom), from within a 5-meter radius. The choice of distance of observations was as a consequence of the findings reported in section 4.3.1, which identified social learning by observations within a 5-meter radius using NBDA. The observation matrices were normalised using the “Normalization” procedure available in UCINET 6.0, along each column, based on the maximum value of that given column. By performing this operation, I take into account individual differences in frequency of solving the lift-pull task (and consequent observation opportunities).

With UCINET 6.0, the in-degree for each node (individual) was calculated for the *observation within 5-meter networks*. The in-degree is a centrality measure, of a directed network, and is indicative of how many edges arrive at the node. In the case of our normalized observation network, in-degree represents the relative frequency a given individual was observed by naïve conspecifics, while it solved the lift-pull task successfully.

A generalized linear model (linear regression) analysis was then conducted to test whether our factors (sex, age, dominance rank) or covariate (success ratio) were predictive of the response variable, *frequency an individual was observed by naïve individuals* (expressed as the in-degree for the model individual normalised for relative to the frequency of successful manipulations).

5.3 Results

5.3.1 Observation records and first successful manipulations

By the end of the open-diffusion field experiment a total of 34 individuals across both groups ($N_{\text{Jurubeba}}=23$; $N_{\text{Pedra Furada}}=11$) had solved the lift-pull task successfully at least once. Two of these monkeys (CHI and Lim) were trained individuals who were excluded from the analysis in this chapter. All the remaining monkeys observed a conspecific solving the task successfully at least once, within a 10 meters radius, before solving the task successfully themselves.

Of the 32 individuals who eventually solved the lift-pull task, after having seen a conspecific solving the task successfully, 14 had observed only one action ($N_{\text{lift}}=12$; $N_{\text{pull}}=2$) being used before subsequently performing the very same action themselves. The remaining 18 individuals had observed both actions (*pull* and *lift*) being used, at least once by conspecifics, before solving the task themselves. For 6 of these 18 individuals the first successful action and the most recent successful action seen were the same ($N_{\text{lift}}= 6$; $N_{\text{pull}}= 0$), impeding us from distinguishing between primacy and recency effect. For the remaining 12 individuals who saw both actions being performed before they solved the task themselves, the vast majority ($N_{\text{recency}} = 11$; $N_{\text{primacy}} = 1$) solved the task using the action they had seen performed most recently, rather than the action they had first observed being used to solve the task.

Both groups developed a bias in the same direction; *lift* being the group prevailing option in both cases. Most individuals, first solved the lift-pull task using the group prevailing option, *lift* ($N_{\text{group prevailing option}}=27$; $N_{\text{alternative option}}=5$). Of the 5 individuals that first solved the task using the alternative action, *pull*, 3 adopted the group bias over time; whilst 2 individuals continued using predominantly *pull*. Only 2 monkeys (CAD and CAP) used the option *pull* predominantly, the remaining 30 monkeys used *lift* predominantly (Figure 5.1).

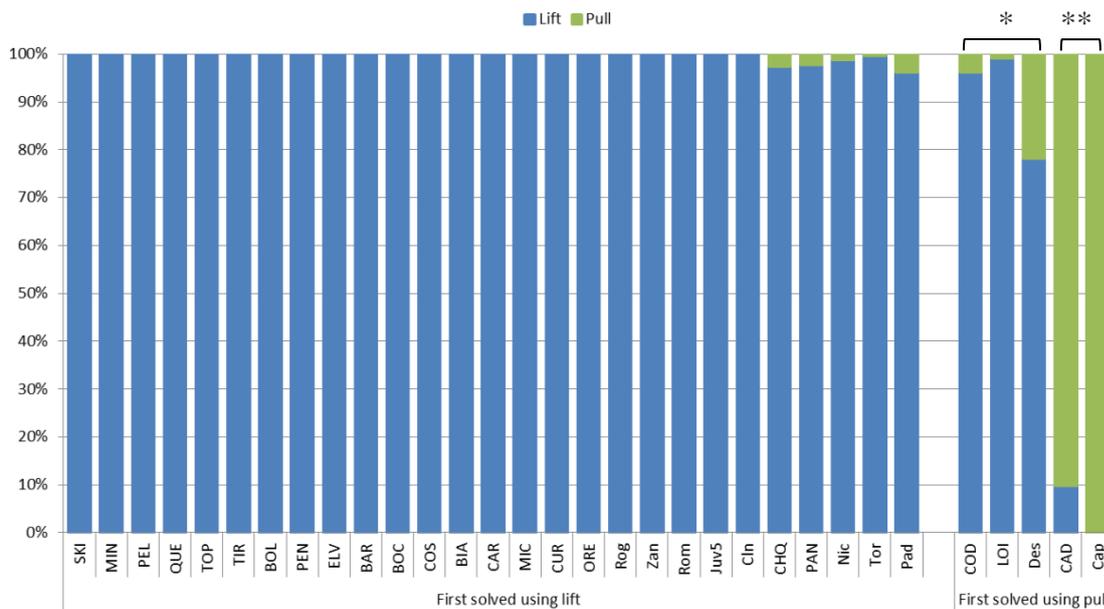


Figure 5.1 Proportion of *lift* (blue) and *pull* (green) actions performed by monkeys in both groups when solving the lift-pull task successfully. * indicates individuals who originally solved the task using the alternative option (*pull*) but shifted to the group prevailing option (*lift*). ** indicates individual who continued to use the alternative option (*pull*).

Overall, in the open diffusion experiment, there was a strong bias towards using the *lift* option, which was employed with 9.8 times more often than pull was ($N_{\text{total lift}}=7867/ N_{\text{total pull}}=804$) of X:X. This bias was almost 4 times stronger than that described for the asocial condition. In the asocial control experiment conducted at Edinburgh Zoo (see sections 2.2.3 and 4.2.2) the *lift* option was 2.6 times more likely to be discovered individually than *pull* ($N_{\text{total lift}}=105/ N_{\text{total pull}}=40$). Whether this difference between the bias described for the open diffusion with the wild groups ($N=32$) and that described for the individually isolated captive

groups (N=7) is consequence of a larger sample size or of a social influence towards a lift bias, requires further investigation.

5.3.2 Frequency-dependent social learning strategies

Copy most frequent variant in group

To test whether, during the lift-pull task experiments, the monkeys were *copying the variant lift* a generalized linear model (henceforth GLM) analysis with gamma log-link function was conducted. Gamma log link was used due to the skewed distribution of the data. The overall fitted model was significant (Likelihood ratio chi-square = 20.82, d.f.=5, p=0.001) when compared against the intercept-only. Age of observer and *proportion of lift actions observed* interacted significantly in predicting the *proportion of lift actions produced* (Table 5.1). When we plot the regression line for each of the age groups, we find that for juveniles the proportion of actions observed seems to reflect the subsequent proportion of actions produced (Figure 5.2), but this was not the case for adults.

Table 5.1 Results for the generalized linear model analysis, testing for frequency dependent bias, *copy variant lift*, in the lift-pull task

Models	Wald Chi-squared	d.f.	Significance (p-value)
Sex	1.615	1	0.204
Age	1.743	1	0.187
Proportion of <i>lift</i> actions observed	2.970	1	0.085
Sex * Proportion of <i>lift</i> actions observed	1.510	1	0.219
Age * Proportion of <i>lift</i> actions observed	4.255	1	0.039**

** p<0.05

Adult individuals varied quite widely in the proportion of actions observed, individual variation ranging between having seen lift in 20% of the times they had seen the task being solved up until those who only saw lift being used. This variation was not reflected in performance of the adults, as most individuals used lift predominantly, despite what they observed. The results from the GLM, on the other hand, points towards juveniles being influenced by the frequency of the variant observed in determining the frequency of the

variants later performed, i.e. a frequency-dependent transmission bias. The juvenile regression line implies that if a juvenile observes *lift* 40% of the times s/he sees the task being solved by a conspecific, s/he is likely to perform lift 60% of the times s/he solves the task her/himself (Figure 5.2).

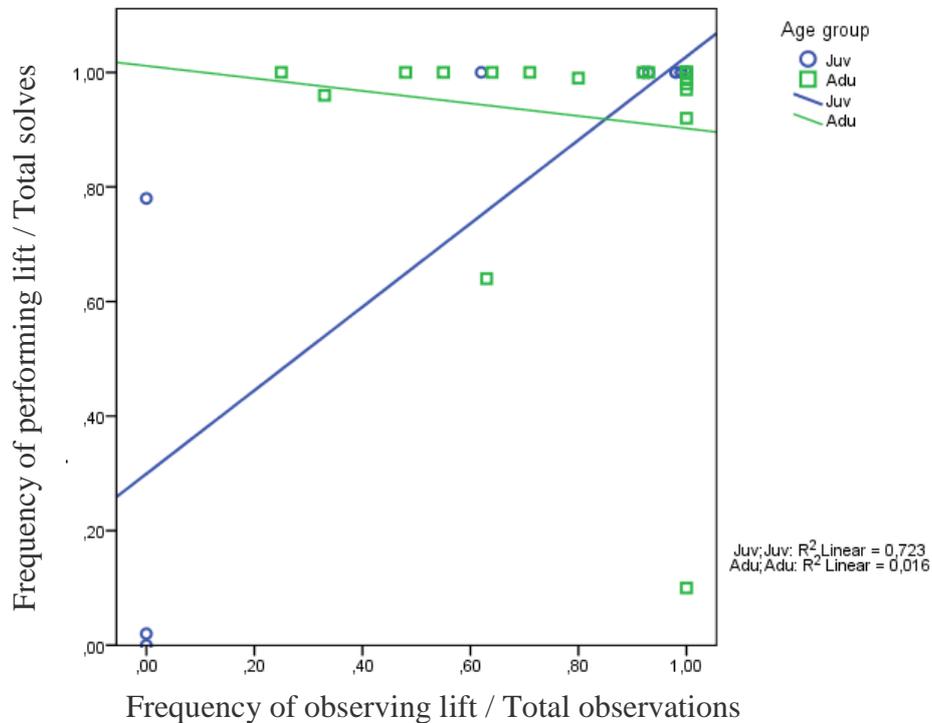


Figure 5.2 Regression of Proportion of actions observed and Proportion of actions produced, throughout the open diffusion, for juveniles (N=8) and adults (N=18) for data on both wild groups (JB and PF) together.

Caution is required in interpreting these results. First the sample size, for juveniles in particular is small. Second, in this analysis I include all observations and all task actions regardless of which observations occurred before which actions. A Bayesian method capable of taking into account this ever changing ‘prior’ influence, as done by Kendal et al (2015) is recommended.

Copy the majority: a conformist bias

To test the *copy the majority* hypothesis a GLM analysis with a binary logistic function was run. A significant fit for the overall model (Likelihood ratio chi-square = 60.01, d.f. = 5, p <0.001) when compared against the intercept-only model was found; presenting evidence for a conformist bias in solving the lift-pull task. The *proportion of individuals seen*

performing lift predominantly was significantly predictive of whether individuals used *lift* predominantly when solving the lift-pull task. Neither sex nor age of observers, as main effects, were significant predictors; nor was the interaction between age or sex and the dependent variable (*proportion of individuals seen performing lift predominantly*) (Table 5.2).

Table 5.2 Results for the generalized linear model analysis, testing for conformity bias in the lift-pull task

Models	Wald Chi-squared	d.f.	Sig.
Sex	0.005	1	0.944
Age	0.334	1	0.564
Proportion of individuals seen performing <i>lift</i> predominantly	17.001	1	0.000**
Sex * Proportion of individuals seen performing <i>lift</i> predominantly	2.494	1	0.287
Age * Proportion of individuals seen performing <i>lift</i> predominantly	5.289	1	0.152

** p<0.05

The interpretation of this data also requires caution, since only two individuals (CAD and Cap) used the *pull* technique predominantly there was a greater opportunity to observe individuals who used the *lift* technique predominantly. It is likely that there was not enough variability in the results to conduct a valid.

5.3.3 Whom do naïve individuals observe? Model-based biases

For the model-based bias hypotheses a GLM analysis with a gamma log link function was run. When the overall fitted model was compared against the intercept-only model a significant fit was found (likelihood ratio chi-square = 80.127, d.f. = 15, p <0.001); indicating that at least one of the factors/covariates regarding the characteristics of individuals (sex, age, dominance) predicts who the most frequently observed individuals were. Both success ratio as a main factor and the interaction between sex and success ratio were predictive of the frequency with which a model was observed by naïve conspecifics (Table 5.3). Sociograms

(Figure 5.3) indicate that, for both social groups, naïve individual's most frequent observation targets were highly successful (at solving the lift-pull task) males.

Table 5.3 Results for the generalized linear model analysis, testing for model-based biases in the choice of observational targets during the lift-pull task experiment.

Model fit	Likelihood ratio Chi-square	d.f.	Sig.
Group	2.740	1	0.098
Sex	0.049	1	0.825
Age	0.526	1	0.468
Dominance	0.638	2	0.727
Success ratio	3.959	1	0.047**
Sex*Age	0.924	1	0.336
Sex*Dominance	1.978	2	0.372
Age*Dominance	2.056	2	0.358
Sex*Success ratio	7.349	1	0.007**
Age*Success ratio	3.168	1	0.075
Dominance*Success ratio	1.093	2	0.579

** p<0.05

The findings from the model-based bias analysis are relative to the types of model that are more often attended too. Therefore, successful males were attended to by naïve individuals more often, however, I cannot, from this data, discern if the individual actually learned from the model, or where attending to these models for scrounging opportunities, for example. Given that NBDA was able to identify social learning based on observation from within 5 meter, I infer that this analysis can, for now function as a proxy for a learning bias.

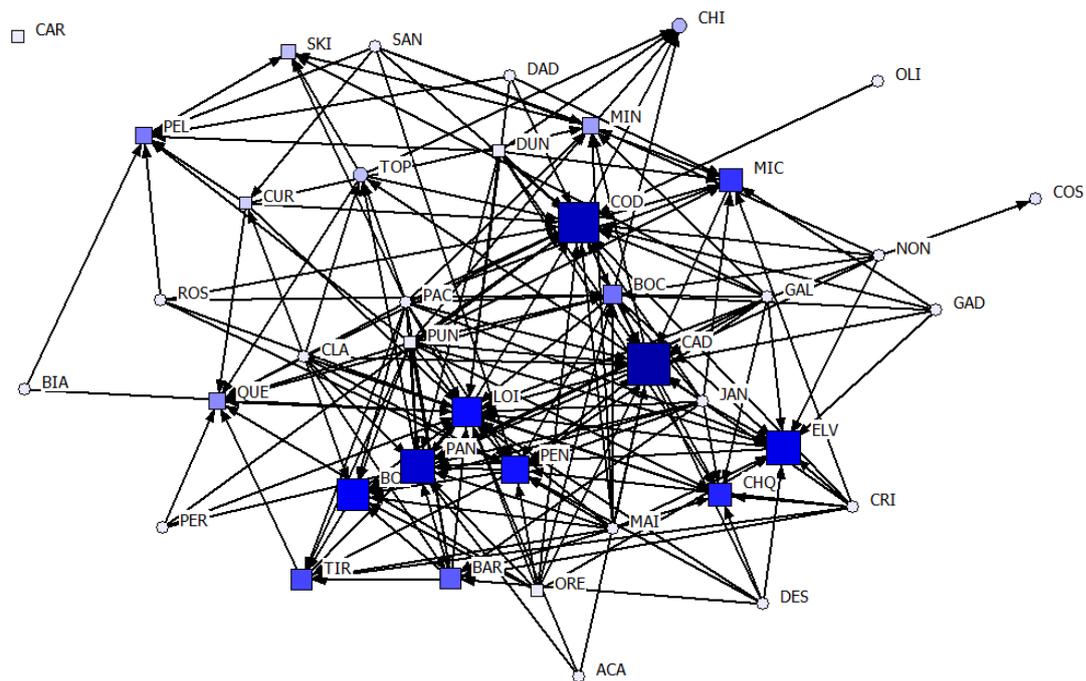
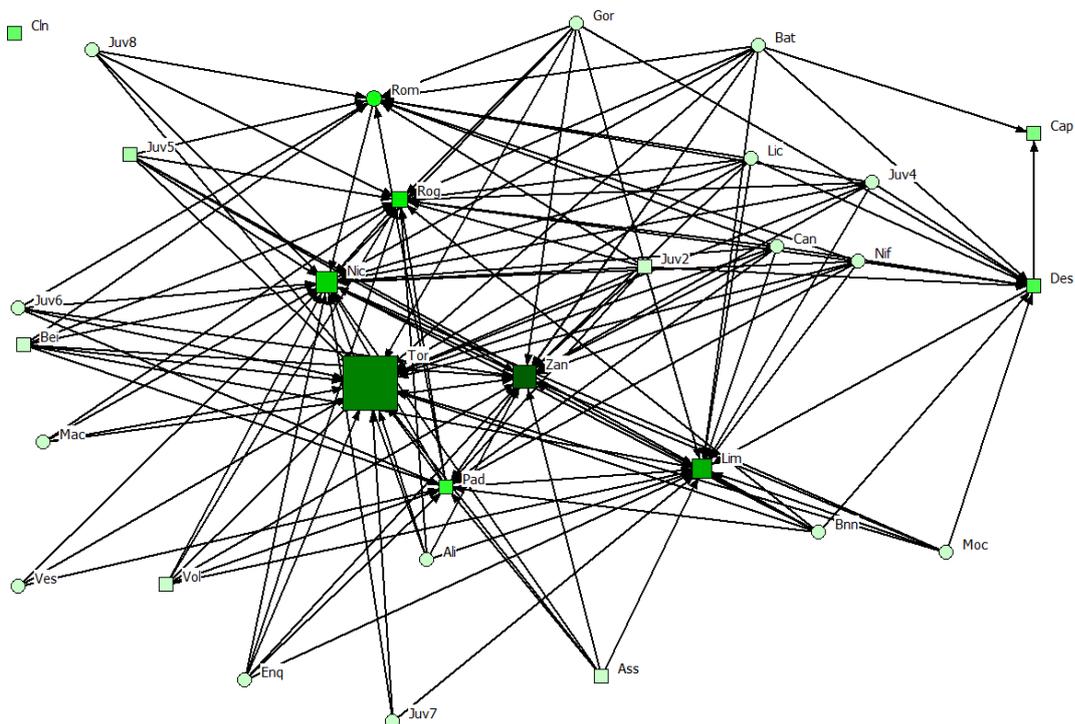
A**B**

Figure 5.3 Observation within 5-meter radius networks for (A) Jurubeba and (B) Pedra Furada. Size of nodes indicates in-degree centrality (i.e. frequency that a monkey was observed by a naïve conspecific, while it solved the task). Colour of nodes code for success ratio: stronger tones for higher success ratios in solving the lift-pull task. Node shapes indicate sex of monkey, *circle*=female and *square*=male.

5.4 Discussion

The findings from this chapter indicate that several transmission biases might be responsible for the final repertoire in both groups, of a group prevalent behavioural variant (*lift* to solve the lift-pull task). Findings presented were consistent with the frequency effect, i.e. *copy the more frequent behavioural variant (lift)* strategy. For frequency-dependent transmission bias, I replicated here that found for feeding techniques in wild capuchin monkeys (Perry, 2009). Perry studied the relative use of pounding and scrubbing variants (for opening *Lucea* fruit) to assess whether young capuchins adopted the technique (variant) more frequently observed. In line with Perry's findings, juvenile (but not adult) capuchins across both groups (JB and PF) performed more frequently the behavioural variant they had observed more frequently, i.e. *lift*, which was the behavioural variant at highest frequency in both groups. This finding leads us to speculate that *copy when unexperienced* might be a social learning strategy employed by the capuchins. In this thesis, I do not directly address social learning strategies based on state-based biases (i.e. when an individual should copy), but studies with primates have shown that individuals are prone to use social information when the behaviour to be learned is more difficult. In fact, copy when uncertain has been reported for many non-human animal species as reviewed in Kendal et al, 2005). In neotropical primates, for example, Day et al's (2003) detected social learning in callitrichid monkeys only when solving the most difficult of the foraging tasks. An alternative interpretation of why only juveniles would be influenced by frequency, is that, given that juvenile capuchins are tolerated by most (if not all) group members, the predominant trait used by the majority of individuals could be less relevant than the total frequency of possibilities for observing a given variant. The latter would be especially true if several observation opportunities are needed before the young capuchin can learn the new behaviour.

I cannot affirm that the findings for the acquisition of the lift-pull task were consistent with a *copy the majority* social learning strategy. For such an affirmation it is necessary a disproportionate tendency to do copy the actions of the majority of individuals would be needed. In my results, the stringent diversity in variants (because the great majority of individuals used the same variant predominantly) meant a disproportionate tendency to copy could not be determined. A tendency to adopt the majority behaviour is what Boyd & Richerson (1985) called positive frequency dependence (also known as cultural inertia) is common in humans, however, its existence in non-human primates has been controversial.

van Leeuwen & Haun (2013), make a strong point in arguing that conformity studies in non-human primates are not conclusive. Furthermore, these studies are not specifically designed to address conformity and often attempt to do so, based on results two-action task experiments, not the most appropriate experimental set-up to investigate conformity.

As regards the model-based biases, success at solving the task predicted the frequency of being observed by conspecifics as a main effect; an interaction effect between the sex of the model and their success at solving the task was also predictive of the frequency with which individuals observed them. These findings were despite the observation networks having been normalized to control for the frequency of activity by the models. One must consider, however that the more frequently targeted individuals, in terms of observation by conspecifics, might have exhibited higher success ratios because, overall, they had more opportunity to manipulate the task; thus either becoming more proficient at solving it or reducing errors due to a larger sample size. These findings should also be examined with caution as they address whom individual observed preferentially, and therefore does not offer a direct measure of whom was copied. However, given that in the previous chapter, social learning was detected based on observation networks within 5 meters distance, for both groups, it is safe to argue that observational context was conducive to learning and that, although an indirect measure it can be taken as an appropriate proxy for the present analysis.

The finding that more proficient individuals (i.e. those better at solving the task) were more frequently observed by naïve conspecifics, echoes findings for semi-free capuchin monkeys with regards to social learning strategies for nut-cracking (Otonari et al, 2005; Coelho et al, 2015). In the latter study (Coelho et al, 2015), proficiency was not the only predictor of choice of observational target, with significant effects of age and dominance rank of models also present. This is similar to the finding for the lift-pull task, where males and more proficient individuals were more frequently observed by naïve conspecifics.

In the following chapter (General Discussion), I discuss in further details the implications of the social learning strategies identified in this study and how these findings resonate with the literature of SLS in non-human animals. I also expand on the debate over the adaptiveness of social learning versus asocial learning in light of arguments made in the introduction about the ultimately individual nature of learning which can (or not) be biased by the social context.

CHAPTER 6:

GENERAL DISCUSSION

The social context: on opportunities of social learning

The wild capuchin monkeys (*Sapajus libidinosus*) at PNSC frequently engage in behavioural coordination in both time and space, which confirms that there are many opportunities in which they can learn from social cues presented by conspecifics. Behavioural coordination in both time and space is of particular interest, as it affords the observer its best opportunity to acquire detailed information from the demonstrator. However, it is important to note that when not coordinating in both space and time, these monkeys, with their cohesive social groups, were constantly coordinating solely in time or solely in space. The two latter forms of behavioural coordination, while not allowing detailed observation, allow individuals to learn about essential characteristics of the environment biased by group members. In coordinating in time, experiences with the environment are biased by synchronism with other group members and, in spatial coordination, experiences are biased by physical alterations of the environment resulting from the activity of conspecifics. All three forms of behavioural coordination provide conditions in which social learning occurs although they can vary in the type of information being transmitted (Coussi-Korbel & Fragaszy 1995).

Coussi-Korbel & Fragaszy's (1995) seminal paper is often cited in the social learning literature to emphasize the importance of taking the social context into consideration, however, seldom have studies attempted to describe animal social structures specifically addressing the opportunities for social learning (for exceptions see Voelkl & Noë 2008 and Carter et al, 2015 discussed below). The findings presented in this thesis give an empirical description of the social learning opportunities available to these wild capuchin monkeys. I confirm Coussi-Korbel & Fragaszy's (1995) predictions that capuchin monkeys have relationships conducive of both non-specific social learning and directed social learning. A portrayal of the groups' social structure based on different measures of relationships allowed for the description of social networks that produced opportunities for non-specific, and directed social learning. Where the social structure was defined by fairly homogenous associations between individuals, such as in the saturated association networks (social proximity and co-feeding), relationships prescribe situations conducive to non-specific social learning. In contrast, where the social structure contained heterogeneous relationships, with networks fragmented into sub-groups or cliques (such as play, grooming and observation networks), relationships sustain conditions conducive to directed social learning.

In a study of intragroup behavioural variation of foraging techniques in white-fronted capuchin monkeys (*Cebus albifrons*), Matthews (2009) applied a novel cluster analysis method based on social networks, and found that the use of certain food processing techniques clustered in a way that mirrored the clustering of individuals regarding frequencies of association. These results differs from my findings given that asymmetry was found in social proximity relationships, while my data for social proximity points towards homogenous relationships conducive of non-specific social learning. This is interesting as it points to a possible difference between *Cebus* and *Sapajus* regarding social proximity; further studies widening the sample size are required. Despite this difference, Matthews' (2009) findings are in line with mine in showing that capuchin monkeys engage in asymmetric relationships, which supplies evidence of the necessary conditions for directed social learning of food processing techniques between individuals.

Directed social learning is expected to generate more intra-group variation in behavioural traits, as opposed to non-specific social learning, given the heterogeneity in relationships (Coussi-Korbel & Fragaszy 1995). Simulation of diffusion of information through both artificial and natural (empirical) primate social networks have shown that the non-human primate social networks, resemble 'small-world' networks found for humans (Voelkl & Noë 2008). 'Small-world' networks are particular in that they are clustered into subgroups but are simultaneously short-pathed (Watts and Strogatz 1998). Under these conditions, although a behavioural trait would be transmitted through subsections of the group, via directed social learning, it could still become wide- spread, given that the total amount of steps needed to connect all group members are relatively few (short-pathed attribute of the network). My findings show that all of the socio-positive and observation networks of the capuchins at PNSC presented some clique formation, as the clustering coefficient (Watts and Strogatz 1998) was always larger than the network density. Overall, the networks did not vary greatly in how clustered they were, with the exception of the observation networks which presented significantly more sub-groupings than grooming and, than social play networks. By analysing the assortative mixing of the social networks, I was able to describe these asymmetric relationships in further detail, identifying the 'pathways' conducive to directed social learning, for the different types of relationships.

Grooming networks presented asymmetrical relationships that describe conditions for directed social learning. Assortative mixing was present based on sex classes and had disparate results for the two groups studied. In JB, most grooming bouts occurred between

the sexes (heterophily), with a predominance of males grooming females. In this group, where the adult male to adult female ratio was 1:1, it is possible that males “cultivated” their relationships with females based on grooming, as the female choice of target during proceptive behaviour mirrored the grooming relationships (Coelho et al 2013). Furthermore, the dominant male in JB (BOL), as determined by agonistic interactions, does not have priority of access over the proceptive females, as is considered the norm for capuchin monkeys. In PF, on the other hand, grooming relationships occurred predominately within the sexes (homophily), specifically between females, the philopatric sex for this species. In PF, the sex ratio of mature individuals was skewed towards females (2 male:3 female), and in addition, only two larger males (Tor and Zan) were seen being targeted by proceptive females; with the dominant male (Tor), as determined by agonistic interactions, having priority over proceptive females. Current literature places the pattern described by PF as typical for capuchin monkeys (including both *Cebus* and *Sapajus*) (Fragaszy et al 2004), however, there is no available information for social and reproductive behaviours specific for the population in question, i.e. *S. libidinosus* inhabiting the *caatinga*. Long-term studies over a larger sample of groups are needed before further assertions can be made.

Overall, the findings for assortative mixing in grooming networks point to the importance of measuring the social context at the time of the diffusion study due to the dynamic nature of such relationships. Given the differences in the grooming networks of the two groups, a behavioural trait associated to grooming, such as hand-clasp grooming in chimpanzees (McGrew et al 2001; Bonnie and de Waal 2006), would have very distinct diffusion possibilities in the two groups. In contrast, assortative mixing in the social play networks was similar for both groups (JB and PF) and was characterised by more frequent interactions among juveniles (homophily of age group) and among males (homophily of sex). The stronger connections between certain classes of individuals prescribe clear pathways for directed social learning. Examples of behaviour likely to spread through play pathways would be the eye-ball poking, hand in mouth and other play traditions in white-fronted capuchin monkeys (Perry 2003), and stone-handling in Japanese macaques (Huffman & Hirata 2003; Nahallage & Huffman 2007).

I also examined assortativity in who observed whom solving the two-action task. Assortative mixing of observation networks based on dominance rank describe how naïve individuals observed models who were generally more dominant than themselves. This is likely the result of higher-ranking individuals being able to monopolise the task. Nonetheless,

it is an interesting finding in itself, as it shows that, within the natural dynamics of a group, dominant individuals are likely to have more frequent chances of solving a foraging problem than subordinate individuals; thus demonstrating their behavioural variant more often. Initially, these findings seem to resonate with other studies where naïve individuals predominantly observed dominant individuals (e.g. chimpanzees: Kendal et al. 2015, starlings: Boogert et al 2006). However, when the observation networks were normalized for the frequency of activity of the models solving the task, frequency of observation was no longer found to be related to dominance rank, indicating directed social learning regarding rank, rather than a transmission bias (I shall explore these finding later on in this chapter). Accordingly, dominant individuals, particularly the dominant male, were found to be more central than other group members in both the socio-positive and the observation networks; indicating that, if information was to be flowing through the networks, dominant individuals would play a crucial role in its spread. These results are in line with findings of Claidiere et al (2013), who used social network centrality measures to identify observational learning in a two-action task with captive squirrel monkeys (*Saimiri sciureus*). They found that eigenvector centrality of observation networks predicted the speed with which an individual first solved the task. Thus, the authors conclude that the monkeys relied on observational learning to acquire the group behavioural trait.

Social network analysis (SNA) can provide useful tools for identifying social learning. However, one must take into consideration the conditions of the social context before considering the appropriate SNA metrics to employ. The eigenvector centrality proved to be useful in Claidiere et al's (2013) study possibly because dominant individuals were trained demonstrators, thus centrality was a key feature in the diffusion. This might not be the case for more egalitarian social groups or situations where the novel behaviours are innovated by subordinate individuals. Here again, I emphasize the importance in considering which are the relevant social contexts for the diffusion of the behaviour being studied.

From this section of the discussion chapter, I conclude that the social context in which the capuchin monkeys live represents a tolerance 'landscape' that is multi-layered, varying according to the relationships and types of interactions between group members, and the activities being performed. This tolerance 'landscape' is important for two main reasons. First, it allows us to determine the opportunities individuals have of learning from conspecifics. Second, the variable opportunities of learning from others can generate patterns

in the transmission of information, that are based on the social context rather than on learning mechanisms and which might appear as confounding variables in studies of transmission biases (or social learning strategies); a point I discuss in further details later in this chapter.

Identifying learning influenced by the social context: on the importance of choosing social networks representative of the relationships underlying diffusion

Network-based diffusion analysis (NBDA) has been in constant development since Franz & Nunn (2009) introduced it (Hoppitt et al 2010; Hoppitt & Laland 2013). Currently it allows us to inform the asocial model with variables that describe individual attributes (e.g. individual neophobia and dominance rank) that could lead to a false-positive identification of social learning. The non-social transmission model (a.k.a. asocial model) compares the rate of diffusion of the new behaviour to the asocial factors alone. The social transmission model (a.k.a. social and asocial model), on the other hand, considers both the asocial factors and the social context (input by the social network) when considering the fit with the rate of diffusion of the novel behaviour. NBDA's strongest point is that it allows us to inform the social model with a social network, therefore improving greatly on previous analysis, which considered that individuals learn from other individuals randomly.

In this thesis, NBDA produced evidence for social learning of the foraging tasks when observation networks informed the social transmission model. This finding reinforces those from previous studies with captive capuchins (Dindo et al 2007, 2009; Crast et al 2010) as well as squirrel monkeys (Cladiere et al 2013), and indicates that these neotropical primates are capable of observational learning even outside controlled experimental contexts. Moreover, where the social context was informed by observation of the task being solved from within 5 meters distance from the observer, the social transmission models presented a significant fit to the diffusion data. In contrast, when the social transmission model was informed by frequency of observations over 5 meters distance, NBDA could not find a significant fit to either models. Hence, observations had to have occurred within a certain distance for the social learning effect to be present.

Other social networks also provided evidence for social learning in both groups, predominantly those based on grooming relations for the lift-pull task and co-feeding relations for the tube-task. One might expect that social learning of a foraging task would be better detected by co-feeding, rather than grooming, since the experiments involved foraging tasks. One major difference in the experimental set-up of the lift-pull task and the tube task

was that for the former the monkeys were presented with a single apparatus, whereas in the latter, three identical tubes were made available to the monkeys. It is thus probable that competition over the lift-pull task was higher than that for the tube task apparatuses. Within a competitive scenario, grooming might be a better measure of the tolerance landscape as it portrays concomitantly a socio-positive relationship and an aspect of hierarchy, better reflecting the access to a resource (here, the lift-pull apparatus) than co-feeding. Along the lines of this hypothesis, Boogert et al's (2014) showed that NBDA found the social model to have a better fit to the diffusion data when perching networks of starlings, but not foraging networks, informed the social model. The authors argue that in perching, the starlings were more prone to choose whom to associate with and thus perching relationships were a better portrayal of who starlings chose to attend to when they learn. Similarly, it may be argued that there is more active choice in whom to groom than whom to feed next to in capuchins.

Boogert et al (2014) argue that previous studies may have found negative results for NBDA because they used a single social network. Accordingly, these authors highlight the importance of considering more than one social network when predicting spread of behaviour through a group. As argued previously in the chapter the first step in identifying social learning should be to give due consideration to what types of social contexts might be more conducive to the spread of a particular behaviour. It is likely that some of the studies that had shown support for social learning with other analysis, but presented inconclusive results regarding NBDA, did so because the social network used to inform the social transmission model did not represent a social context conducive to social learning. For, example, Kendal et al (2010b) informed the social model with a network containing the absolute rank difference between individuals. Ring-tailed lemurs (*Lemur catta*) have a strongly hierarchical social system and the dominant females actively monopolised the several apparatuses offered to the wild groups. The authors therefore reasoned that a dominance hierarchy network would be a propitious one; however, the authors found a negative result for NBDA despite other analysis having identified social learning. It is possible that the network chosen was not the most appropriate to portray the social opportunities of learning to solve this task. By investigating which social contexts might result in a better fit to the diffusion data, one can portray the relationships (association and interactions patterns) that make up the tolerance landscape within which social learning is occurring

Overall, NBDA, applied to the lift-pull task, was able to find better fits for the diffusion data when the social model was informed by socio-positive networks characterised by high flow betweenness centralities (such as observation and grooming networks). Given that

NBDA uses the strength of connections between individuals in a network as a predictor of the rate of diffusion between them, for the social model, it is likely to have stronger power to identify directed social learning rather than non-specific social learning. In fact, my findings show that, where the rate of diffusion for the social model was informed by networks portraying relationships of varying strengths between individuals, conducive to directed social learning (i.e. interaction and observation networks), NBDA was better able to clearly discern between the asocial and social-and-asocial agent-based models by finding conclusive selection for one of the two models. This was true whether finding a better fit for the social-and-asocial model (as for the grooming and observation networks) or for the asocial learning model (as for the play networks). My findings indicate that, for tufted capuchin monkeys (*Sapajus sp.*), among the socio-positive networks, interaction networks seem to provide more power for the NBDA, likely as consequence of the clear pathways described by asymmetric relationships. Association networks might not be able to inform NBDA adequately. The latter is one possible reason why NBDA could not find a better fit for either social or asocial models in Schnoell & Fichtel's (2012) study of social learning among red-fronted lemurs (*Eulemur rufifrons*).

So far, two studies have presented positive results for social learning using NBDA with social models informed by association networks, namely Lob-tail fishing in humpback whales (Allen et al 2013) and patch discovery in wild song-birds (Aplin et al 2012). Unlike the fully connected, homogenous association networks described for primates (Kasper & Voelkl 2009), who generally live in relatively cohesive social groups, the studies of whales and song-birds used pod and flock composition, respectively, as measures of association. I suspect that association networks sampled from such fluid fission-fusion social grouping are likely to be more heterogeneous and thus better suited for NBDA. Unfortunately, SNA metrics are seldom provided in NBDA studies, thus making it hard to verify such assumptions.

More recently, Hobaiter et al (2014) developed a novel, dynamic version of NBDA, capable of evaluating how successive observations by an individual influence its acquisition of the novel behaviour. By applying this version of NBDA they found evidence for the social transmission of variants of moss sponging in wild chimpanzees. A better fit to the diffusion data was found for the social-and-asocial model, than for the asocial model, when it was based on observation frequency, thus detecting observational learning. It would be interesting to run this new version of NBDA for my data to determine how including temporal aspects of

acquisition (such as the number of observations made while naïve) might alter the detection power of NBDA.

On the group repertoire and social learning strategies

By the end of the lift-pull experiment, most individuals in both groups had learnt to solve the task using both the available actions, despite showing a clear preference for using one of the actions to solve the task. In addition, even though both actions yielded the same amount and quality of rewards, the action lift was used predominantly by most individuals and in most of their interactions with the task (as reported in chapters 4 and 5). In the classic two-action task two groups paradigm - where social learning is inferred to be occurring only if two distinct group repertoires (in terms of the behavioural variants) are established- I would have no basis to argue for social learning. However, as argued in the introduction the group contrast approach (a.k.a. ethnographic approach) is liable to falsely rejecting a behavioural tradition because two groups present the same behavioural repertoire, and the classic two-action task experiment is subject to the same problem. As argued previously, NBDA is capable of making a more informed inference of social learning and the findings indicate that social learning is underlying the spread of the knowledge of how to solve the task. In addition, NBDA showed that observing a conspecific at close proximity while s/he solved the task, predicted the diffusion of solving the task, thus some knowledge is acquired during observation, rather than mere attraction to the task as a whole (which is possible at greater observation distances). The field experimental set-up was not intended to address social learning processes. Hence, the question will remain whether observation led to the monkeys learning something more general such as ‘do something to that colourful part of the box with things sticking out’ (stimulus/local enhancement), more specific, such as ‘lift the blue square’ and ‘pull the green rod’ (imitation) or something intermediary. Given the constraints of field experiments, I am thus unable to address whether one of the options (blue door, green knob) or actions (lift, pull) was more prominent tactilely or visually and therefore more likely to be cued in the demonstrations observed. However, contextual variables, such as the characteristics of the demonstrators and/or observers, could also be biasing social learning, and consequentially influencing the final distribution of the behavioural trait.

The establishment of *lift* as a group wide practice in PF group could, for example, have been due to the a low ‘virulence’ of the subordinate juvenile male Lim in spreading the

seeded option (*pull*) and/or a tendency for observers to copy dominant individuals (e.g. the dominant male who used the *lift* option). Consistent with the latter argument, van de Waal's (2010) study of vervet monkeys found that when the inception of the novel behaviour (whether seeded or innovated) came from a dominant female (rather than male), the new behaviour seemed to be more 'virulent' and spread through the group, generating a clear group predominant bias. The author thus argues in favour of the group repertoire being established by a 'copy the philopatric sex' social learning strategy.

Besides the importance of the origin of the new behavioural trait, the subsequent spread of the behaviour among group members is also prone to social biases. In line with this argument, Cadieu et al. (2010) reported that male canaries were more innovative than females, however, the novel behaviour only spread to females, since males did not tolerate each other. The authors concluded that although females were not the most innovative they were the best demonstrators to ensure the transmission of information throughout the flock as both males and females could learn from them. Interested in how biases during the spread of the behaviour might have influenced the overall repertoire, I set out to address characteristics of the models that might be biasing the use of the different variants (*lift/pull*). In chapter 5, I presented findings consistent with model-based biases. Similar to the argument that more than one social learning process might be underlying the acquisition of behaviour by new practitioners, several transmission biases may be acting together in biasing the spread of information among group members. Dominance rank was a clear factor in the opportunities of observation, mirroring the ability dominant individuals had of monopolising the task. Once the frequency of activity was controlled for, however, successful (in terms of solving the *lift-pull* task) males, emerged as the preferred target of observation in both groups. Selective attention towards proficient individuals has been described for tool-aided nut cracking in semi-free capuchin (*Sapajus spp.*: Ottoni et al 2005, Coelho et al, 2015) and wild capuchin monkeys (*Sapajus libidinosus*) (Coelho et al 2008). In capuchin monkeys, males are usually the most frequent tool users and often the target of observation by group members (Mannu & Ottoni 2008; Spagnoletti et al 2011; Falótico & Ottoni 2014; Coelho et al 2008).

Some of the monkeys who had originally solved the *lift-pull* task using the action *pull*, shifted from their original behavioural variant, adopting *lift*, the group predominant variant. The reduced sample size means only assumptions can be made regarding a conformity bias based on this information, thus, I investigate possible frequency-dependent transmission biases at the population-level in an attempt to further understanding of how these transmission biases might be influencing the final group repertoire.

My findings concerning frequency-dependent social learning strategies, seem to be consistent with both the frequency effect ('fad bias') and conformist bias (but see criticism below). The frequency effect or 'fad-bias' (i.e. copy the action most seen performed by conspecifics) was present, however, only for juvenile observers. This resonates with the findings of Matthews (2009) and Agostini & Visalberghi (2005), described below. In his study of food processing techniques in white-fronted capuchins, Matthews (2009) reported mixed results for social learning as only one of the two versions of the cluster analysis ran, revealed social learning. When the cluster analyses involved a binary value (presence-absence) for the food processing techniques within the individual's repertoire, there was substantiated evidence for social learning. However, when the cluster analysis included the frequency of the food processing techniques no such result was found. This finding suggests that, while the existence of a behavioural trait within an individual's repertoire might mirror the repertoire of group members with whom s/he associates, the frequency of performing such traits across individuals might not reflect patterns of association. Rather, variation in frequency of traits could be driven by ecological, developmental and/or social factors, such as transmission biases. Matthews (2009) in fact argues in favour of a combination of developmental and transmission bias effects and states: "*there may be a window of time during development when social learning of substrate processing frequencies occurs. Individuals may be biased while young to learn about these frequencies from older individuals with whom they have contact (Agostini & Visalberghi, 2005), but beyond some point in development the frequency with which they use techniques is more influenced by their own experiences of food processing payoffs.*" (pg. 319). Agostini & Visalberghi (2005) studied foraging patterns across age and sex classes of wild tufted capuchin monkeys (*Sapajus nigritus*) in Iguazu National Park and found that the acquisition of foraging behaviours by juvenile males was socially biased by their closeness to adults of the same sex. In summary, and in accordance with other authors, the frequency with which a juvenile capuchin monkey observes a given behavioural variant (e.g. food processing technique) being performed is predictive of the behavioural variants the juvenile capuchins will perform themselves. In line with the findings here reported, these studies also report a model-based bias, whereby young capuchins' acquisition of food repertoire would be biased by that of older individuals of the same sex as them.

However, given the homogeneity of option choices (i.e. predominance of lift) in both groups there is little I can safely affirm regarding frequency-dependent biases; a more sophisticated analysis is required before a case for conformity bias can be made.

Furthermore, as discussed in chapter 5, care must be taken when interpreting conformist bias as one must show disproportionate copying is occurring and the analysis conducted currently does not account for this. Finally, van Leeuwen et al. (2013) has argued that two-action task experiments are not the most propitious set-ups to address frequency-dependent transmission bias; a specific experimental set-up is required to test for conformity.

On integrating social context, learning processes and transmission biases

Although many social learning studies have examined relevant relationships in the spread of information, few studies (fish: Swaney et al 2001; Katz & Lachlan 2003; ravens: Schwab 2008; vervet monkeys: van de Waal et al 2012 and lemurs: Kendal et al 2010) have referred specifically to the types of social learning as proposed by Coussi-Korbel & Fragaszy (1995). Here types of social learning (namely non-specific and directed social learning) do not refer to social learning processes; rather they are defined by the social context (i.e. determined by different relationships or group social structure). This is in line with the viewpoint that learning is ultimately individual and that social learning is therefore the consequence of the social context biasing an individual's learning (Fragaszy & Visalberghi 2001; Heyes 2011).

At times, the definition of directed social learning has been used in ways that stray a little from how it seems to have been originally proposed. For example, van de Waal et al (2012) found that social learning of a novel foraging behaviour (a two-action task) was greater when dominant females, rather than dominant males, acted as trained demonstrators. Their analysis showed that this difference was the result of selective attention to females and not due to a higher tolerance on the part of females or aggression on the part of males. van de Waal et al (2010) thus conclude that there was a “*favoured role of dominant females as a source for ‘directed’ social learning in a species with female philopatry*“. This is certainly an interesting result as it addresses a crucial point of behavioural traditions seldom touched on by other studies, namely how a new behaviour (be it an innovation or seeding by a trained individual) begins its social diffusion (discussed above). However, the results from this study cover the first step of the putative diffusion, i.e. the introduction of the behaviour, and then ‘jumps’ to the final outcome. To characterise as directed social learning one would have to describe relationship ‘pathways’ through which information is directed as it spreads to other group members, becoming a shared practice. Although the findings are potentially consistent

with directed social learning (according to female philopatry) further analysis is required to claim it. Moreover, throughout the paper, the authors use terminology related to directed social learning and transmission biases interchangeably. Typical of directed social learning, the females (philopatric sex) are described as a favoured relationship and source for social learning, while at other points “copying the philopatric sex” is referred to. It is not uncommon that terminology from these approaches are used interchangeably.

Considering the following scenario can help to better elucidate the pit falls where directed social learning and transmission biases become confounded. In a hypothetical primate species with a female philopatric society, older juveniles of different sexes live within very distinct tolerance landscapes. Female juveniles are tolerated by both male and female adults. Male juveniles, on the other hand, will be often tolerated by its mother and a few other adult females but only rarely by adult males. If we were to consider only the social context, one would expect non-specific social learning for female juveniles since they are amply tolerated by all and thus can acquire information from anyone in the group, and directed social learning for juvenile males who can acquire information from the few individuals who tolerate them (e.g. mother or other adult female sisters). However, if transmission of information, besides being directed by the group social structure (opportunities for social learning), was also being biased by motivational forces (transmission bias) a quite different transmission outcome can be expected. If we add the motivational force to the hypothetical scenario and suppose juvenile females are highly motivated to attend to adult females and juvenile males are highly motivated to attend to adult males. Now, one might expect a strong influence of adult female behaviour upon juvenile female behaviour consequent of and added effect of directed social learning and transmission biases. While for juvenile males, one might predict a continued directed social learning from some females occurring alongside a transmission bias to attend to males, that is, making the most of the few opportunities the juvenile males have of observing adult males, by attending to them whenever possible.

The transmission outcome of female juveniles from adult females, as motivation added to tolerance, will result in optimal scenario for social learning. Furthermore, at group level one might be inclined to argue in favour of a ‘copy the philopatric sex’ since both female and male juveniles learn from adult females (the philopatric sex). However, in accordance with my argument here present, interpreting the transmission outcome as a transmission bias would be erroneous. This is because the transmission outcome does not result from any heuristics that are present because they are selectively adaptive, a requirement to constitute a

transmission bias (Richerson & Boyd 2005). Rather, the transmission outcome is the consequence of social learning being directed along the tolerance pathways present in a female philopatric society. Of course, female philopatry is also the consequence of natural selection, however one would argue this is a less flexible characteristic than psychological mechanisms (such as motivation to attend to a particular sex), thus the first can be described as the opportunities, while the latter as rules of transmission. .

By giving due attention to the social influences resulting from of the social context (directed social learning) and those resulting from transmission modes, I expect that a better understanding of the levels of social influences affecting the spread of a behavior and of the establishment of a maintained behavioural practice, can be reached.

On tolerance, social learning and behavioural traditions

According to van Schaik's (2003) *opportunities for social learning hypothesis*, social tolerance affects both the initial spread and the subsequent maintenance of a behavioural tradition. The hypothesis further posits that a greater tolerance and the consequent increase of social learning opportunities should generate more diverse local traditions. The highly connected association networks describe the capuchins at PNSC as forming cohesive groups. Furthering the understanding of cohesiveness in primate groups might elucidate why behavioural traditions vary amongst primate groups. For example, the lack of tool-use (such as sticks as probes) amongst forest dwelling *Sapajus* species might be, in part, consequence of their fission-fusion societies (Izar et al 2012). In socially fragmented groups a novel behavioural trait is unlikely to spread sufficiently to become a group-wide behavioural tradition. Although, large cohesive groups, such as the *S. libidinosus* of PNSC are likely to have come about due to ecological factors (e.g predation risks), the result is that these large groups are subject to ideal conditions under which group-wide maintained behavioural traditions may occur.

Large social groups would be expected to generate a greater number of innovations. A relatively high tolerance between individuals allows new behaviours to spread and to be maintained, through social learning. The combination of these two factors make for ideal conditions for behavioural traditions. Here I posit that the large tool kit present in the SCNP capuchin monkeys might be, at least in part, explained by a combination of large group sizes (more innovations) and high levels of tolerance between individuals (diffusion and

maintenance of a shared behavioural practice). Capuchin monkeys exhibit a high degree of interindividual tolerance, especially towards infant and juveniles (Fragaszy et al 2004) and are often described as exhibiting an intermediary society in the despotic-egalitarian spectrum of primate societies (Coussi-Korbel & Frigaszy 1995, Frigaszy et al 2004). Such characteristics point towards capuchins having a particularly conducive social context for the establishment of behavioural traditions. New behaviours are expected to be introduced into wild groups through innovation, usually by subordinate individuals under pressure to find alternative resources, and/or young individual, who are typically less neophobic and more prone to manipulate elements in their environment in novel or different ways (Reader 2004, Kummer & Goodall 1985). It is therefore likely that, as these young, neophilic and manipulative, male capuchin monkeys, are forced out of the female philopatric groups, and assume a subordinate position in new groups, they are pressured into having to come up with novel foraging techniques to survive. In a more despotic society, the behaviours of the subordinate individuals would be unlikely to spread through the group as subordinates are not paid attention to. However, in the partially and asymmetrically tolerant society of capuchin monkeys, these novel behaviours may spread into the main component of the social group, via directed social learning, and become a maintained shared behavioural tradition.

Considering opportunities of social learning and transmission biases together allow us to further the understanding of how distinct traditions in neighbouring populations that share ecology and migrants, might occur. In chimpanzees, traditions are unlikely to homogenise across group as consequence of a conformity influence on immigrants (Luncz et al 2012) and/or copy dominant individuals (Kendal et al, 2015), meaning subordinate immigrants are usually ignored. As the picture of the social influences in the transmission of behaviour in capuchin monkeys becomes clearer, we further our understanding of the dynamics involved in the spread of behavioural traditions across populations.

Behavioural traditions can have important fitness consequences for their practitioners. The biological significance of these long-lasting shared behavioural practices is that behavioural innovations, which can be rare occurrences, need only occur once. Through social learning, this novel behaviour, product of a single innovation, can then become widespread among group members, be maintained over time and passed on to new generations and migrant individuals. Social learning can thus be thought of as contributing to niche construction and enhancing the species' potential for feedback to natural selection (Odling-Smee et al, 1996). When these shared behavioural practices impact fitness positively they are maintained over time and by such the behavioural traditions can become part of the

constructed niche. By removing the individual from a passive condition as simply a target of natural selection, the concept of niche construction enriches the evolutionary processes and allows us to consider how individuals and their behaviours feedback into the evolutionary process (Laland et al, 2000).

Future directions

As studies identifying behavioural traditions in non-human animals accrue, we move away from the original human-centred perspective towards broader questions focusing on cognitive, ecological and social factors fostering the emergence and maintenance of behavioural traditions (Ottoni, 2015). This thesis strengthens the ground on which we can claim behavioural traditions for wild capuchin monkeys. It also ends with the advent of new questions to be addressed. Among some of the questions still ripe for investigation are: what are the individual and social processes behind the appearance of novel behavioural traits in wild populations? How frequent are these behavioural innovations? What is the likelihood these will spread among group members? What are the social conditions necessary for the novel traits to be transmitted between group members becoming a maintained shared practice in wild populations? How do ecology, cognition and group social dynamics interplay in each stage of establishing and maintaining a behavioural tradition? Long term studies are required to address core issues in the origin of traditions in wild capuchin monkeys. Developmental approaches coupled with a multi-faceted comprehension of group social dynamics are also important to further the understanding of inception, spread and maintenance of behavioural traditions.

REFERENCES

- Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In *Selected Papers of Hirotugu Akaike* (pp. 199-213). Springer New York.
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), 485-488.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, rspb20121591.
- Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge University Press.
- Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees: Enculturation, temperament, and cognition. Reaching into thought: The minds of the great apes, 235-256.
- Barta, Z., & Giraldeau, L. A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology*, *42*(3), 217-223.
- Bonnie, K. E., & de Waal, F. B. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, *47*(1), 27-34.
- Boogert, N. J., Nightingale, G. F., Hoppitt, W., & Laland, K. N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. *Behavioural processes*, *109*, 135-144.
- Boogert, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, *72*(6), 1229-1239.
- Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. London: SAGE Publications Limited.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Brown, C., & Laland, K. (2002). Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon. *Journal of Fish Biology*, *61*(4), 987-998.
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: a hierarchical approach. *Behavioral and brain sciences*, *21*(05), 667-684.
- Caldwell, C. A., & Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, *65*(6), 1085-1092.

- Caldwell, C. A., & Whiten, A. (2004). Testing for social learning and imitation in common marmosets, *Callithrix jacchus*, using an artificial fruit. *Animal cognition*, 7(2), 77-85.
- Campbell, F. M., Heyes, C. M., & Goldsmith, A. R. (1999). Stimulus learning and response learning by observation in the European starling, in a two-object/two-action test. *Animal Behaviour*, 58(1), 151-158.
- Cardoso, R. (2014). Resolução de problemas por macacos-prego selvagens (*Sapajus libininosus*) de duas populações com diferentes repertórios de uso de ferramentas. (Tese de Doutorado). Instituto de Psicologia, Universidade de São Paulo, São Paulo.
- Claidière, N., & André, J. B. (2012). The transmission of genes and culture: a questionable analogy. *Evolutionary Biology*, 39(1), 12-24.
- Claidiere, N., Messer, E. J., Hoppitt, W., & Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Current Biology*, 23(13), 1251-1255.
- Coelho, C. G. (2009). Observação por co-específicos e influências sociais na aprendizagem do uso de ferramentas para quebrar cocos por macacos-prego (*Cebus* sp.) em semi-liberdade. (Dissertação de mestrado). Instituto de Psicologia, Universidade de São Paulo, São Paulo.
- Coelho, C. G., Falótico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal cognition*, 1-9.
- Coelho, C. G., Kendal, R. L., & Ottoni, E. B. (2013, January). Female Mate Choice and Male Mating Strategies in Wild Bearded Capuchin Monkeys (*Sapajus libidinosus*). In *Folia Primatologica* (Vol. 84, No. 3-5, pp. 259-260). Allschwilerstrasse 10, Ch-4009 Basel, Switzerland: Karger.
- Coussi-Korbel, S., & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal behaviour*, 50(6), 1441-1453.
- Crast, J., Hardy, J. M., & Frigaszy, D. (2010). Inducing traditions in captive capuchin monkeys (*Cebus apella*). *Animal Behaviour*, 80(6), 955-964.
- Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton: Princeton University Press.
- Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 113(1), 13.
- Custance, D., Whiten, A., Sambrook, T., & Galdikas, B. (2001). Testing for social learning in the "artificial fruit" processing of wildborn orangutans (*Pongo pygmaeus*), Tanjung Puting, Indonesia. *Animal Cognition*, 4(3-4), 305-313.
- Cutrim, F. H. R. (2013). *Padrão comportamental e uso de ferramentas em macacos-prego (Sapajus libidinosus) residentes em manguezal* (Tese de doutorado) Instituto de Psicologia, Universidade de São Paulo, São Paulo.

- Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal behaviour*, 13(4), 470-474.
- Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, 65(3), 559-571.
- Dean, L. G., Hoppitt, W., Laland, K. N., & Kendal, R. L. (2011). Sex ratio affects sex-specific innovation and learning in captive ruffed lemurs (*Varecia variegata* and *Varecia rubra*). *American journal of primatology*, 73(12), 1210-1221.
- Dindo, M., Thierry, B., & Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society B: Biological Sciences*, 275(1631), 187-193.
- Dindo, M., Whiten, A., & de Waal, F. B. (2009). In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PLoS One*, 4(11), e7858.
- Drea, C. M., & Wallen, K. (1999). Low-status monkeys “play dumb” when learning in mixed social groups. *Proceedings of the National Academy of Sciences*, 96(22), 12965-12969.
- Drewe J. A. & Perkins, S.E. Disease transmission in animal social networks. In: J. Krause, R. James, D. Franks & D. Croft. *Animal Social networks* (pp. 95-109). Oxford: Oxford University Press.
- Falótico, T. (2011). Uso de ferramentas por macacos-prego (*Sapajus libidinosus*) do Parque Nacional da Serra da Capivara. (Tese de doutorado). Instituto de Psicologia, Universidade de São Paulo, São Paulo.
- Falótico, T., & Ottoni, E. B. (2013). Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. *PloS one*, 8(11), e79535.
- Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS biology*, 4(9), e302.
- Ferreira, R. G., Izar, P., & Lee, P. C. (2006). Exchange, affiliation, and protective interventions in semifree-ranging brown capuchin monkeys (*Cebus apella*). *American journal of primatology*, 68(8), 765-776.
- Fragaszy, D. M., & Perry, S. (2003). Towards a biology of traditions. In: D. M. Frigaszy, & S. Perry (Eds.), *The biology of traditions: models and evidence* (pp. 1-32). Cambridge: Cambridge: University Press.
- Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Visalberghi, E. (2013). The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120410.
- Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus*. Cambridge: Cambridge University Press.

- Fragaszy, DM, Visalberghi, E (2001) Recognizing a swan: socially-biased learning. *Psychologia* 44, 82-98
- Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, 276(1663), 1829-1836.
- Galef, B. G. (2004). Approaches to the study of traditional behaviors of free-living animals. *Animal Learning & Behavior*, 32(1), 53-61.
- Galef, B.G. (1976). Social Transmission of Acquired Behaviour: a Discussion of Tradition and Social Learning in Vertebrates. *Advances in the Study of Behavior*, 3, 77-100.
- Gariépy, J. F., Watson, K. K., Du, E., Xie, D. L., Erb, J., Amasino, D., & Platt, M. L. (2014). Social learning in humans and other animals. *Frontiers in neuroscience*, 8.
- Haslam, M., & Falótico, T. (2015). Nasal probe and toothpick tool use by a wild female bearded capuchin (*Sapajus libidinosus*). *Primates*, 1-4.
- Heyes, C. & Saggerson, A. (2002). Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour*, 64(6), 851-859.
- Heyes, C. (2012). What's social about social learning?. *Journal of Comparative Psychology*, 126(2), 193.
- Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*, 69(2), 207-231.
- Heyes, C., & Pearce, J. M. (2015). Not-so-social learning strategies. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1802), 20141709.
- Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. *PLoS biology*, 12(9), e1001960.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2013). When given the opportunity, chimpanzees maximize personal gain rather than “level the playing field”. *PeerJ*, 1, e165.
- Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, 73(6), 1021-1032.
- Hoppitt, W., & Laland, K. N. (2011). Detecting social learning using networks: a users guide. *American Journal of Primatology*, 73(8), 834-844.
- Hoppitt, W., & Laland, K. N. (2013). *Social learning: an introduction to mechanisms, methods, and models*. Princeton: Princeton University Press.
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, 263(4), 544-555.

- Hoppitt, W., Kandler, A., Kendal, J. R., & Laland, K. N. (2010). The effect of task structure on diffusion dynamics: Implications for diffusion curve and network-based analyses. *Learning & Behavior*, *38*(3), 243-251.
- Hoppitt, W., Samson, J., Laland, K. N., & Thornton, A. (2012). Identification of learning mechanisms in a wild meerkat population. *PLoS One*, *7*(8), e42044.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PLoS One*, *5*(5), e10625.
- Huffman, M. A. (1984). Stone-play of *Macaca fuscata* in Arashiyama B troop: transmission of a non-adaptive behavior. *Journal of Human Evolution*, *13*(8), 725-735.
- Huffman, M. A. (1996). Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In: C. M. Heyes, B. J. Galef Jr (Eds.). *Social learning in animals: the roots of culture* (pp. 267-286). San Diego, CA: Academic Press.
- Huffman, M. A., & Hirata, S. (2003). Biological and ecological foundations of primate behavioral tradition. *The biology of traditions: Models and evidence*. In: D. M. Fragaszy, & S. Perry (Eds.), *The biology of traditions: models and evidence* (pp. 267-296). Cambridge: University Press.
- Huffman, M. A., & Quiatt, D. (1986). Stone handling by Japanese macaques (*Macaca fuscata*): implications for tool use of stone. *Primates*, *27*(4), 413-423.
- Huffman, M. A., Spiezio, C., Sgaravatti, A., & Leca, J. B. (2010). Leaf swallowing behavior in chimpanzees (*Pan troglodytes*): biased learning and the emergence of group level cultural differences. *Animal cognition*, *13*(6), 871-880.
- Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159.
- Itani, J., & Nishimura, A. (1973). The study of infrahuman culture in Japan. *Precultural primate behavior*. Karger, Basel, 26-50.
- Izar, P., Ferreira, R. G., & Sato, T. (2006). Describing the organization of dominance relationships by dominance-directed tree method. *American Journal of Primatology*, *68*(2), 189-207.
- Izar, P., Verderane, M. P., Peternelli-dos-Santos, L., Mendonça-Furtado, O., Presotto, A., Tokuda, M., ... & Fragaszy, D. (2012). Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. *American Journal of Primatology*, *74*(4), 315-331.
- Jacobs, A., & Petit, O. (2011). Social network modeling: a powerful tool for the study of group scale phenomena in primates. *American journal of primatology*, *73*(8), 741-747.
- Kanakogi, Y., & Itakura, S. (2010). The link between perception and action in early infancy: From the viewpoint of the direct-matching hypothesis. *Japanese Psychological Research*, *52*(2), 121-131.

- Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, 50(4), 343-356.
- Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L., & Rasamimanana, H. (2010b). Evidence for social learning in wild lemurs (*Lemur catta*). *Learning & Behavior*, 38(3), 220-234.
- Kendal, R. L., Galef, B. G., & Van Schaik, C. P. (2010a). Social learning research outside the laboratory: How and why?. *Learning & Behavior*, 38(3), 187-194.
- Kendal, R. L., Kendal, J. R., Hoppitt, W., & Laland, K. N. (2009). Identifying social learning in animal populations: a new 'option-bias' method. *Plos One*, 4(8), e6541.
- Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65-72.
- Koops, M. A., & Giraldeau, L. A. (1996). Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. *Animal Behaviour*, 51(4), 773-783.
- Krause, J., Lusseau, D., & James, R. (2009). Animal social networks: an introduction. *Behavioral Ecology and Sociobiology*, 63(7), 967-973.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, 32(1), 4-14.
- Laland, K. N., & Galef, B. G. (Eds.). (2009). *The question of animal culture*. Harvard: Harvard University Press.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542-547.
- Laland, K. N., & Kendal, J. R. (2003). What the models say about social learning. *The biology of traditions: Models and evidence* (pp. 33-55). Cambridge: Cambridge University Press.
- Laland, K. N., Kendal, J. R., & Kendal, R. L. (2009). Animal culture: problems and solutions. In: K. N. Laland & B. G. Galef. *The question of animal culture* (pp. 174-197). Harvard: Harvard University Press.
- Laland, K. N., Odling-Smee, J. & Feldman, M. W. (2000) Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, 23, 131–175.
- Lefebvre, L. (1995). Culturally-transmitted feeding behaviour in primates: evidence for accelerating learning rates. *Primates*, 36(2), 227-239.
- Leonardi, R., Buchanan-Smith, H. M., Dufour, V., MacDonald, C., & Whiten, A. (2010). Living together: behavior and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, 72(1), 33-47.
- Lonsdorf, E. V., & Bonnie, K. E. (2010). Opportunities and constraints when studying social learning: Developmental approaches and social factors. *Learning & Behavior*, 38(3), 195-205.

- Luncz, L. V., Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology*, 22(10), 922-926.
- Lynch Alfaro, J. W., Boubli, J. P., Olson, L. E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G. A., ... & Alfaro, M. E. (2012). Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *Journal of Biogeography*, 39(2), 272-288.
- Mannu, M., & Ottoni, E. B. (2009). The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. *American Journal of Primatology*, 71(3), 242-251.
- Matthews, L. J. (2009). Intragroup behavioral variation in white-fronted capuchin monkeys (*Cebus albifrons*): mixed evidence for social learning inferred from new and established analytical methods. *Behaviour*, 146(3), 295-324.
- McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. G. (2001). Intergroup Differences in a Social Custom of Wild Chimpanzees: The Grooming Hand-Clasp of the Mahale Mountains¹. *Current Anthropology*, 42(1), 148-153.
- Mendes, F. D. C., Cardoso, R. M., Ottoni, E. B., Izar, P., Villar, D. N. A., & Marquezan, R. F. (2015). Diversity of nutcracking tool sites used by *Sapajus libidinosus* in Brazilian Cerrado. *American journal of primatology*, 77(5), 535-546.
- Mesoudi, A., & Whiten, A. (2004). The hierarchical transformation of event knowledge in human cultural transmission. *Journal of cognition and culture*, 4(1), 1-24.
- Mesoudi, A., & Whiten, A. (2008). The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), 3489-3501.
- Mesoudi, A., Whiten, A., & Laland, K. N. (2006). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences*, 29(04), 329-347.
- Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (1996). Niche construction. *American Naturalist*, 641-648.
- Ottoni, E. B. (2015). Tool use traditions in nonhuman primates: the case of tufted capuchin monkeys. *Human Ethology Bulletin*, 30(1), 22-40.
- Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews*, 17(4), 171-178.
- Ottoni, E. B., & Mannu, M. (2001). Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology*, 22(3), 347-358.
- Ottoni, E. B., de Resende, B. D., & Izar, P. (2005). Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal cognition*, 8(4), 215-219.

- Pasquaretta, C., Levé, M., Claidière, N., Van De Waal, E., Whiten, A., MacIntosh, A. J., ... & Sueur, C. (2014). Social networks in primates: smart and tolerant species have more efficient networks. *Scientific reports*, 4.
- Perry, S. (2009). Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal cognition*, 12(5), 705-716.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., ... & Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, 44(2), 241-268.
- Reader, S. M., & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning & Behavior*, 38(3), 265-283.
- Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in cognitive sciences*, 15(2), 68-76.
- Resende, B. D. (2004). Ontogenia de comportamentos manipulativos em um grupo de macacos-prego (*Cebus apella*) em situação de semi-liberdade. (Tese de doutorado). Instituto de Psicologia, Universidade de São Paulo, São Paulo.
- Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception–action perspective. *Developmental science*, 11(6), 828-840.
- Richerson, P. J., & Boyd, R. (2005). *Not by genes alone*. Chicago: the University of Chicago Press.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review Neuroscience*, 27, 169-192.
- Schnoell, A. V., & Fichtel, C. (2012). Wild redfronted lemurs (*Eulemur rufifrons*) use social information to learn new foraging techniques. *Animal cognition*, 15(4), 505-516.
- Shettleworth S.J. (2010). *Cognition, Evolution and Behavior*. New York: Oxford University Press.
- Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63(7), 975-988.
- Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution*, 61(1), 97-107
- Strier, K. B. (1990). New World primates, new frontiers: Insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). *International Journal of Primatology*, 11(1), 7-19.

- Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal behaviour*, 82(4), 845-852.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford: Oxford University Press.
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340(6131), 483-485.
- van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, rspb20092260.
- van Leeuwen, E. J., & Haun, D. B. (2013). Conformity in nonhuman primates: fad or fact?. *Evolution and Human Behavior*, 34(1), 1-7.
- van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PloS one*, 8(11), e80945.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., ... & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299(5603), 102-105.
- Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60(2), 195-202.
- Voelkl, B., & Noe, R. (2008). The influence of social structure on the propagation of social information in artificial primate groups: a graph-based simulation approach. *Journal of Theoretical Biology*, 252(1), 77-86.
- Vries, H. D. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, 55(4), 827-843.
- Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, 393(6684), 440-442.
- Webster, M. M., Atton, N., Hoppitt, W. J., & Laland, K. N. (2013). Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *The American Naturalist*, 181(2), 235-244.
- Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, 63(5), 765-778.
- Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, 21, 239-285.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685.
- Whiten, A., Horner, V., & De Waal, F. B. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437(7059), 737-740.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In: C. Heyes & B. G. Galef, Jr *Social learning in animals: The roots of culture* (pp. 221-243). San Diego, CA: Academic press.

APPENDIX A – Dominance Hierarchy and Ranking

For both groups the same protocol was carried out. Only agonistic interactions in which (i) both individuals were identified and (ii) the reaction of individual B was submissive (moved away, submissive grin or vocalization) as a response to the action (threat, lunge, chase, physical aggression) of individual A, were used for determining dominance hierarchy. This is in accordance with Clutton-Brock et al. (1979) argument that only the win or loss of a fight is relevant in determining dominance hierarchy and not the overall agonistic interactions.

Based on the agonistic interactions as described above we calculated Vries et al (1995)'s index of linearity test (more conducive to our data as it deals with unknown dyadic dominance relationships). Although our data shows low degree of linear hierarchy for both groups, in both cases the test also rejected the null hypothesis of random dyadic dominance (Table A1).

Table A1: Vries (1995): Measure of linearity (h') where 0 is non-linear (each animal dominates half of the others) and 1 is completely linear hierarchy. A modification of Landau's index (1951) as it deals with unknown dyadic dominance relationships.

	Result	Conclusion
Jurubeba	$h'=0.142$	Low degree of linearity
	$p=0.012$ (1000 permutations)	Rejects the null hypothesis of random dyadic dominance
Pedra Furada)	$h'=0.313$	Low degree of linearity
	$p<0.001$ (1000 permutations)	Rejects the null hypothesis of random dyadic dominance

There are several methods for assigning individuals in a dominance hierarchy to a dominance rank; however, these should not be attempted if the hierarchy is too distant to linear or if the test (Vries 1995) does not reject the null hypothesis of random dyadic dominance. In our case the test (Vries et al 1995) did reject the null hypothesis so there is some form of dyadic dominance however it is likely to be of a partial hierarchy.

Considering that in a less linear hierarchy, there is likely to be more discordance between ranking methods (Whitehead, 2008) our next step was to calculate dominance rankings and dominance indices by different methods and verify whether an overall pattern could be identified (Table A2).

Table A2: Dominance ranks and dominance indices for Jurubeba group

	Dominance ranking		Dominance indices		
	'I&SI' (Vries 1998)	Brown (1975)	Proportion of contests won	David's (1987) score	Modified David's score (Vries et al. 2006)
BOL	1	1	1.00	118.67	69.39
LOI	2	2	1.00	86.37	46.16
PAN	3	3	0.89	73.97	41.71
ELV	4	4, 5	0.85	56.40	31.25
QUE	5	6	0.88	12.23	6.72
ROS	6	7, 8	1.00	18.23	8.54
NON	7	29	0.57	16.50	8.27
PEN	8	4, 5	0.71	55.17	33.19
OLI	9	9	0.67	1.87	-0.49
ORE	10	10, 18	0.60	4.00	2.67
TIR	11	8, 9	0.71	11.90	11.39
BAR	12	7, 12	0.31	15.03	-1.97
MAI	13	11, 13	0.77	21.10	13.88
SKI	14	17, 25	1.00	5.10	2.43
CHQ	15	12, 15	0.42	3.33	0.97
TOP	16	13, 20	0.46	-6.30	-3.41
BIA	17	16, 21	0.64	-8.53	-3.25
COD	18	10, 14	0.56	-0.93	2.04
GAL	19	17, 24	0.20	-14.00	-6.51
CHI	20	20, 28	0.33	-7.40	-7.10
GAD	21	14, 24	0.40	-4.53	-2.03
CLA	22	19, 28	0.46	-10.40	-6.28
DES	23	18, 25	0.40	-6.43	-3.38
PER	24	19, 31	0.50	1.10	0.64
MIN	25	16	0.33	3.00	0.33
PUN	26	41	0.00	-1.00	-0.08
CAD	27	11, 15	0.31	-7.50	-8.65
CAR	28	21	0.18	-44.73	-24.43
BOC	29	26, 30	0.58	-0.73	2.68
JAN	30	31	0.60	12.67	6.77
CRI	31	30	0.56	-9.33	-4.40
SAN	32	27	0.33	-16.40	-7.94
PAC	33	29	0.25	-28.63	-16.11
ACA	34	35	0.17	-45.17	-20.96
DUN	35	36, 37	0.35	-36.33	-18.91
MIC	36	36, 37	0.32	-65.17	-33.65
COS	37	27, 42	0.50	-11.23	-5.61
CUR	38	38	0.21	-67.57	-41.09
DAD	39	39	0.00	-27.10	-13.92
PEL	40	40	0.14	-85.37	-53.40

Table A3: Dominance ranks and dominance indices for Pedra Furada group

	Dominance ranking		Dominance indices		
	'I&SI' (Vries 1998)	Brown (1975)	Proportion of contests won	David's (1987) score	Modified David's score (Vries et al. 2006)
Tor	1	1	0.99	219.9	154.7
Rom	2	2, 3	0.76	99.08	59.62
Bei	3	3, 4	0.93	70.88	38.98
Gor	4	3, 4, 5	0.87	112.55	71.45
Zan	5	6, 7	0.63	105.88	53.21
Nic	6	4, 7	0.81	103.47	60.18
Lic	7	8, 9, 11	0.83	43.22	34.97
Rog	8	8, 9	0.67	47.06	21.55
Bnn	9	9, 10, 11	0.77	38.8	31.04
Nif	10	10, 11, 13	0.74	44.29	27.32
Ali	11	12, 14	0.56	7.14	3.77
Bat	12	5, 6	0.56	40.8	21.99
Can	13	14, 18, 21	0.35	-14.52	-14.62
Pad	14	13, 15	0.35	-19.55	-16.77
Des	15	15, 16	0.5	-37.79	-14.79
Vol	16	16, 17, 18	0.31	-41.27	-31.67
Ass	17	17, 18	0.26	-47.03	-38.49
Moc	18	18, 19	0.5	-35.03	-15.75
Cap	19	24, 28, 30	0.17	-7.45	-5.97
Mac	20	20, 21, 27	0.26	-51.25	-32.31
Mal	21	12, 22, 24	0.23	-16.99	-15.63
Juv6	22	25, 26, 32, 33	0.27	-32.63	-16.77
Lim	23	14, 15, 19, 20	0.47	-17.92	-16.56
Mol	24	28, 29, 31, 32	0	-22.37	-6.94
Nar	25	20, 23	0.25	-50.79	-23.85
Juv8	26	25, 26, 30, 31	0.3	-35.47	-13.03
Hal	27	23, 26, 27, 28	0.22	-80.72	-43.89
Enq	28	22, 24, 25, 30	0.19	-93.62	-60.21
Ves	29	29, 31, 32	0.18	-71.26	-49.84
Cln	30	26, 27, 28, 30	0.07	-113.33	-77.49

Gammell et al. (2003) recommends the use of David's score as a more appropriate dominance index and therefore ranking method and Vries et al. (2006) further elaborate on this score to include the amount of data available for each dyad. The I&SI (Vries 1998) is argued to be the best straight ranking technique (Whitehead, 2008).

If we look at age groups and sex classes separately, the null hypothesis of random hierarchy was confirmed between Infants and between Juveniles for both groups and between Adult

females (Jurubeba) but rejected between Adults. Adult males seem to present a more linear hierarchy than females in both groups studied (Table A4).

Table A4: Vries (1995): Measure of linearity (h') where 0 is non-linear (each animal dominates half of the others) and 1 is completely linear hierarchy. A modification of Landau's index (1951) as it deals with unknown dyadic dominance relationships.

	All	Infants	Juveniles	Adults	Adult females	Adult males
Jurubeba	$h'=0.121$ $p=0.016$	$p=0.628$	$p=0.554$	$h'=0.230$ $p=0.002$	$p=0.336$	$h'=0.604$ $p=0.000$
Pedra	$h'=0.313$			$h'=0.518$	$h'=0.564$	$h'=0.779$
Furada)	$p<0.001$	$p=0.816$	$p=0.478$	$p<0.001$	$p=0.026$	$p=0.029$

1000 permutations

To avoid problems with inversions of individuals between ranks, the top quartile (first 10 in JB and first 7 in PF) of individuals according to the 'I&SI' ranking system (Vries 1998) (Tables A2 and A3) were considered to be of high rank. The bottom quartile (last 10 in JB and last 7 in PF) individuals, according to the same ranking system, were considered to be of low rank and all the individuals in between these were considered mid-ranking members of their social group. The decision of the breakdown of individuals into the categories as described above was due to the fact there were fewer inversion of positions in the extremes (high and low ranks) than amongst individuals ranked in the middle. We therefore made the mid-ranking section larger, in terms of number of individuals, as a conservative measure. Table A5 presents the allocation of individuals in each group to these three categories.

Table A5 – Allocation of group members to the categories of high, mid and low-ranking according to the quartile they were placed in by the I&I rank (Vries).

Jurubeba		Pedra Furada	
BOL LOI PAN ELV QUE ROS NON PEN OLI	High- ranking	Tor Rom Bei Gor Zan Nic Lic	High- ranking
ORE TIR BAR MAI SKI CHQ TOP BIA COD GAL CHI GAD CLA DES PER MIN PUN CAD CAR BOC JAN	Mid-ranking	Rog Bnn Nif Ali Bat Can Pad Des Vol Ass Moc Cap Mac Mal Juv6 Lim	Mid-ranking
CRI SAN PAC ACA DUN MIC COS CUR DAD PEL	Low-ranking	Mol Nar Juv8 Hal Enq Ves Cln	Low-ranking

APPENDIX B – Novel objects experiment: measuring neophobia

I presented each group with three novel objects: a fluffy toy, a football and a sink plunger in a randomised order (section 4.2.2), five times throughout the day in five different locations within the area the monkeys were using that day; each trial lasted 5 minutes and there was at least 10 minutes between trials. The experiment was filmed and coded from video; for details of methods see Chapter 2.

All 30 individuals of the PF group and 37 of the 40 individuals of JB came within 10 meters of at least one novel object and looked in its direction. For PF 27 individuals (90% of the group) came within five meters of the novel objects, 14 monkeys (46.7%) touched the objects and the mean latency to touch the novel objects for the first time was 711 seconds (S.D \pm 511 seconds). For JB 25 monkeys (62.5%) came within five meters of the novel objects, of which 9 (22.5%) touched the objects and the mean latency to touch the objects for the first time was of 867seconds (S.D \pm 568 seconds). The difference in latency between groups approached statistical significance (Mann-Whitney: $p=0.067$)

PF group's home range covers some of the most visited locations of the Serra da Capivara National Park (SCNP) and therefore they have frequent contact with tourists. I would expect them to be less neophobic towards novel objects than monkeys in JB group which only has very infrequent encounters with non-researchers. Furthermore, PF group has been now subject to two experimental studies, the present one, and a molasses dipping task by Cardoso (unpublished) the previous year to this study, whereas this is the first experimental study conducted with JB. Our results seem to portray this as proportionally fewer monkeys came within 5 meters of the novel objects and interacted with them at JB than at PF; also the latency to touch the novel objects was lower (but not significantly so) for PF than for JB. As a group it seems JB are more neophobic towards novel objects than PF.

Typically, experiments to evaluate neophobia are conducted in isolated individuals so as to eliminate the influence that seeing a conspecific interact with the novel object might have in facilitating another individual's interaction with the same object. However, I argue that in a natural context individuals would have an opportunity to see conspecifics interacting with novel elements in their environment. Thus for the context of use (open diffusion) the group-level measure of neophobia was considered appropriate.

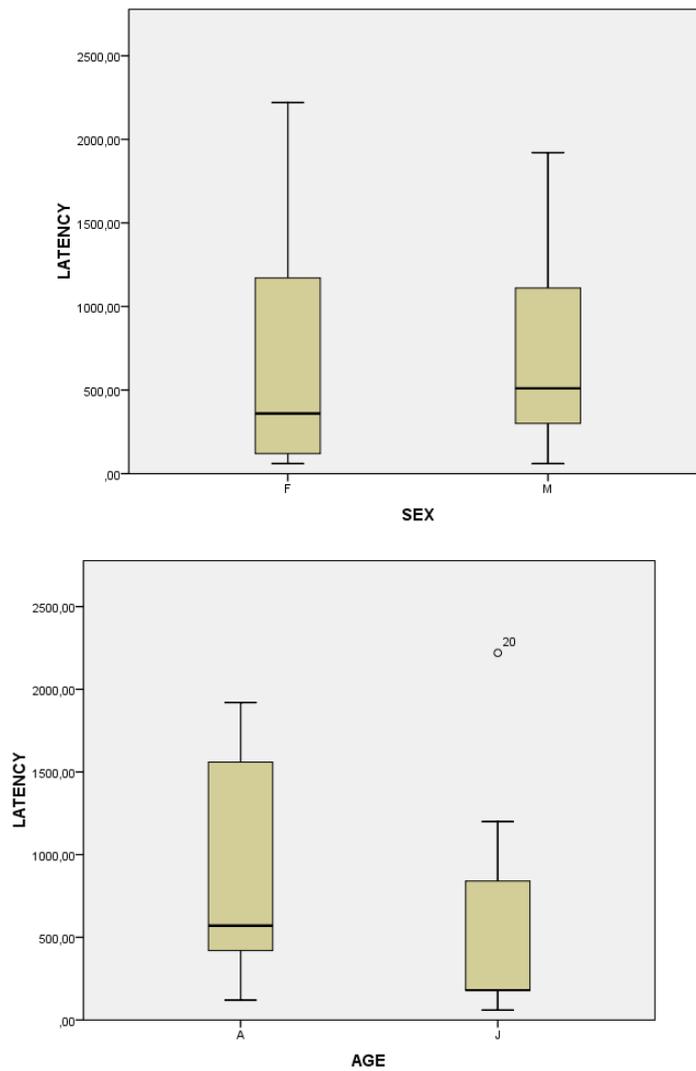


Figure B1

I calculated two indexes of neophobia that were factored into the OADA in Chapter 4. As most monkeys in the group didn't even approach (i.e. come within 5 meters of the novel object) my first measure of neophobia (neophobia1) gave a score of -1 to individuals who never came within five meters of the novel objects, score 0 to monkeys that came within five meters but didn't touch any of the objects and +1 to individuals that touched at least one of the novel objects. The second measure of neophobia (neophobia2) was conducted only for individuals who came within 5 meters of the novel objects. For these subjects I calculated the mean latency of touching novel objects in each group and the comparison of individual latency to mean group latency. Table B1 presents the individual-level variables of neophobia attributed to each individual.

Table B1 – Neophobia measures

JURUBEBA			PEDRA FURADA		
	novObj1	novObj2		novObj1	novObj2
BOL	0	866	Tor	-1	1136
LOI	1	866	Rom	-1	-546
PAN	1	866	Bei	-1	896
ELV	0	866	Gor	-1	116
QUE	0	866	Zan	0	664
ROS	1	866	Nic	-1	-244
NON	1	866	Lic	0	664
PEN	0	866	Rog	-1	-64
OLI	1	866	Bnn	0	664
ORE	0	866	Nif	-1	-544
TIR	-1	-326	Ali	-1	-304
BAR	-1	153	Bat	0	664
MAI	1	866	Can	1	664
SKI	-1	-686	Pad	0	664
CHQ	0	866	Des	-1	-184
TOP	0	866	Vol	-1	-484
BIA	1	866	Ass	1	664
COD	-1	-446	Moc	0	664
GAL	0	866	Cap	-1	536
CHI	0	866	Mac	-1	896
GAD	0	866	Mal	0	664
CLA	1	866	Juv6	0	664
DES	0	866	Lim	-1	664
PER	1	866	Mol	0	664
MIN	1	866	Nar	-1	664
PUN	1	866	Juv8	0	664
CAD	-1	-386	Hal	0	664
CAR	-1	-686	Enq	0	664
BOC	-1	-26	Ves	0	664
JAN	1	866	Cln	1	664
CRI	0	866			
SAN	0	866			
PAC	0	866			
ACA	0	866			
DUN	0	866			
MIC	1	866			
COS	1	866			
CUR	1	866			
DAD	-1	1353			
PEL	-1	1053			

APPENDIX C – Supplementary material for NBDA

Table C1 Order and time (minutes) of acquisition of the trait (solve the task) used in the diffusion analysis, for the Jurubeba group. Time of acquisition is the time elapsed from the beginning of the task's introduction until the moment each individual solved the task for the first time.

	Order	Time (min)
CHI	1	67
SKI	2	84
MIN	3	95
PEL	4	98
QUE	5	106
CHQ	6	136
CAD	7	153
COD	8	154
TOP	9	182
PAN	10	202
LOI	11	207
TIR	12	246
BOL	13	247
PEN	14	248
ELV	15	260
BAR	16	271
BOC	17	319
COS	18	399
BIA	19	410
CAR	20	470
MIC	21	615
CUR	22	628
ORE	23	811

Table C2 – Order and time (minutes) of acquisition of the trait (solve the task) used in the diffusion analysis, for the Pedra Furada group. Time of acquisition is the time elapsed from the beginning of the experiment application until the moment each individual solved the task for the first time.

	Order	Time (min)
Lim	1	138
Cap	2	157
Des	3	165
Nic	4	225
Rog	5	243
Zan	6	409
Rom	7	417
Tor	8	423
Mol	9	849
Cln	10	1019
Pad	11	1196

Table C3 – Individual-level variables used to inform the asocial learning model. For I&SI rank and social ranking refer to Appendix A, for neophobia towards novel objects (novObj1 and novObj2) refer to Appendix B. Approach task is the frequency individuals were seen within 10 meters radius of the task without a conspecific model at the apparatus.

JURUBEBA						PEDRA FURADA					
	I&SI dominance rank	social ranking	novObj 1	novObj2	frequency approach task		I&SI dominance rank	social ranking	novObj 1	novObj2	frequency approach task
BOL	1	high	0	866	45	Tor	1	high	-1	1136	11
LOI	2	high	1	866	66	Ro m	2	high	-1	-546	26
PAN	3	high	1	866	42	Bei	3	high	-1	896	22
ELV	4	high	0	866	4	Gor	4	high	-1	116	31
QUE	5	high	0	866	45	Zan	5	high	0	664	28
ROS	6	high	1	866	10	Nic	6	high	-1	-244	16
NON	7	high	1	866	26	Lic	7	high	0	664	39
PEN	8	high	0	866	32	Rog	8	mid	-1	-64	26
OLI	9	high	1	866	40	Bnn	9	mid	0	664	18
ORE	10	high	0	866	28	Nif	10	mid	-1	-544	36
TIR	11	mid	-1	-326	43	Ali	11	mid	-1	-304	22
BAR	12	mid	-1	153	38	Bat	12	mid	0	664	28
MAI	13	mid	1	866	39	Can	13	mid	1	664	18
SKI	14	mid	-1	-686	38	Pad	14	mid	0	664	38
CHQ	15	mid	0	866	6	Des	15	mid	-1	-184	34
TOP	16	mid	0	866	40	Vol	16	mid	-1	-484	46
BIA	17	mid	1	866	38	Ass	17	mid	1	664	66
COD	18	mid	-1	-446	65	Moc	18	mid	0	664	1
GAL	19	mid	0	866	41	Cap	19	mid	-1	536	17
CHI	20	mid	0	866	73	Mac	20	mid	-1	896	12
GAD	21	mid	0	866	2	Mal	21	mid	0	664	20
CLA	22	mid	1	866	50	Juv6	22	mid	0	664	0
DES	23	mid	0	866	42	Lim	23	mid	-1	664	44
PER	24	mid	1	866	25	Mol	24	low	0	664	4
MIN	25	mid	1	866	25	Nar	25	low	-1	664	24
PUN	26	mid	1	866	51	Juv8	26	low	0	664	13
CAD	27	mid	-1	-386	19	Hal	27	low	0	664	19
CAR	28	mid	-1	-686	12	Enq	28	low	0	664	27
BOC	29	mid	-1	-26	27	Ves	29	low	0	664	6
JAN	30	mid	1	866	52	Cln	30	low	1	664	17
CRI	31	low	0	866	83						
SAN	32	low	0	866	24						
PAC	33	low	0	866	63						
ACA	34	low	0	866	20						
DUN	35	low	0	866	45						
MIC	36	low	1	866	0						
COS	37	low	1	866	11						
CUR	38	low	1	866	13						
DAD	39	low	-1	1353	65						
PEL	40	low	-1	1053	23						

Results for OADA

Based on the *order of acquisition*, the social (and asocial) learning model was a better fit for the diffusion data than the purely asocial model in both groups, irrespective of the observation distance networks used to inform the social learning models. This was true for all the diffusions investigated: solving the lift-pull task irrespective of the option used, solving task using lift and solving task using pull. The sole exception was for the diffusion of solving task using *pull* with observation within 1 meter in JB, although the difference was in the correct direction.

Table C4 – Results for the OADA based on Observation networks. * indicates a difference of at least two AIC values between both models conveying strong support of the model with the lowest AIC value.

Diffusion	Network	Model	JURUBEBA	PEDRA FURADA
			AIC	AIC
Lift-pull task irrespective of option used	Observation within 1 meter	social and asocial learning	102.52*	62.29*
		asocial learning	153.63	70.63
	Observation within 5 meters	social and asocial learning	108.57*	62.46*
		asocial learning	153.63	70.63
Observation within 10 meters	social and asocial learning	111.70*	61.09*	
	asocial learning	153.63	70.63	
Observation between 5 and 10 meters	social and asocial learning	115.95*	59.97*	
	asocial learning	153.63	70.63	
Lift-pull task using lift	Observation within 1 meter	social and asocial learning	102.39*	49.64*
		asocial learning	153.63	64.64
	Observation within 5 meters	social and asocial learning	111.42*	44.28*
		asocial learning	153.63	64.64
Observation within 10 meters	social and asocial learning	111.00*	45.37*	
	asocial learning	153.63	64.64	
Observation between 5 and 10 meters	social and asocial learning	113.72*	46.74*	
	asocial learning	153.63	64.64	
Lift-pull task using pull	Observation within 1 meter	social and asocial learning	42.83	35.20*
		asocial learning	43.48	39.74
	Observation within 5 meters	social and asocial learning	37.99*	35.11*
		asocial learning	43.48	39.74
Observation within 10 meters	social and asocial learning	36.24*	35.21*	
	asocial learning	43.48	39.74	
Observation between 5 and 10 meters	social and asocial learning	36.75*	33.84*	
	asocial learning	43.48	39.74	

APPENDIX D - Supplementary material Tube task experiment

Methods

For methodology, see section 2.3.2 Tube task (chapter 2 – Methods) and section 4.3.2 Experimental set-up (chapter 4 – Identifying social learning in the wild).

Results

In JB, tail-dipping was used to solve the tube task by monkeys of all sex-age classes; sticks as probe tools were used less frequently but also by members of all sex-age classes; stones were rarely used to solve the task and this was a strategy of males only, both juveniles and adults (Figure 3.11A). No significant difference was found in the frequency with which each sex-age group solved the task for any of the three techniques analysed (KW for *tail-dipping*: $\chi^2=6.309$ $df=3$ $p=0.098$; *stick probe*: $\chi^2=0.815$ $df=3$ $p=0.846$ and *stone hammer*: $\chi^2=1.872$ $df=3$ $p=0.599$).

In PF, tail-dipping was used to solve the tube task by adults only; sticks as probe tools was used by both adults and juveniles, but not by adult females; stones were rarely used to solve the task (Figure 3.11B). No significant difference was found in the frequency with which each sex-age group solved the task for the three techniques analysed (KW for *tail-dipping*: $\chi^2=3.716$, $df=3$, $p=0.294$; *Stick probe*: $\chi^2=4.009$, $df=3$, $p=0.261$ and *Stone hammer*: $\chi^2=1.00$ $df=3$, $p=0.801$).

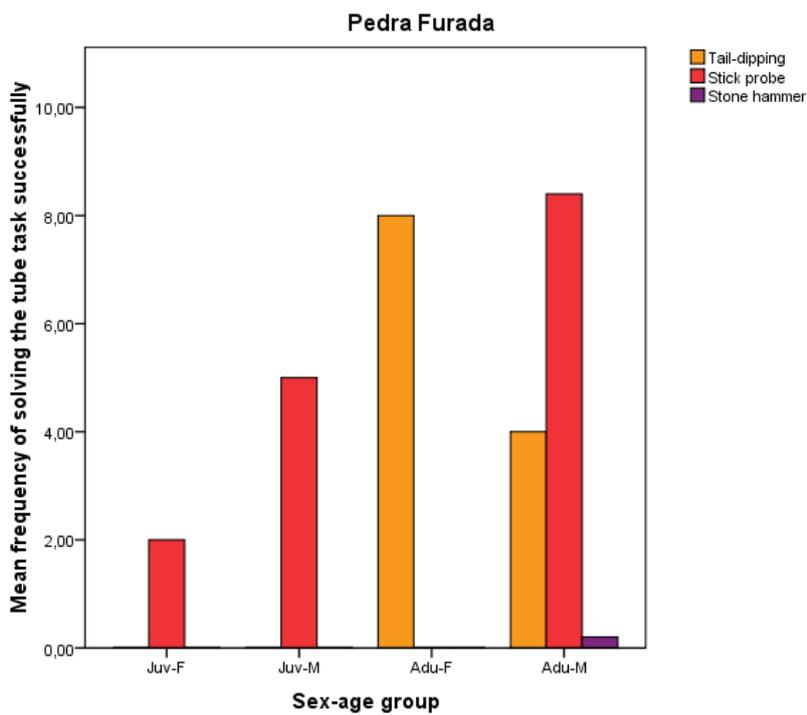
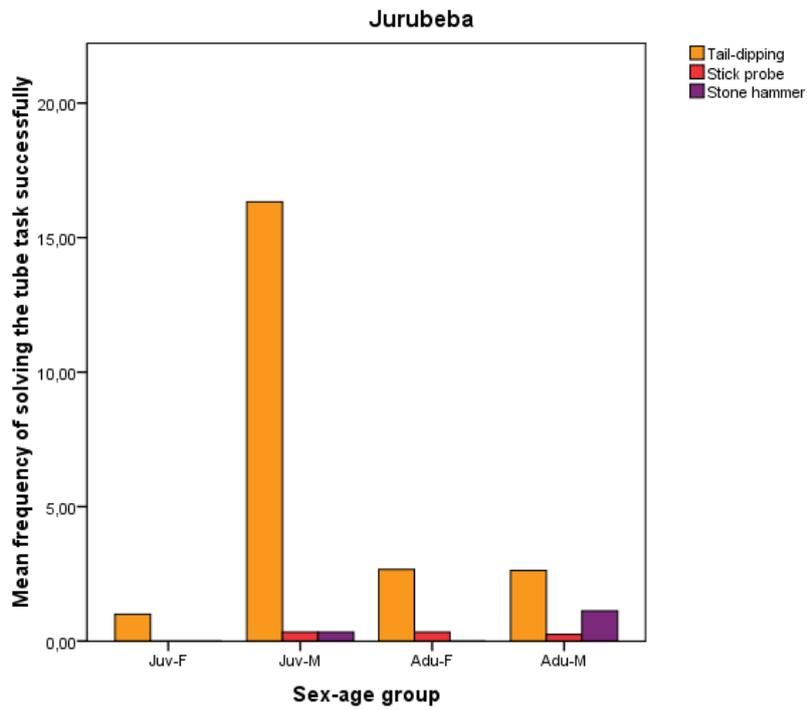
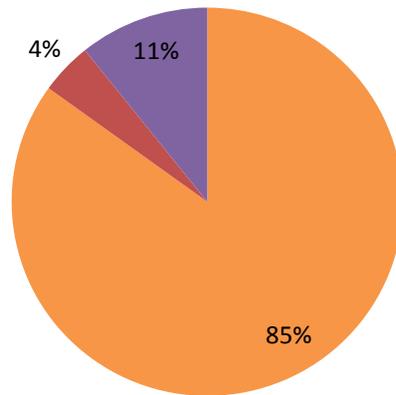
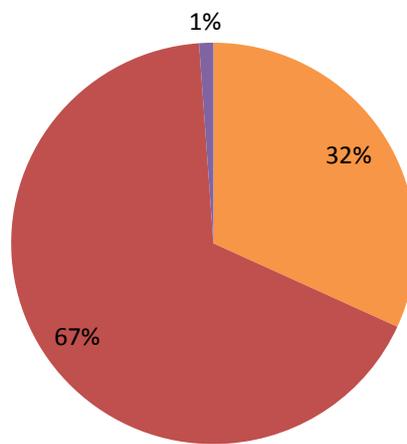


Figure D1 Mean frequency of solving the tube task successfully for each sex-age group by technique used: tail-dipping, stick probe and stone hammer for groups (A) Jurubeba and (B) Pedra Furada.

TAIL-DIPPING STICK PROBE STONE HAMMER



A



B

Figure D2 Proportion of tail-dipping, stick probe and stone hammer solutions to the tube task for groups (A) Jurubeba and (B) Pedra Furada.

APPENDIX E – GLM analysis chapter 5

Table E1 - Data input for GLM analysis for identifying for transmission bias (chapter 5).

	ID	Sex	Age	Option used predominantly	Dominance rank	Success ratio	Observation network	
							In-degree	Out-degree
<i>Jurubeba</i>	PAN	M	Adu	Lift	High	0,926	2,571	1,333
	PEN	M	Adu	Lift	High	0,922	1,889	1,571
	BOL	M	Adu	Lift	High	0,878	2,238	1,286
	QUE	M	Juv	Lift	High	0,865	0,492	2,700
	LOI	M	Adu	Lift	High	0,832	2,111	2,000
	ELV	M	Adu	Lift	High	0,751	2,460	1,750
	NON	F	Adu	Lift	High	0,000	0,000	0,000
	OLI	F	Juv	Lift	High	0,000	0,000	0,000
	ROS	F	Juv	Lift	High	0,000	0,000	0,000
	CHQ	M	Adu	Lift	Mid	0,918	1,349	3,500
	CAD	M	Adu	Pull	Mid	0,904	3,603	1,500
	TIR	M	Adu	Lift	Mid	0,884	1,000	0,000
	BOC	M	Juv	Lift	Mid	0,870	0,889	3,115
	MIN	M	Juv	Lift	Mid	0,856	0,429	3,167
	COD	M	Adu	Lift	Mid	0,850	3,349	1,640
	TOP	F	Adu	Lift	Mid	0,835	0,159	1,947
	BAR	M	Adu	Lift	Mid	0,829	0,905	2,750
	CHI	F	Adu	Lift	Mid	0,810	0,238	1,500
	SKI	M	Juv	Lift	Mid	0,794	0,159	1,444
	BIA	F	Adu	Lift	Mid	0,686	0,000	4,400
	CAR	M	Juv	Lift	Mid	0,667	0,000	3,115
	ORE	M	Juv	Lift	Mid	0,400	0,000	2,500
	CLA	F	Adu	Lift	Mid	0,000	0,000	4,115
	DES	F	Adu	Lift	Mid	0,000	0,000	1,158
	GAD	F	Adu	Lift	Mid	0,000	0,000	1,500
	GAL	F	Juv	Lift	Mid	0,000	0,000	2,242
	JAN	F	Adu	Lift	Mid	0,000	0,000	1,000
	MAI	F	Adu	Lift	Mid	0,000	0,000	3,095
	PER	F	Adu	Lift	Mid	0,000	0,000	3,698
	PUN	M	Juv	Lift	Mid	0,000	0,000	1,000
	COS	F	Juv	Lift	Low	1,000	0,016	1,000
	PEL	M	Adu	Lift	Low	0,814	0,587	2,800
	CUR	M	Adu	Lift	Low	0,810	0,111	1,438
	MIC	M	Adu	Lift	Low	0,784	1,286	4,282
	ACA	F	Adu	Lift	Low	0,000	0,000	0,000
	CRI	F	Adu	Lift	Low	0,000	0,000	2,091
	DAD	F	Juv	Lift	Low	0,000	0,000	2,875
	DUN	M	Adu	Lift	Low	0,000	0,000	0,001
	PAC	F	Adu	Lift	Low	0,000	0,000	1,200

	SAN	F	Adu	Lift	Low	0,000	0,000	2,333
<i>Pedra Furada</i>	Zan	M	Adu	Lift	High	0,921	0,864	0,105
	Tor	M	Adu	Lift	High	0,894	4,109	0,040
	Nic	M	Adu	Lift	High	0,800	0,672	0,358
	Rom	F	Adu	Lift	High	0,759	0,232	0,203
	Bei	M	Adu	Lift	High	0,000	0,000	0,161
	Gor	F	Adu	Lift	High	0,000	0,000	0,105
	Lic	F	Adu	Lift	High	0,000	0,000	0,000
	Lim	M	Juv	Lift	Mid	0,863	0,494	0,000
	Rog	M	Adu	Lift	Mid	0,761	0,255	0,004
	Pad	M	Juv	Lift	Mid	0,691	0,071	0,498
	Des	M	Juv	Lift	Mid	0,585	0,046	0,877
	Cap	M	Juv	Pull	Mid	0,214	0,006	1,010
	Ali	F	Adu	Lift	Mid	0,000	0,000	0,105
	Ass	M	Adu	Lift	Mid	0,000	0,000	1,128
	Bat	F	Juv	Lift	Mid	0,000	0,000	0,090
	Bnn	F	Adu	Lift	Mid	0,000	0,000	0,073
	Can	F	Adu	Lift	Mid	0,000	0,000	0,192
	Mal	M	Juv	Lift	Mid	0,000	0,000	0,199
	Juv6	F	Juv	Lift	Mid	0,000	0,000	0,000
	Mac	F	Adu	Lift	Mid	0,000	0,000	0,094
	Moc	F	Adu	Lift	Mid	0,000	0,000	0,054
	Nif	F	Adu	Lift	Mid	0,000	0,000	0,000
	Vol	M	Juv	Lift	Mid	0,000	0,000	0,695
	Cln	M	Adu	Lift	Low	0,583	0,000	0,228
	Mol	M	Juv	Lift	Low	0,036	0,000	0,025
	Enq	F	Adu	Lift	Low	0,000	0,000	0,015
	Hal	F	Juv	Lift	Low	0,000	0,000	0,000
	Nar	F	Juv	Lift	Low	0,000	0,000	0,167
	Juv8	F	Juv	Lift	Low	0,000	0,000	0,322
	Ves	F	Adu	Lift	Low	0,000	0,000	0,002