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

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.

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

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 **i**n 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:_____

Prof. Dr._____

Instituição:_____

Assinatura:_____

Prof. Dr._____

Instituição:_____

Assinatura:_____

Prof. Dr._____

Instituição:_____

Assinatura:_____

Prof. Dr._____

Instituição:_____

Assinatura:_____

ACKNOWLEDGEMENTS

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 leaning 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, permite-nos 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

LIST OF TABLES

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 enhancement[1] (Campbell et al, 1999), emulation, and various kinds of imitation[2] (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

---

[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"

[2] The 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).

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 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 Fragaszy 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.

14

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, adult 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 Fragaszy et al, 2004) and more revent branchin 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 & Fragaszy (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 Fragaszy (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).

SPACE

-visiting and interacting with same elements, same location

-does not involve physical proximity

SPACE AND TIME

-individuals present together, same place same time

-involves physical proximity

TIME

-synchronized with the activities of others but in different locations

-does not involve physical proximity
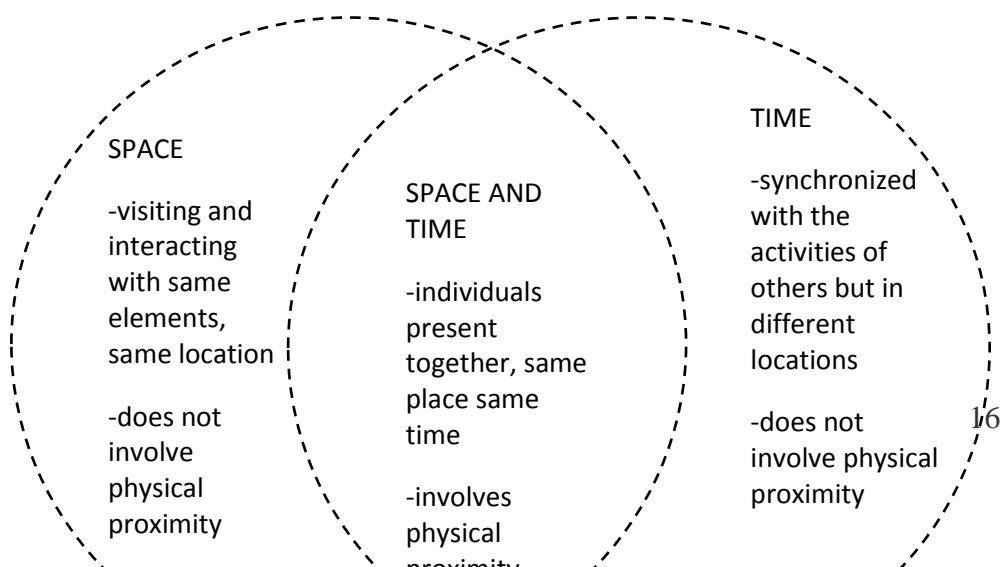
Figure 1.1 Three dimensions of behavioural coordination, in space, in time and in space-time, according to Coussi-Korbel & Fragasy (1995)

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 & Fragaszy (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 identify 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 & Fragaszy, 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 Fragaszy (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). Capuchins 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 (Falotico, 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.

CONCLUSION

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). Capuchins 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 & Fragaszy 1995, Fragaszy 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 leaning 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., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal behaviour*, *50*(6), 1441-1453.

Crast, J., Hardy, J. M., & Fragaszy, 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. Fragaszy, & 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.