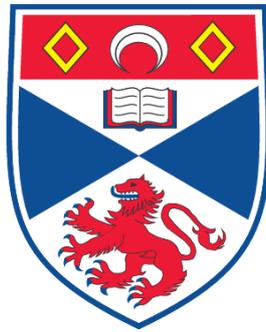


**SOCIAL LEARNING AND BEHAVIOUR TRANSMISSION IN  
BROWN CAPUCHIN MONKEYS (*CEBUS APELLA*)**

**Marietta Dindo**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



**2009**

**Full metadata for this item is available in the St Andrews  
Digital Research Repository**

**at:**

**<https://research-repository.st-andrews.ac.uk/>**

**Please use this identifier to cite or link to this item:**

**<http://hdl.handle.net/10023/740>**

**This item is protected by original copyright**

**SOCIAL LEARNING AND  
BEHAVIOUR TRANSMISSION IN  
BROWN CAPUCHIN MONKEYS (*Cebus apella*)**

**Marietta Dindo**

Thesis submitted for the degree of Doctor of Philosophy  
School of Psychology  
University of St Andrews  
March 2009



## **Abstract**

The research aims of this thesis are to experimentally investigate how behaviours spread socially, and what factors contribute to the development of group-wide social traditions in capuchins (*Cebus apella*). Given the apparent convergent evolution between such monkeys and great apes, capuchin traditions are of great interest anthropologically and for a biological and psychological understanding of culture. Several studies have investigated social learning in capuchins, but few have made headway into understanding how it supports the development of traditions either in the wild or in captivity. By experimentally introducing novel foraging behaviours into several captive groups, the studies included in this thesis simulate the development of foraging behaviours so that their spread can be studied from various viewpoints. Five experiments are presented investigating: (1) the chained transmission of foraging behaviours, (2) the role of social facilitation on the rate of individual learning, (3) the fidelity of learning from localised stimulus enhancement & object-movement re-enactment, (4) the quality of individual relationships in the social transmission of novel foraging techniques, and (5) the open diffusion of group-specific foraging behaviours in capuchin monkeys. Together, these experiments explore how traditions may develop, ranging from individual learning to how behaviour patterns may spread socially based on social ties within the group.

## **Acknowledgements**

I owe a great deal of thanks to many people for making this thesis possible. First, I would like to thank Kristin Bonnie for her countless manuscript revisions and moral support. Her insight and patience is invaluable to me. A report on social learning in primates would not be possible without acknowledging how much I have learned from her.

I thank Bernard Thierry and Odile Petit for welcoming me into their research team in Strasbourg. My work there would not have been possible without Valerie Dufour's assistance and support, as well as her friendship and good advice. Thanks also goes to Marie Pele, Cedric Sueur, and Pierre Uhlrich.

I am especially grateful to Frans de Waal for years of mentoring that made it possible for me to pursue a PhD and for allowing me to conduct research at the Capuchin Lab. My words fall short of my gratitude. I would like to thank Kristi Leimgruber specifically for the time she spent assisting me with the observer preference study, but also for her enthusiasm for my work in general. Being in such a supportive work environment made the process of completing my studies so enjoyable. I would also like to thank Dan Brubaker, Jen Pokorny, Colleen Gault, Malini Suchak, and Teresa Romero for various assistance at Capuchin Lab. And lastly, I thank Vicky Horner for introducing me to the fascinating study of social learning in primates, "Scottish culture", and for encouraging me to pursue a PhD at St Andrews.

At St Andrews, a huge thanks goes to Andy Burnley for making all the foraging boxes in my experiments. Without his skillful work my projects would not have been possible. I thank Stephanie Braccini, Lydia Hopper, Emma Flynn, Erica Cartmill, Lynn Watson, and Jamie Lawson for thoughtful discussions. Thank you to Simon Townsend for being an great friend and colleague to look up to. Most

importantly, I am thankful for the support of my supervisor, Andrew Whiten for our many discussions and his continual enthusiasm for my research endeavours.

I never thought one of the hardest parts of writing my thesis would be the acknowledgements section, as it seems impossible to find the right words to finish these thanks. I thank Sarah Pearse for being an exceptionally great friend, for always being just a phone call away, and for keeping the red sofa empty for me. I thank Andrew Sinclair for being my constant. And finally I thank my extremely supportive family for always believing that their 'little monkey' would someday be a 'monkey doctor'.

# Contents

<b>DECLARATION</b> .....	<b>II</b>
<b>ABSTRACT</b> .....	<b>III</b>
<b>ACKNOWLEDGEMENTS</b> .....	<b>IV</b>
<b>CONTENTS</b> .....	<b>VI</b>
<b>LIST OF FIGURES AND TABLES</b> .....	<b>X</b>
<b>CHAPTER 1: INTRODUCTION</b> .....	<b>2</b>
<b>The Study of Social Learning in Animals: A brief history</b> .....	<b>3</b>
<b>Forms of Social Learning</b> .....	<b>5</b>
Enhancement.....	7
Stimulus and Local Enhancement.....	7
Social Facilitation (Social Enhancement) .....	8
Copying .....	9
Emulation and Object Movement Re-enactment .....	9
Imitation.....	10
<b>The question of animal culture</b> .....	<b>11</b>
Captive Studies on Social Learning and Culture .....	20
Two-action task studies.....	21
Diffusion studies .....	22
Social Learning and Behaviour Transmission in Capuchins .....	26
<b>Thesis Aims and Scope</b> .....	<b>30</b>
<b>CHAPTER 2: SOCIAL DIFFUSION OF NOVEL FORAGING METHODS IN CAPUCHIN MONKEYS</b> .....	<b>34</b>
<b>INTRODUCTION</b> .....	<b>34</b>
<b>METHODS</b> .....	<b>38</b>
Subjects & Housing .....	38
Apparatus.....	40
Procedure .....	41
Controls.....	41
Model training.....	42
Demonstration tests and observer tests .....	43
Data collection and analysis.....	44
<b>RESULTS</b> .....	<b>46</b>
Controls .....	46
Observers.....	47

DISCUSSION.....	49
<b>CHAPTER 3: CONDITIONAL COPYING FIDELITY IN CAPUCHIN MONKEYS.....</b>	<b>54</b>
INTRODUCTION .....	54
<b>EXPERIMENT 1:.....</b>	<b>58</b>
<b>METHODS.....</b>	<b>58</b>
Subjects & Housing .....	58
Apparatus (a) .....	59
Procedure .....	63
Controls.....	63
Model training and selection.....	63
CdP models .....	63
Yerkes models.....	64
Demonstration sessions and observer tests .....	65
Data collection and analysis.....	66
<b>RESULTS.....</b>	<b>67</b>
Controls .....	67
Demonstration sessions.....	67
Test sessions .....	68
<b>EXPERIMENT 2:.....</b>	<b>72</b>
<b>METHODS.....</b>	<b>72</b>
Subjects & Housing .....	72
Apparatus (b) .....	72
Procedure .....	74
Model training and selection.....	74
Demonstration sessions and observer tests .....	74
<b>RESULTS.....</b>	<b>74</b>
Demonstration sessions.....	74
Test sessions .....	75
<b>DISCUSSION.....</b>	<b>77</b>
<b>CHAPTER 4: SOCIAL FACILITATION OF EXPLORATORY FORAGING BEHAVIOUR IN CAPUCHIN MONKEYS.....</b>	<b>82</b>
INTRODUCTION .....	82
<b>METHODS.....</b>	<b>86</b>
Subjects & Housing .....	86
Apparatus.....	87
Procedure .....	89
Alone and Social Conditions.....	90
Non-learner post-testing.....	91
Data Collection and Analysis.....	92
<b>RESULTS.....</b>	<b>92</b>
Learners .....	94

Non-learners .....	96
<b>DISCUSSION.....</b>	<b>97</b>
<b>CHAPTER 5: OBSERVER PREFERENCE DURING OBSERVATION OF FORAGING TASKS IN CAPUCHIN MONKEYS .....</b>	<b>103</b>
<b>INTRODUCTION .....</b>	<b>103</b>
<b>METHODS.....</b>	<b>107</b>
Subjects & Housing .....	107
Apparatus & Test Chamber .....	108
Procedure .....	113
Model selection and training.....	113
Baseline observer preference .....	114
Observer preference tests .....	115
Method preference tests .....	115
Data collection .....	116
<b>RESULTS.....</b>	<b>117</b>
Baseline observer preference .....	117
Observer preference tests .....	117
Method preference tests .....	120
<b>DISCUSSION.....</b>	<b>121</b>
<b>CHAPTER 6: IN-GROUP CONFORMITY SUSTAINS DIFFERENT FORAGING TRADITIONS IN CAPUCHIN MONKEYS .....</b>	<b>125</b>
<b>INTRODUCTION .....</b>	<b>125</b>
<b>METHODS.....</b>	<b>128</b>
Subjects and Housing.....	128
Apparatus .....	129
Procedure .....	132
Model Training .....	132
Baseline Observation Phase .....	134
Open Diffusion Test Phase.....	135
Data Collection and Analyses .....	136
<b>RESULTS.....</b>	<b>136</b>
Baseline Observation Phase .....	136
Open Diffusion Test Phase .....	137
<b>DISCUSSION.....</b>	<b>141</b>
<b>CHAPTER 7: GENERAL DISCUSSION.....</b>	<b>145</b>
<b>Physical factors .....</b>	<b>145</b>
<b>Social and individual factors.....</b>	<b>147</b>
<b>Overview of experiments.....</b>	<b>149</b>

Conclusions .....	161
<b>REFERENCES .....</b>	<b>162</b>
<b>APPENDICES.....</b>	<b>183</b>
Appendix A – Family Trees .....	183
Appendix B – Study subjects, ranks, and reference codes .....	184
Appendix C – Research site home enclosures .....	186

## List of Figures and Tables

Figure 1.1. Handclasp grooming in chimpanzees.....	14
Figure 1.2. Potato-washing in Japanese macaques.....	17
Figure 1.3. Social conventions in capuchins.....	20
Figure 2.1. The doorian apparatus.....	41
Figure 2.2. Experimental condition.....	45
Figure 2.3. Diffusion chain results.....	46
Figure 3.1. The Veegie apparatus front view.....	61
Figure 3.2. The Veegie apparatus back view.....	61
Figure 3.3. Experimental conditions.....	62
Figure 3.4. Veegie results by trial.....	70
Figure 3.5. The Veegie apparatus side condition.....	73
Figure 4.1. The test apparatus.....	88
Figure 4.2. Test condition and chamber.....	89
Figure 4.3. Test results by individual.....	95
Figure 5.1. The observer preference test chamber and panels.....	109
Figure 5.2. The observer preference test apparatus.....	110
Figure 5.3. The observer preference test condition.....	111
Figure 5.4. Subject's view through peep-holes.....	112
Figure 6.1. Open diffusion camera angles.....	131
Figure 6.2. The doorian apparatus.....	132
Figure 6.3. Open diffusion study site and setup.....	133
Figure 6.4. Group diffusion chart.....	138
Table 1.1. Forms of social learning.....	7
Table 1.2. Components of culture.....	12
Table 1.3. Diffusion experiments.....	25
Table 2.1. Subject observations by group.....	47
Table 3.1. Individual results by subject.....	71
Table 4.1. Individual results by subject.....	93
Table 5.1. Subject status and performance.....	119
Table 6.1. Method of acquisition chart.....	140

## CHAPTER 1: INTRODUCTION

*Parts of this chapter appear in:*

**Dindo, M.** (invited chapter, *in press*). Social learning and behavior transmission. In *Encyclopedia of Behavioral Neuroscience*, Eds. George Koob, Richard F. Thompson & Michel Le Moal. Elsevier Press, Oxford.

## CHAPTER 1: INTRODUCTION

The objective of this thesis is to investigate the social learning abilities of brown capuchin monkeys (*Cebus apella*), and how these abilities support the spread and maintenance of traditions consistent with those in the wild. Field reports indicate that capuchins (*Cebus libidinosus* and *capucinus*) have group-specific social conventions and unique methods for foraging that are not explained by genetics or local ecology alone, suggesting that these behaviours may spread through social learning (Panger et al. 2002; Perry et al. 2003). In contrast to these reports, extensive experimental evidence indicates that capuchins do not exhibit the social learning abilities that appear to be necessary for the spread and maintenance of group specific traditions (see Frigaszy and Visalberghi 2004 for a review). The experiments completed for this thesis aim to resolve this conflict and test whether capuchins do or do not in fact learn through observation.

The experimental study of animal social learning has predominantly focused on a narrow slice of social learning, imitative abilities, and in many respects has neglected the importance of alternative ways in which animals may learn to copy behaviours socially. This focus on imitation has also greatly influenced the study of animal traditions, as debates over terminology such as ‘tradition’ and ‘culture’ have been deeply rooted in the ability to imitate others.

In this chapter, I will first address the history of social learning research and reports of primate traditions in the wild, followed by how the body of work presented in this thesis aims to bridge the apparent disconnect between field studies of traditions and captive experiments on social learning in capuchin monkeys.

### ***The Study of Social Learning in Animals: A brief history***

The definition of imitation and the significance of the ability to imitate have seen many transformations since the turn of the 19<sup>th</sup> century. A century ago, imitation was not viewed as particularly sophisticated, and it was assumed that most animals could copy others, albeit not to the extent that humans do (Darwin 1871; Romanes 1884). One of the first definitions of imitation focused simply on an animal's ability to match the behaviours of others (Romanes 1884). This broad definition did not distinguish the many different ways in which matching-matching can occur, but it did pave the way for the future of social learning research in animals. Romanes sparked an interest in social learning in animals, despite the fact that his evidence was largely anecdotal.

Later, the definition of imitation became more focused, and it was also acknowledged that imitation may not be a single mechanism, but rather one with distinguishable components. For example, James Baldwin (1895) suggested that there are many imitative-like processes that can account for behaviour matching. Baldwin proposed one of the first 'stage' theories of imitation by dividing imitation into (1) *organic* and (2) *conscious* imitation, and further dividing *conscious*

imitation into *simple* and *persistent* imitation. Baldwin's theory of behavioural change (now called "the Baldwin Effect") viewed imitation as a fundamental process in evolutionary change, as learned behaviours could be advantageous in adapting to environmental changes (Baldwin 1902). Baldwin's distinction of *conscious* imitation into simple and persistent imitation was a crucial turning point in the study of social learning; it emphasized the difference between an instinctual response to a stimulus versus the motivational response to imitate others.

More rigorous evaluation of learning in animals gained momentum with the work of Edward Thorndike. Thorndike (1898; 1911) described his use of a puzzle-like box that required a levering technique to open the box. A cat was placed inside and left to individually discover the escape method. Critics of Thorndike's work have noted that the puzzle-boxes were too small and triggered stressful responses in his study subjects, and furthermore, his lever-systems for escaping the boxes were designed from an anthropocentric perspective that did not take into account the behavioural repertoire of his subjects (Whiten & Ham 1992). Nevertheless, Thorndike contributed to social learning theory by dismissing the use of anecdotes by those like Romanes. He encouraged a more operational definition of imitation, as: "learning to do an act from seeing it done", thus building upon Romanes' earlier view of imitation as any socially biased change in behaviour (Romanes 1884; Thorndike 1911, p. 50).

Morgan (1900), like Baldwin, believed that anecdotes did not provide direct evidence for the kinds of imitation taking place. In addition, Morgan proposed that

imitation is not a homogeneous phenomenon, but rather could be separated into three 'stages': (1) *instinctive* (2) *intelligent* and (3) *reflective*. What Morgan called *instinctive* imitation is now commonly referred to as social *contagion*, where a hardwired or pre-existing behaviour is copied without thought in the presence of others that exhibit the same behaviour. Morgan referred to *intelligent* imitation as when an individual's attention is influenced by the social behaviour of others, emphasizing that the behaviour would not occur without the enhanced motivational state. Morgan believed that *reflective* imitation was not seen in animals, as it required an individual to intentionally copy the actions of another. Morgan's attempt to identify different forms of imitation provided an invaluable contribution to social learning theory and gave way to the practice of distinguishing mechanisms of social learning. However, today the field of social learning still struggles to define and agree upon what exactly these different forms of social learning are.

### ***Forms of Social Learning***

Imitation was initially considered one of the few traits that animals had in common with humans, and many languages even have terms that involve the words 'ape' or 'monkey' to describe imitation (e.g. aping). However, great debate exists over whether or not monkeys, apes, and other animals are able to truly imitate, with a particular focus being placed on what the definition of imitation should be. Sometimes imitation can be confused with more subtle forms of social influence that lead to learning the same behaviours as others. For this reason, the literature on animal learning has made distinctions in terminology for the different kinds of

learning mechanisms at work. While the many different definitions contribute to the confusion in the literature, they also highlight the various ways in which social influences affect animal social learning and behaviour transmission.

As the following sections will highlight, social learning research in capuchin monkeys (*Cebus spp.*) has provided strong evidence that capuchins' behaviour patterns can be socially biased by their group-mates, but nevertheless they do not imitate others with the same degree of fidelity as humans or even great apes (see Visalberghi & Fragaszy 2002 for review). Therefore, this thesis does not strive to find imitative learning in capuchins, but instead focuses on overall copying abilities and how they may be enhanced socially. The following forms of social learning are addressed within this thesis (Table 1.1).

**Table 1.1** Categories of Social Learning. Social learning within this thesis will address two main components, enhancement effects and copying. Specific terms are divided into these two categories and presented along with basic definitions.

<b>Social Learning</b>	
'learning that is influenced by observation of, or interaction with, a conspecific or its products' (Hoppitt & Laland 2008)	
<b>Enhancement</b> (learning <i>with</i> )	<b>Copying</b> (learning <i>from</i> )
<p style="text-align: center;"><b>Stimulus Enhancement</b></p> <p>A form of social influence in which an individual is drawn to a stimulus based on the behavior or byproducts of another individual (Spence 1937)</p>	<p style="text-align: center;"><b>Object Movement</b></p> <p style="text-align: center;"><b>Re-enactment</b></p> <p>A form of copying where the observer learns about how an object or parts of an object move (Custance et al. 1999)</p>
<p style="text-align: center;"><b>Local Enhancement</b></p> <p>A motivational effect that leads an individual to focus on the location in which another individual is or was present or interacting with objects at that location (Thorpe 1963)</p>	<p style="text-align: center;"><b>Emulation</b></p> <p>A form of copying in which an observer achieves the end state goal of the demonstrator's actions but not necessarily the actions themselves (Tomasello 1990)</p>
<p style="text-align: center;"><b>Social Facilitation</b></p> <p>The process in which the mere presence of another individual either enhances or inhibits the observer's behavior (Thorpe 1963; Zajonc 1965)</p>	<p style="text-align: center;"><b>Imitation</b></p> <p>The most faithful form of copying in which an observer not only replicates the actions required to achieve an end result, but may also copy the unnecessary actions involved (Horner &amp; Whiten 2006)</p>

## Enhancement

### Stimulus and Local Enhancement

One of the most common forms of social influence occurs when an individual's attention is drawn to a stimulus by another individual. This is referred to as *stimulus enhancement* (Spence 1937). Similarly, when an individual is drawn to a specific location because of the actions or by-products of the actions of another

individual, it is called *local enhancement* (Thorpe 1963). It is not always possible to distinguish these two forms of enhancement, as an object or stimulus may also be associated with a specific location.

Some have argued that stimulus and local enhancement are not learning mechanisms per se, rather they are social influences that lead to individual trial-and-error learning, or in some cases facilitate opportunities for observational learning to take place (Heyes et al 2000). Nevertheless, local and stimulus enhancement are generally recognized as important processes in social learning, and therefore will be addressed in this thesis. In addition, it is not always possible to distinguish evidence for imitative learning from simpler forms of social influence such as local and stimulus enhancement (Tomasello & Call 1997).

### **Social Facilitation (Social Enhancement)**

The presence of another individual may enhance or inhibit existing behaviour in an individual (Clayton 1978; Zajonc 1965). This is commonly referred to as *social facilitation*, but is also referred to as *social enhancement*, as the motivational state of an individual is enhanced by another (be it an increase or decrease in motivation). The mere presence of another individual has the potential to lead to synchronization of behaviours over space and time, which is crucial in group-living species with regards to group cohesion, behavioural coordination, foraging efficiency and predator avoidance (Boinski & Garber 2000). While social facilitation alone does not lead to complex behaviour matching, like stimulus and

local enhancement, it has the potential increase opportunities in which observational learning can occur.

## **Copying**

Within this thesis, the term *copying* will in general refer to instances in which an individual replicates the actions of a model. The following section addresses the various forms of copying behaviours.

### **Emulation and Object Movement Re-enactment**

*Emulation* was first suggested by Tomasello (1990) to refer to a form of learning about the affordances of a task, or changes in the environment as a result of a conspecific's behaviour. As used by Tomasello (1990, 1996), the term implies less advanced cognitive abilities than imitation, as the lack of copying the actions of another could have resulted from a lack of overall understanding of the other's mental state and intentions.

Within the literature, four distinct aspects of emulation learning, which all relate to learning about the affordances of an object, have been defined: (1) setting a goal, (2) learning the physical properties of objects, (3) learning relationships among objects, and (4) learning what can be done with an object (Byrne 1998; Tomasello 1996; Tomasello & Call 1997; Whiten & Ham 1992). Furthermore, as it is changes in the environment that are replicated by the learner, the demonstrator's identity or even presence may be irrelevant in instances of emulation, so long as the

movements are observed. Other terms for emulation include goal enhancement and affordance learning.

## **Imitation**

Imitation, as a unique form of social learning and not as a term to describe social learning in general, has been the cornerstone to the study of social learning for over a century, and yet agreement over the definition of imitation remains a rather contentious issue (see Galef 1988; Heyes 1993). The term imitation has been used to refer to instances of motor, auditory, and cognitive copying, but for the purpose of this thesis, only motor imitation will be addressed. Imitation is defined here as a form of copying in which an observer not only replicates the end-result of observed actions (as in emulation), but also replicates the specific actions themselves.

While copying (Table 1.1) is perhaps the most fundamental aspect of imitation, the ability to imitate, i.e. to copy all aspects of a task, has been associated with more advanced overall cognitive abilities. Deficits in imitative abilities in humans have been found in individuals with higher cognitive impairments, such as autism (Meltzoff and Gopnik 1993). Because imitation is considered a more advanced form of copying and is associated with cognitive ability, some have argued it may be unique to humans. The argument that imitation is unique to humans has also often been at the heart of the debate over whether or not culture exists in animals.

## *The question of animal culture*

While few would disagree about the complexity of human culture, restricting the definition of culture to the domain of humans is quite limiting. The debate over culture has been, to a large part, definitional (Galef 1992; McGrew 1998, 2004; Whiten & Ham 1992), both in terms of what is culture, and how to define the social learning mechanisms that are thought to support the transmission of cultural behaviour (Boyd & Richerson 1985; Galef 1992; Whiten & Ham 1992; Whiten et al. 2004). Another important component of this debate surrounds the terms used to describe behaviours that are potentially cultural in nature. Early reports described such behaviours as proto-culture, or pseudo-culture (Kawai 1965). More recently, some have employed the term tradition, e.g. in Frigaszy and Perry's book, *The Biology of Traditions*, they make an explicit case for calling them traditions versus cultures. Still others prefer to use the terms *tradition* and *culture* interchangeably (Laland & Hoppitt 2003; Laland & Janik 2006), which has sometimes contributed to the confusion and debate over the question of animal culture (Galef 1992; Laland & Galef *in press*). Within this thesis, a tradition is defined as a behaviour that is socially acquired and that endures throughout a population (Frigaszy 2003), and it is considered a component of culture in humans as well as animals (Kroeber 1928).

In terms of defining culture, Kroeber (1928) was one of the first to present set criteria for determining culture in animals. Specifically, Kroeber addressed the question of chimpanzee culture in his examination of Köhler's (1927) publication, *The Mentality of Apes*. As indicated in the brackets [below], Kroeber presented six

components that he believed were defining features of cultural behaviour, and from these criteria, he concluded that apes do not provide evidence for culture. This approach for assessing culture, however, focuses on the processes involved, and therefore requires longitudinal studies that were rare during Kroeber's time, if not non-existent (Köhler 1927).

If one ape devised or learnt a new dance step, or a particular posture, or an attitude toward the object about which the dance revolved [1. *innovation*]; and if these new acts were taken up by other chimpanzees, and became more or less standardized [2. *standardization* and 3. *dissemination*]; especially if they survived beyond the influence of the inventor [4. *durability* and 5. *diffusion*], were taken up by other communities, or passed on to generations after him [6. *tradition*] – in that case, we would legitimately feel that we were on solid ground of an ape culture.

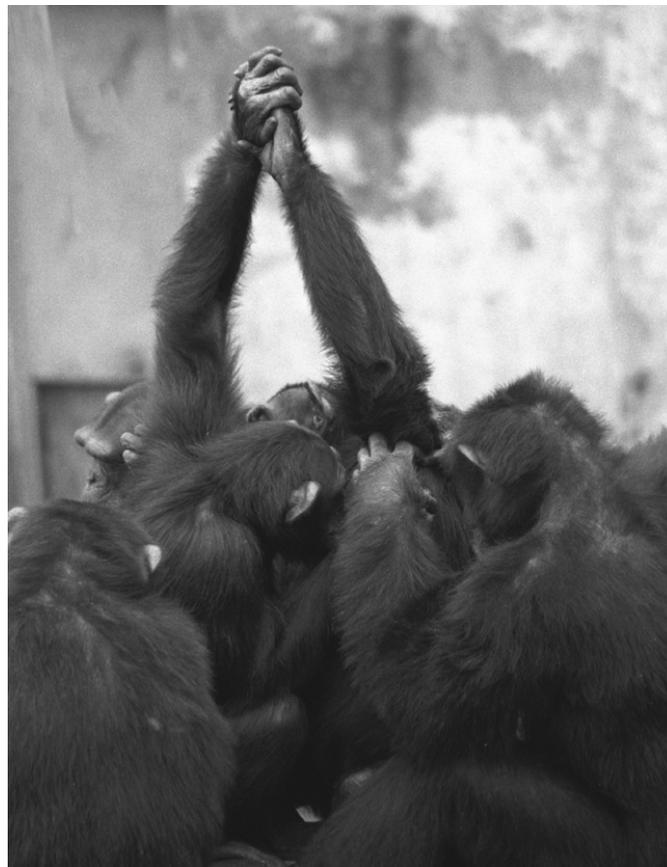
Kroeber 1928, p. 331

**Table 1.2.** Components of culture. Twelve defining features of culture are presented along with the presence ( + ), absence ( x ), or debate (?) in humans, apes and monkeys (adapted from Subiaul 2007).

Components of Culture		Humans	Apes	Monkeys
<b>Innovation</b>	<i>New Behavioural pattern is invented</i>	+	+	+
<b>Dissemination</b>	<i>Transmitted from individual to individual</i>	+	+	+
<b>Durability</b>	<i>Pattern endures beyond demonstrator's presence</i>	+	+	?
<b>Diffusion</b>	<i>Pattern spreads across groups</i>	+	+	+
<b>Tradition</b>	<i>Pattern endures across generations</i>	+	+	?
<b>Standardization</b>	<i>Pattern is consistent and stylized</i>	+	+	?
<b>Species-valid</b>	<i>Not an artefact of human influence</i>	+	+	+
<b>Transcendent</b>	<i>Not determined by biophysical environment</i>	+	+	+
<b>Accumulation</b>	<i>Multiple traditions build over time</i>	+	?	x
<b>Imitation</b>	<i>Ability to copy novel motor responses</i>	+	+	x
<b>Variability</b>	<i>Two or more patterned behaviours in more than one domain</i>	+	+	+
<b>Conformity</b>	<i>Preference for groups' standard</i>	+	+	?

The last several decades have now provided us with evidence in primates for Kroeber's six components of culture, as well as adding additional features to his list. Table 1.2 is adapted from Subiaul (2007) and presents twelve defining components of culture as suggested by Kroeber (1928), Galef (1992), McGrew (1998), Tomasello and Call (1997), and Whiten and van Schaik (2007). An influential breakthrough for studying cultural variation in primates came from a combination of longitudinal studies in wild populations of chimpanzee throughout Africa (Whiten et al. 1999). By systematically comparing the cultural variants for each site with regards to ecological conditions, Whiten and colleagues were able to identify 39 distinct behavioural variants among seven chimpanzee research sites (i.e. *standardization*). Chimpanzees in some areas of Africa use stones as tools to crack open nuts (Boesch & Boesch 1990; McGrew 1992), while chimpanzees at other sites select and modify tools for ant dipping, a foraging technique for consuming ants by using sticks (Humle & Matsuzawa 2002). Chimpanzees also engage in traditions that do not have direct survival benefits. One example of this is the handclasp grooming (McGrew 2004; McGrew et al. 2001a,b). The handclasp groom involves holding and supporting the arm of a grooming partner by the wrist or hand over the grooming pairs' heads (Figure 1.1). This behaviour is seen at specific field sites, and entirely absent in others; for example, McGrew (2004) observed the handclasp groom in the Mahale Mountains but not at Gombe, a chimpanzee research site only about 150 miles distant. The handclasp groom has also been shown to endure (*durability*) despite extreme changes in-group composition (Nishida et al. 1985; Nakamura & Uehara 2004; Uehara et al. 1994). This behaviour has also been seen in captivity. Chimpanzees in the FS1 group at

the Yerkes Primate Center handclasp groom, while a second group at the centre with the same housing conditions and group size do not (de Waal & Seres 1997). It is believed that the FS1 hand-clasp groom originated with an adult female (*innovation*) and records show it first spread to her kin and close social partners before it became a group-wide behavioural occurrence (*diffusion* and *tradition*; Bonnie & de Waal 2006).



**Figure 1.1.** Handclasp grooming in chimpanzees. Two individuals from the FS1 group at the Yerkes Primate Center engage in the handclasp groom (photo: de Waal 2003).

Using the same approach as Whiten and colleagues (1999), van Schaik and others (2003) compared cultural variants in wild orangutan populations (*Pongo pygmaeus*) in Southeast Asia. Orangutans are relatively solitary, yet still social animals whose

interactions with conspecifics are mostly limited to mother-offspring pairs and mating partners (van Schaik et al. 1999). Opportunities for social learning are inherently limited by the number of social encounters between individuals, so the opportunities for studying cultural learning in orangutans have also been limited (van Schaik 2006). Despite this confine, van Schaik and colleagues' comparison of six field sites concluded that orangutans also exhibit cultural variants, including 6 social signals (e.g. kiss-squeaks), and 10 specialized feeding techniques, two of which involved tool-use. As with the chimpanzee cultures collaborative, data collected from these different sites confirmed that the reported cultural variants could not be attributed to ecological differences across sites, and furthermore, found correlations between the opportunities for social learning and the size of the local repertoire.

Of the twelve components of culture (Table 1.2), apes and humans appear to share all features except possibly *accumulation*. On one end of the spectrum, Tomasello (1999) has proposed that cumulative culture, or the *ratchet effect*, is unique to humans as it allows for complex technologies and traditions to develop. On the opposite end, McGrew (2001) has argued that even monkeys show evidence for *accumulation* of traditions. The modification of the wheat-washing tradition in Japanese macaques is cited as an example of accumulation, because monkeys improved, and therefore built upon, the technique by digging small pools in the sand so that the wheat did not float away during washing bouts (McGrew 2001, pp. 250-1). In contrast with apes and humans, monkeys share only half these components, with capuchins presenting the strongest support among monkeys for

*innovation, dissemination, diffusion, species-valid, and variability* in traditions (Panger et al. 2002; Perry et al. 2003; see Perry 2006 for review).

It seems unlikely that a tradition that can be transmitted across generations would not also endure beyond the original innovator. Nevertheless, with regards to *durability* (as defined in Table 1.2), it remains to be precisely shown if a tradition endures beyond the original innovator as it is not always possible to determine when and where the innovation began. With one notable exception, few studies have specifically identified the initial point of innovation of a tradition (Kawai 1965). Similarly to chimpanzees and orangutans, we have longitudinal evidence for traditions in Japanese macaques (*Macaca fuscata*). The long-term data on Japanese macaques suggests *durability*, but not to the extent it has been seen in apes (Leca et al. 2007a). Solid evidence for *durability, standardization, accumulation, imitation and conformity* has yet to be shown in monkeys. One of the first reports for ‘proto-culture’ in macaques came from the island of Koshima, where a group of Japanese macaques washed sweet potatoes that were provisioned to them (Imanishi 1957; Kawai 1965; Nishida 1987). Potato-washing was innovated by one female, Imo, and within 10 years, the behaviour diffused to most of her group (Watanabe 1994; Figure 1.2). The spread of potato washing was initially slow, with only one or two individuals acquiring the behaviour per year. Galef (1990, 1992) suggested that imitation seemed unlikely to explain such a slow transmission. If Japanese macaques were imitating what they observed, Galef argued that the transmission rate would be much higher. What Galef did not take into consideration was the strict hierarchical nature of macaque species (Chapais 1992; de Waal 1996; Flack et

al. 2006), which restricts the proximity between unrelated individuals and those with the greatest rank disparity, and therefore limits social opportunities for individuals to observe this behaviour. Furthermore, Galef was assuming that cultural behaviours could only spread by complex social learning mechanisms such as imitation (Galef 1990, 1992; Heyes 1994, 1996; Whiten & Ham 1992). While it is now widely assumed that the potato washing did not spread by imitation, it is accepted as a tradition of the monkeys at Koshima (de Waal 2001; Whiten 2004).



**Figure 1.2.** Potato-washing. Japanese macaques (*Macaca fuscata*) submerge potatoes on the shore at Koshima (photo: de Waal 2003).

Another tradition in Japanese macaques is the handling of stones as an object-play behaviour (Huffman 1982; Huffman & Quiatt 1986). Stone handling in Japanese macaques may not have a specific functional purpose beyond social play, and it is possible this object-play behaviour is a precursor of tool-use (Huffman & Quiatt 1986). What is particularly interesting is that object-play behaviour is not rewarded and does not involve food or food processing, just like the handclasp groom in

chimpanzees. New reports are emerging for variants of stone handling between groups, including stone throwing, as well as a novel fish eating method in Japanese macaques, adding further support for *variability* of kinds of traditions in monkeys (Leca et al. 2007a,b).

The best evidence for *variability* of traditions comes from the long-term study of capuchin monkeys (*Cebus capucinus*) in Costa Rica (Panger et al. 2002; Perry et al. 2003; Perry 2006). A collective 19,000-hours of field observations from 13 social groups over 13 years were combined from four field sites, Lombas Barbudal, Santa Rosa, Palo Verde, and Curu (Perry et al. 2003). Five social conventions were described: (1) hand-sniffing – when an individual takes the hands or feet of another individual and deeply inhales, (2) body part sucking – when an individual engages in lengthy period of time sucking a body part of another individual (e.g. ear, finger, tail), (3) finger-in-mouth game – when an individual puts his or her fingers in the mouth of another individual that then clamps down firmly for a lengthy period of time, (4) hair game – when two individuals take turns biting hair from each other, and (5) toy game – when two individuals repeatedly take turns pulling non-food objects from each other's mouths (Perry et al. 2003). Additionally, different food processing methods were described for some of the 13 field sites (Panger et al. 2002; Rose et al. 2003). For example, at Lomas Barbudal, capuchins hunt squirrels by biting them on the back of the neck, whereas this method is not seen at all in Santa Rosa, and in Lomas Barbudal and Palo Verde, groups within and between sites vary in their use of pounding and rubbing foods. Panger and colleagues (2002) compared within group association patterns with method preferences and

found that those dyads that spent more time in proximity were also likely to share the same method preference, suggesting that these behaviours are socially influenced. Perry and colleagues (2003) suggested that the social conventions capuchins exhibit are also socially acquired, as the dyadic nature of these behaviours requires individuals to match another's behaviour. Social conventions in capuchins are another example of primate traditions that are not subsistence related; in fact, they appear to be potentially costly since they require individuals to put fingers and other body parts in the mouths of others (Perry 2006; Figure 1.3). Thus, it has been argued that these behaviours function mainly to strengthen social bonds (Perry & Manson 2003; Perry 2006). Lack of imitation may be one of the key features that distinguishes monkeys from apes and humans with regards to culture in Table 1.2, but whether imitation is a necessary component of culture remains debatable (Heyes 1993, 1994; Tomasello et al. 1993a; Zentall et al. 1996; Zentall 2006). As with the handclasp groom in chimpanzees, monkeys match the behaviour of other group members despite a lack of material gain (i.e. non-material traditions). It is possible that copying group-members in some form may have an intrinsic appeal in primates. Galef (1990) has suggested that being reinforced with food is a necessary part of cultural learning in animals and without it the behaviour quickly disappears. This claim has been disputed by others such as de Waal (2001; de Waal & Bonnie *in press*; Bonnie & de Waal 2007) who suggests that acting like others is in itself an intrinsic reward. De Waal (2001) refers to this as Bonding- and Identification-based Observational Learning (BIOL). The tradition of object-play provides no apparent benefit other than social bonding to the monkeys who perform this act; perhaps this underlying motivation to act like others is what connects

human and ape imitation to other forms of copying in monkeys. The precise social learning mechanisms that support these traditions remain to be seen, and researchers are continuing to investigate opportunities for social learning at these field sites in Costa Rica (Perry & Ordonez 2007). Regardless of how similar or dissimilar these components are between humans, apes and monkeys, collectively identifying key features of culture brings us closer to presenting a “biologically meaningful understanding of culture” (Fragaszy 2003, p. 69).



**Figure 1.3.** Social conventions in capuchins. Two white-faced capuchins (*Cebus capucinus*) engage in the 'finger-game' and 'hand-sniffing' (Perry et al. 2003).

### **Captive Studies on Social Learning and Culture**

Longitudinal studies in the wild (such as those mentioned above) are costly, both in time and money spent by researchers, which has in turn limited the amount of information available. In order to assess if wild traditions are the result of social learning, it is also necessary to conduct captive experiments that allow us to control for all instances of social influence. Two of the most influential experimental paradigms for uncovering social learning in the spread of behaviours are the 'two-action task' and the 'group-diffusion' methods.

### **Two-action task studies**

The two-action task (Dawson & Foss 1965) has mainly been used to control for the effects of local and stimulus enhancement on social learning while examining the imitative abilities of subjects in observational learning experiments. The test involves two distinct methods for solving a task. One method for solving the task is demonstrated to an experimental subject before the subject is presented with the task. Although both methods are possible, the subject only observes one of the two tasks. Therefore, if a subject performs the same task as the demonstrator, it is most likely a result of imitative learning. The two-action task is considered one of the best methods for testing imitation in animals (Galef 2003; Zentall et al. 1996; Zentall 2006).

Animals differ in their physical abilities (e.g. primates use their hands, while birds use their beaks for most foraging behaviours), and so an advantage of the two-action test, is that it can be designed specifically for the physical abilities of a given species. Two-action task experiments have been used to study imitation in pigeons (Zentall et al. 1996), budgerigars (Galef et al. 1986), Japanese quails (Akins & Zentall 1996), rats (Heyes & Dawson 1990), hamsters (Prato Previde & Poli 1996), capuchin monkeys (Custance et al. 1999), gorillas (Stoinski et al. 2001), orangutans (Stoinski et al. 2003) and chimpanzees (Whiten 1998), among other species. These experiments have typically investigated test subjects in pairs, and have suggested imitative, or imitation-like, learning in the context of the two-action task paradigm.

However, it is apparent that each of these species is distinct from the next with regards to social structure and cognitive abilities, and it is, therefore, to be expected that we shall see differences in how socially acquired information spreads among group members, and how new behaviours develop into group-specific traditions.

### **Diffusion studies**

One approach to studying traditions in animals is to investigate the diffusion of a behaviour pattern throughout a social group. In the wild, it is virtually impossible to witness or recognize the innovation of a novel behaviour. It is also difficult to study the transmission of that behaviour in a controlled manner, with some exceptions, such as potato washing and stone handling in Japanese macaques (Huffman & Quiatt 1986; Imanishi 1957; Kawai 1965). Even in the Japanese macaque studies, which have years of behavioural data available, the underlying social learning processes involved still remain a point of issue and debate (Galef 1990, 1992).

As described above, the two-action test allows us to study the extent to which individuals learn to copy by observation, and in most experiments to date, this paradigm has been used in a dyadic context. The ‘diffusion experiment’ can provide us with further details about how a behaviour spreads socially beyond the artificial dyadic context imposed upon subjects. The ‘open diffusion’ experimental paradigm has been used before in a wide range of captive as well as wild experiments with primates and other animals (see Table 1.3, as well as Whiten &

Mesoudi 2008, for review). Whiten and colleagues' (2005) study was the first 'open diffusion' experiment to use the two-action test with two large non-human primate groups and an additional control group. This approach showed that two distinct tool-use tasks could be seeded into two groups of chimpanzees, respectively, through demonstrations in each group by one high-ranking group member. Both study groups showed conformity to the method employed by the original demonstrator, and the experiment tracked the acquisition pattern among group members. The 'open diffusion' paradigm is an ideal method for investigating the role of social relationships and observational requirements involved in the spread of a tradition, and will be addressed with regards to capuchin monkeys in Chapters 2 and 6.

A further point of interest for how culture spreads socially is how long a tradition is maintained socially (Fragaszy 2003, Laland & Plotkin 1990, 1992; Laland & Williams 1998). Some shared behaviours are short-lived, lasting a few days or a few months (Fragaszy 2003; Laland & Hoppitt 2003; Laland et al. 2000; Perry et al. 2003), while others may be preserved across generations (McGrew 1998; Nishida 1987; Whiten et al. 1999). It has been argued that in order for a shared behaviour to become a tradition, it must persist in the absence of the innovator of that behaviour (Fragaszy 2003; Nishida 1987). An experimental approach for studying this is the 'diffusion chain' test. The 'diffusion chain' paradigm begins with an 'innovator,' a trained model of a behaviour, who demonstrates that behaviour to a naïve individual. If the naïve individual learns the behaviour, he or she then becomes the model for a second naïve individual, and so on.

The 'diffusion chain' test was first used by Bartlett in 1932. The experiment resembled the game 'telephone' or 'Chinese whispers,' where a message is transferred verbally from one person to the next. If the message is misunderstood, the information transfer is corrupted and a different message is passed along, ending the chain of the original message. The 'diffusion chain' approach was first used with chimpanzees to study habituation to novel play objects (Menzel 1972). It has been used for studying foraging and food preferences in guppies and rats (Reader & Laland 2000; Laland & Plotkin 1990, 1992, 1993; Laland & Reader 1999; Laland & Williams 1997, 1998), and avoidance tasks in callitrichids and birds (Boogert et al. 2006; Curio et al. 1978, Kendal et al. 2005). More recently, Horner and colleagues (2006) completed a 'diffusion chain' study with the same two groups of chimpanzees in the Whiten et al. (2005) 'open diffusion' study. One task was introduced to each of the two test groups and was successfully passed along two chains of six and seven chimpanzees. These results are consistent with the conclusion that chimpanzee traditions in the wild pass from one generation to the next, and are known to persist even long after the innovator has left the group (McGrew 1998; Whiten et al. 1999).

**Table 1.3** Diffusion Experiments. The diffusion experiment has been used in a variety of species and in combination with other experimental paradigms. A selection of studies reviewed by Whiten & Mesoudi (2008) are presented here to highlight the many ways in which the diffusion paradigm has been used to explore traditions in various species.

<b>Study</b>	<b>Species</b>	<b>Experimental design &amp; results</b>
<b>Menzel et al. 1972</b>	chimpanzees	First diffusion with replacement experiment with primates in which subjects were gradually replaced in order to look at the maintenance of a tradition in the absence of original study group
<b>Curio et al. 1978</b>	blackbirds	First linear diffusion study in which the original model demonstrated a fear response in reaction to the presence of a stuffed owl, while an observer was shown a non-predator. The learned fear response of the observer to the non-predator was then modelled in the presence of a new observer, and this response was passed along to future observers
<b>Cambefort 1981</b>	baboons and vervets	First open diffusion experiment with primates in which hidden food was discovered, and the foraging for those hidden foods was tracked in two species of monkeys. While it was not clear to what extent the behaviour spread by observational learning versus individual learning, the two different social styles showed how behaviours may spread differently based on the species.
<b>Laland &amp; Plotkin 1993</b>	rats	First studies investigating the diffusion of foraging style, as there were two different ways for finding food
<b>Laland &amp; Williams 1998</b>	guppies	First study to present two different shoaling routes where one was shorter and less costly in energy expenditure, while the longer less efficient method was initially preferred based on observation, eventually the tradition eroded in favour of the less costly route
<b>Fragaszy et al. (unpublished) Reported in Frigaszy et al. 2004, pp. 254-255</b>	capuchins	First open diffusion experiment in capuchin monkeys where different experimental methods for collecting juice were demonstrated to juveniles in two locations, however only one of the methods was possible at each apparatus, and the data were never published
<b>Whiten et al. 2005</b>	chimpanzees	First open diffusion of two experimental foraging techniques requiring the use of a tool. Two different groups were presented with the same apparatus that could be manipulated for food using two distinctly different methods. Both techniques were always available, and subjects significantly preferred to use the method the observed modelled for them
<b>Horner et al. 2006</b>	chimpanzees	First diffusion chain of a two-action task, where subjects again had two possible means for extracting food from a foraging apparatus and chose to employ the method they observed. Observer subjects then became the model for a naive individual, and continued the tradition in the absence of the original 'innovator'
<b>Bonnie et al. 2007</b>	chimpanzees	First open diffusion of arbitrary conventions in which chimpanzees recognized the arbitrary act of depositing tokens in different receptacles at different locations
<b>Price &amp; Caldwell 2007</b>	colobus monkeys	First published open diffusion experiment with monkeys in which a video of a conspecific monkey served as a model for a novel foraging behaviour

These combinations of the two-action task and diffusion methods appear to be our best opportunity for bridging the gap between field and experimental studies on social learning and traditions in primates (Whiten & Mesoudi 2008) and data will be presented for capuchin monkeys using these methods in Chapters 1 and 6.

## **Social Learning and Behaviour Transmission in Capuchins**

Brown capuchin monkeys (*Cebus apella*) are the subjects of this thesis on social learning and behaviour transmission. Although reports for traditions in the wild appear only for white-faced capuchins (*Cebus capucinus*), there is recent evidence to suggest that these close cousins may also exhibit group-specific behavioural traditions involving substrate manipulation, and stone tool-use (Boinski et al. 2003; Moura & Lee 2004; Ottoni & Mannu 2001). One reason for the lack of field reports on social learning and culture in brown capuchins is in part due to a gap in research coverage (Boinski et al. 2003). In Costa Rica, long-term projects have been in place to specifically and systematically address social learning and behaviour transmission in capuchins (Perry 2006), whereas established field sites for brown capuchins have focused more on cognitive and ecological effects on group travel, foraging strategies and predator avoidance (Boinski 1998; Boinski et al. 2000b). It is only in the last decade that the study of social learning and traditions has been applied to brown capuchins in the field (Ottoni & Mannu 2001, 2003; Verderane et al. 2007; Visalberghi et al. 2005); by contrast the study of social learning in captivity has been a particular focus for brown capuchin researchers for decades (see Frigaszy & Visalberghi 2004).

Brown capuchin monkeys are particularly interesting research subjects for captive studies of cognition and social learning in primates because, like chimpanzees, they are characterized by a high brain to body ratio (Rilling & Insel 1999), tool use capabilities (Ottoni & Mannu 2001; Westergaard 1998), and a prolonged period of infant development (Fragaszy et al. 2004). However, in contrast with chimpanzees, capuchins have shown no strong evidence for imitative learning in captive experiments (Adams-Curtis & Frigaszy 1995; Visalberghi 1987; Visalberghi & Trinca 1989; Visalberghi & Fragaszy 1990; Visalberghi & Limongelli 1994; Fragaszy & Visalberghi 1996). Most of these experiments suggest that social facilitation and stimulus enhancement are responsible for social learning in capuchins (Coussi-Korbel & Fragaszy 1995; Fragaszy et al. 2004).

Most research on the social learning abilities of capuchin monkeys can be attributed to Elisabetta Visalberghi and Dorothy Fragaszy (Fragaszy & Visalberghi 2004; Fragaszy et al. 2004; Visalberghi & Fragaszy 1990; 2002). Over the course of twenty years, these authors have completed numerous experiments on capuchin social learning, which all concluded that capuchins do not learn by imitation. In one particular study, capuchins were given a tool-use task called the ‘trap-tube’ test (Visalberghi & Limongelli 1994). The ‘trap-tube’ was a clear, horizontal tube that had a ‘trap’, i.e. a cup, in the centre of the tube. A food reward was placed inside the tube and a stick was provided with which the food could be pushed out of the tube. If the subject pushed from the wrong direction, the food would fall into the trap, but if the subject pushed from the opposite direction the food would be pushed

out for collection. The capuchins in this study consistently failed to learn the task by imitation, and the authors concluded that the lack of imitation was due to the monkeys' failure to understand the cause and effect relationship that was necessary to infer the end goal of the task. In another study, these authors were interested in the effects of adult presence on juvenile learning opportunities (Fragaszy et al. 1994). Adult capuchins were presented in their group enclosure with a familiar apparatus from which they knew how to extract juice. In a separated section of the home enclosure, juveniles had access to a second apparatus. The authors examined the juveniles' interactions under three conditions (1) adults had access to the first apparatus in their home area and juveniles had access to the second apparatus in the sub-area, (2) only the first apparatus was presented in the home area, and (3) only the second apparatus was presented in the sub-area. In condition 1, juveniles spent half their time between the two apparatuses. Juveniles spent more time at the first apparatus with adults, than at the second apparatus when only one was available. The authors concluded that juveniles were only weakly motivated by adult presence, and that adult presence was not necessary for learning the task by individual trial-and-error learning. The focus of this study was to examine coordination of activities in adults and juveniles, and so it did not elaborately detail the observations that occurred between adults and juveniles. In a study with 3 hand-raised capuchins, Fragaszy and colleagues (1998, as reported in Fragaszy & Visalberghi 2004, p. 25) had human experimenters show subjects actions with objects in relation to their own body, and then videotaped the capuchins' actions. Two of the three subjects reached for the correct object most of the time, while the third was ambiguous with his choices and only selected the correct object on 30

percent of the trials. All three subjects were not consistent in matching the actions demonstrated to them by the human model. The difficulty in assessing capuchin social learning from studies such as these, is that (1) the actions presented for imitation testing may not be suitable for capuchin monkeys, and (2) the social relationships between models and subjects are not taken into consideration, or at least not explained within the reports. Nevertheless, these reports show that capuchins do not learn in the sophisticated way that apes do.

It has been suggested that capuchins learn *with* each other instead of *from* each other (Fragaszy & Visalberghi 2004; Visalberghi & Fragaszy 2001). Fragaszy & Visalberghi (2004) thus prefer the term ‘socially biased learning’ instead of ‘social learning’ because capuchins do not necessarily gain *direct* information from others; rather, they are affected by the mere presence of a conspecific and will increase their exploratory behaviour in the presence of others. While it is possible that capuchins do not learn by imitation, this matter is still unclear in certain contexts (e.g. Fredman & Whiten 2008; Bonnie & de Waal 2007). Furthermore, if they do not imitate others at all, then it is particularly interesting to understand how capuchin traditions are spread and maintained by less complex social learning processes.

### *Thesis Aims and Scope*

Whether or not traditions in capuchin monkeys spread by imitative means remains to be seen (Panger et al. 2002; Perry et al. 2003; Perry 2006). It is likely that such behaviours have spread in capuchins via social learning mechanisms such as social facilitation, stimulus or local enhancement, and possibly emulation or object movement re-enactment (Galef 1992; Frigaszy & Visalberghi 2004). Nevertheless, the majority of research investigating social learning in capuchins, and other monkey species, has focused on their inability to imitate the actions of others. Few studies have specifically aimed to address alternative means for copying in capuchins. Instead, reports conclude from the absence of imitation that other forms of social learning are at work (Visalberghi & Fragaszy 2002). In the absence of imitation, how then do traditions develop that are unique to one social group and not found in another? Which of the lower-level mechanisms can account for the spread of behaviours and the eventual development of a group-wide tradition? And finally, what social factors enhance or inhibit the transmission of novel behaviours. These questions are the basis for this thesis and the research herein.

It is virtually impossible to be present at the discovery of an innovation and to then document the gradual spread of that novel behaviour in the wild. Experimental research provides the opportunity to bridge the gap between field reports and captive experiments on social learning and traditions in capuchin monkeys. The following studies were conducted at two study sites, the Living Links Center Capuchin Laboratory at the Yerkes National Primate Research Center in Atlanta,

Georgia, USA, and the Centre de Primatologie at Louis Pasteur Université in Strasbourg, France. Each research chapter within this thesis documents specific details about the study subjects and group composition as it relates to each study (see also Appendices A & B). This was done in part to emphasize the importance of group dynamics and individual subject identity, but also because these dynamics changed over the three years in which these five studies were conducted. Therefore, any redundancy in methodology by chapter is a reflection of this.

As noted at the beginning of some chapters, the data therein have been submitted for publication. I carried out all testing, coding and analyses involved in the research. As first author, I wrote all the manuscripts that were submitted, and additional authors were the lab supervisor(s) and my advisor, Andrew Whiten, who supervised the experiments and contributed feedback on subsequent revisions of the manuscripts.

The first four research chapters examine specific components of social learning and behaviour transmission in capuchin monkeys. These studies were designed to investigate elements of social learning that have previously been neglected in the literature. Chapter 2 begins with the simple question, can capuchin monkeys observationally learn to copy the foraging methods of another group member? If so, how long can this behaviour endure throughout a group once the original ‘innovator’ is gone? The next chapter, Chapter 3, expands upon the research questions of Chapter 2, by investigating *when* monkeys will faithfully copy conspecifics, and *how* motivational factors may reduce the fidelity in copying

necessary for a tradition to spread. Chapter 4 investigates the issue of motivation further by examining how the presence of another foraging monkey may enhance an individual's exploratory behaviour and motivation to potentially innovate. Chapter 5 asks the question, what influences an individual's choice to observe another foraging group member? The social status of foraging partners is examined by presenting monkey subjects with a choice in whom they observe. Finally, Chapter 6 builds upon the previous four chapters and connects these findings with reports from the wild by presenting an experiment in the 'open-diffusion' context. This study essentially removes the experimental confines found in previous chapters, where subjects were specifically selected and tested in dyads or triads, and examines the spread of a novel foraging behaviour in a more ecologically representable context.

## CHAPTER 2: SOCIAL DIFFUSION OF NOVEL FORAGING METHODS IN CAPUCHIN MONKEYS

The data in this chapter were published in:

**Dindo, M.,** Thierry, B., & Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society of London: Series B*, 275 (1631), 187-193.

## **CHAPTER 2: SOCIAL DIFFUSION OF NOVEL FORAGING METHODS IN CAPUCHIN MONKEYS**

### ***INTRODUCTION***

In the last twenty years there has been a major expansion in the study of social learning in animals, driven principally by the study of behavioural traditions in the wild, and experimental analyses of the learning process, undertaken mostly in the laboratory (Fragaszy & Perry 2003; Galef & Giraldeau 2001; Galef & Heyes 2004; Perry 2006). Social learning includes all those processes whereby individuals acquire new behaviour or information about their environment through observation or interaction with others, or the results of their actions. This may give rise to the group-level phenomenon of local traditions or cultures, in which case the social learning is often referred to as ‘cultural transmission’. Understanding such learning is important for evolutionary biology generally, because it provides an alternative transmission system to genetics that can powerfully shape behavioural evolution (Boyd & Richerson 1985; Whiten 2005). At more specific levels, studies of animal social learning and traditions have become influential in behavioural ecology (Danchin et al. 2004), ethology (Fragaszy & Perry 2003) anthropology (Perry 2006) and comparative psychology (Hurley & Chater 2005; Shettleworth 2001).

This body of work has provided increasing evidence for social learning and traditions among fish, birds and mammals (Brown & Laland 2006; *Learning & Behavior*, whole issue 32 (1) 2004; Stanley et al. 2008). However, the traditions

described in most species studied tend to be limited to single behaviour patterns, such as pine-cone opening in black rats (Aisner & Terkel 1992; Terkel 1996). By contrast, in a small number of primate species that have been the subjects of long-term field study, multiple traditions have been described that define relatively complex local ‘cultures’ that have been suggested to be somewhat more comparable to the multifarious nature of human culture (chimpanzees: Goodall 1973; Nishida et al. 1983; Whiten et al. 1999; orangutans: van Schaik et al. 2003; Japanese macaques: Leca et al. 2007a; see Whiten & van Schaik 2007, for a review). Recent studies of capuchin monkeys (*Cebus* spp.) have provided the richest of such information for any monkey, extending to several forms of social conventions including finger-sniffing and dyadic games, and locally-varying types of foraging behaviour that include nut-cracking and fruit-processing (Otoni & Mannu 2001; Panger et al. 2002; Perry et al. 2003).

These reports rely on circumstantial evidence that genetic and environmental influences are unlikely to be responsible for the appearance of the group-specific behaviours described. However, the weakness of the field studies is that direct evidence implicating social learning, of the kind provided unambiguously through experimental manipulation of opportunities for social versus non-social learning, remains unavailable (Fragaszy 2003; Galef 2003; Laland & Hoppitt 2003). Accordingly, researchers have turned to laboratory experiments to complete studies of social learning that complement the field research.

The majority of such experiments with capuchin monkeys have converged on a

conclusion that appears at odds with that drawn from the field studies: that capuchin monkeys are not imitators and that the limited transmission of information recorded results from simpler social learning mechanisms such as social facilitation or localised stimulus enhancement, in which attention is merely drawn to relevant stimuli (Visalberghi & Fragaszy 1990, 2002). The authors of these studies have interpreted them as supporting the conclusion that monkeys do not imitate or learn *from* one another; rather, they simply learn *with* each other (Fragaszy & Visalberghi 2001; Bonnie & de Waal 2007), the presence of a conspecific merely facilitating an individual's ability to learn independently. The results of numerous experimental studies (Fragaszy & Visalberghi 2001 and Fragaszy & Visalberghi 2004 review over 30 studies) therefore appear in conflict with the inference of field researchers that group specific behaviours are culturally transmitted in capuchin monkeys, because processes as simple as stimulus enhancement would be insufficient to generate the behavioural variants documented in wild capuchins, which concern particular foraging and social behaviours rather than preferences for objects or locations.

These social learning experiments, however, have been based on dyadic tests in which a single observer watches a single, trained model (Adams-Curtis & Fragaszy 1995; Coussi-Korbel & Fragaszy 1995; and see reviews by Visalberghi and Fragaszy 1990, 2002). This is a limited paradigm for the study of culture, which requires the spread of novel forms of behaviour through a group. Our study therefore aimed to bridge the gap between dyadic experimental studies of social learning and the population-level cultural phenomena inferred in the wild, by

investigating whether brown capuchin monkeys (*Cebus apella*) are capable of transmitting a novel foraging task along a chain of individuals. Moreover, we applied a two-action paradigm (Dawson & Foss 1965; Galef et al. 1986), which controls for individual learning by having each of two alternative foraging methods performed by an initial model in front of a naive subject. The particular two-action design of this study also controls for localised stimulus enhancement by having both of the alternative, modelled foraging methods focussed on the same locus of the task (the handle of a door, which can either be lifted or slid open to retrieve food). This paradigm was further strengthened by testing three groups of individuals: one group for each method, and a third control group not exposed to a demonstrator of either method.

To address the fidelity of information transfer and the ability of a group to maintain an experimentally introduced foraging behaviour beyond the original model, we employed a diffusion chain paradigm. The diffusion chain paradigm, like the game “telephone”, involves information being transferred from one individual to the next. Although at each step in the experiment, we are again testing only a dyad, in this diffusion paradigm there is a realistic possibility for the information to be corrupted, if it is not copied exactly. If the latter occurs, the original behaviour will not spread to become a tradition. Thus, the diffusion chain simulates one ‘thread’ through a series of potential cultural transmission events.

The diffusion chain paradigm was first used with humans (Bartlett 1932) and has more recently been employed in a still-small set of studies to test the transmission of foraging, food preferences and predator avoidance in fish, birds and rats (Curio

et al. 1978; Laland & Plotkin 1990, 1992; Laland & Williams 1998). Recently, the three-group, two-action paradigm used in the current study demonstrated high fidelity transmission of alternative foraging methods along diffusion chains involving up to six steps in chimpanzees (*Pan troglodytes*), as well as in human children (Horner *et al.* 2006). It should be noted that other diffusion paradigms exist, such as ‘open diffusion’ in which a model is introduced into a whole group (Kendal et al. 2005; Whiten et al. 2007). The merit of the ‘chain’ paradigm is that it allows the course of the transmission to be known and ‘cultural generations’ showing faithful replication to be accurately counted.

Given the apparent lack of imitation in monkeys, it remains unknown whether such transmission chains would be sustained in the capuchins we studied. In the light of the experimental studies summarised above, one might instead expect corruption to occur early, since capuchins may not copy the behavioural variants seeded in their chain. The field research, however, would suggest transmission will be sustained. By employing the diffusion chain paradigm in conjunction with a two-action social learning task, it should be possible to gain further insight into the transmission processes that support group-specific cultural variation in capuchins.

## ***METHODS***

### **Subjects & Housing**

Subjects were 4 male and 10 female brown capuchin monkeys ranging in age from 3 to 30 years (median age = 5.5 years; mean age = 9). They lived in a group of 20

individuals (6 males, 11 females, and 3 infants) ranging in age from 2 months to an estimated 35 years, housed at the Centre de Primatologie of Université Louis Pasteur in France.

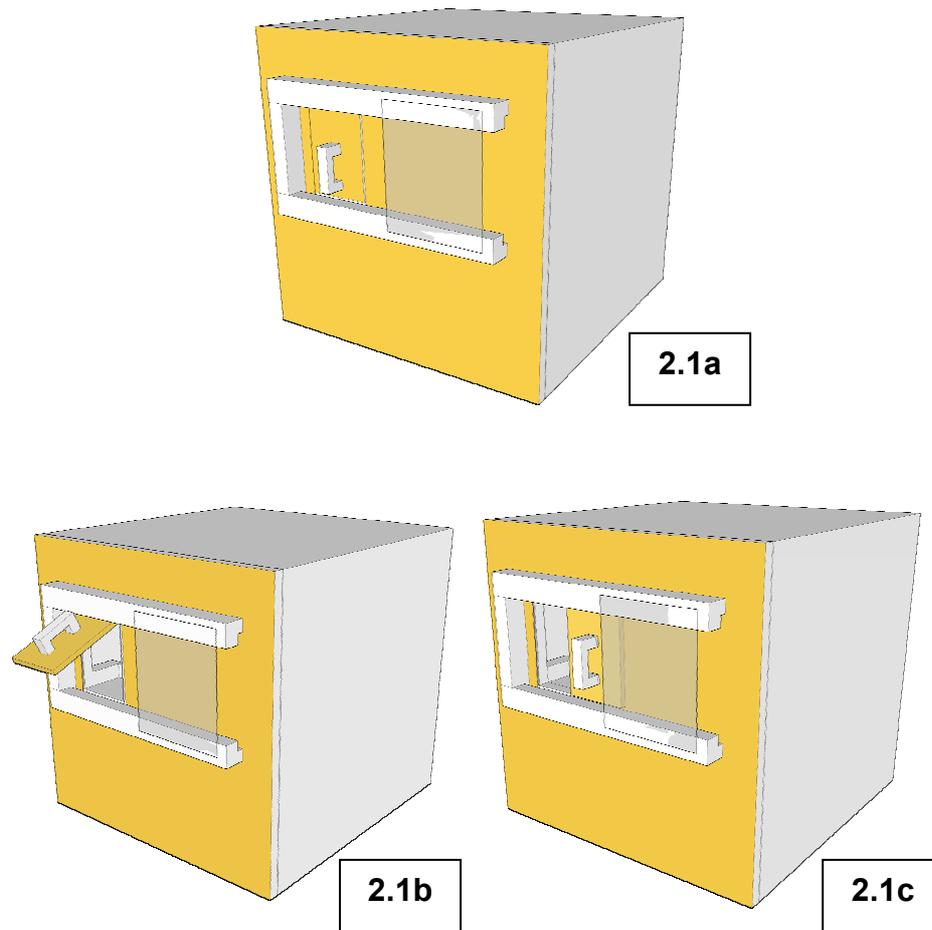
Monkeys were housed in an enclosure consisting of two indoor areas measuring 33 m<sup>2</sup> in total and three inter-connected outdoor areas measuring 45 m<sup>2</sup> in total. The outdoor enclosures were connected by 1 m long tunnels that could be closed off using sliding doors. All tests were conducted in the first outdoor enclosure area, where both subjects could move freely. A visual barrier was placed so as to prevent future test subjects from observing the test condition from the second enclosure. Each test pair was separated from their group for testing, but for no more than 30 minutes. They had *ad libitum* access to monkey chow and water and were never food deprived.

Subject pairs were selected based on observations made by the first author, focusing on social tolerance during grooming bouts and food interest interactions in pairs. The demonstrator for each test was slightly higher ranking than the observer monkey. This was done so that the model would be able to manipulate the device without being displaced by the observer. The rank difference, however, was small enough that the observer was tolerated by the model. Prior to the first test session, all pairs were given a ‘compatibility check’, to see if they could both be presented with food without conflict or displacement. This was deemed important since observer subjects had the opportunity to move about the 15 m<sup>2</sup> enclosure and avoid the model, if there was conflict.

## **Apparatus**

An ‘artificial fruit’ was constructed from Lexan and measured 28 x 28 x 28 cm. This was modelled on the device used by Horner et al. (2006), nicknamed the ‘Doorian Fruit’ (henceforth ‘the Doorian’) scaled down appropriately for capuchin monkeys. The back of the Doorian was open to allow the experimenter to insert food items. Pieces of cereal were used as the food rewards. The door could be opened by either of two actions: (1) lifting or (2) sliding (Figure 2.1). This two-action task controlled for stimulus and local enhancement because either method was possible at the same location.

Our Doorian differed from that used by Horner et al. (2006) in three small but probably important ways for our subjects. First, the Doorian was elevated to monkey shoulder-level, allowing the capuchins to explore and manipulate the apparatus with both hands more naturally while in the seated position (the chimpanzee version was lower). Second, unlike the ape version, the slide method had no spring mechanism to return the door to the closed position, so preventing the monkeys from trapping their smaller fingers in the door. The Doorian had an opening in the back, which allowed the experimenter, sitting behind it, to re-set the door to the closed position and to bait the device with food rewards. Thirdly, a protruding door handle was added so that enough surface area existed for the monkeys to use their entire hand and wrist to open the door, since they appeared less capable of the grips employed by children and chimpanzees. In these ways we contrived to make the task suitable for the known manipulative competencies of our subjects.



**Figure 2.1.** The front panel of the ‘Dorian Fruit’ apparatus was presented to subjects with the door in the closed, resting state (a). In the resting state, subjects could manipulate the door handle to open the apparatus by either lifting (b) or sliding (c) the door.

## Procedure

### Controls

To discover if both methods were similarly difficult, four subjects were presented with the Dorian without any prior training or demonstrations. These individuals were given 15 minutes to manipulate the Dorian in order to extract food rewards. If the subject was successful using either method, the box was re-baited for 20 trials. A trial terminated with food retrieval from the box using either method, or if

the monkey was unsuccessful, the control test ended after 15 minutes.

### **Model training**

Each of two models was given three training sessions spread over three separate days, with each session consisting of 20, 30 and 40 trials respectively. The range of 20-40 trials was employed in order to assess when a demonstrator became satiated. This occurred between 20-30 trials, with longer delays occurring between food retrieval attempts for trials 30-40. Because models and observers could not easily be separated after observations, satiating the demonstrator gave the observer the opportunity to go on to manipulate the Doorian. During the first training session, both models were shown their respective method by having the experimenter open the box twice. Both models were able to open the Doorian using the trained technique during the first training session after only two demonstrations.

The two models were selected based on rank. High-ranking models are most likely to be able to perform the task repeatedly without being displaced. Unfortunately, one of the models, the group's beta male, did not behave the same when paired with some individuals as had been expected from the group context. After his training, he was presented with a 'compatibility test' to see if he would allow a partner to take food from the experimenter in his presence, and he behaved antagonistically towards the partner. Therefore, this originally-intended slide model was replaced by the alpha female, who performed the slide method during her control test. She performed 80% slide (i.e. 4 lift / 16 slide) during her control test, but then later

performed 100% slide once exposed to training sessions. After three sessions of 20, 30, and 40 trials, she was considered a proficient model. Because there were a limited number of monkeys available for this study, there was one less subject in the slide group than in the lift (i.e. 1 trained model and 4 slides observers; 1 trained model and 5 lift observers).

### **Demonstration tests and observer tests**

Prior to testing, all potential test pairs were given a ‘compatibility check’ during which food was presented to the pair in the test area. The experimenter showed two hands holding food rewards and then presented this food to both monkeys with hands apart. If the dominant allowed the subordinate to take food without aggression or major displacement, the pair was considered compatible for testing.

A ‘test’ consisted of two phases. In the first phase, a subject was given the opportunity to watch a demonstrator monkey open the Doorian and collect food for a minimum of 20 trials and a maximum of 40 trials. Subjects were considered ‘watching’ when facing the apparatus within arms reach of the demonstrator. A minimum of 20 trials was set so that subjects had multiple opportunities to watch in close proximity to the demonstrator (Figure 2.2). A maximum of 40 trials was set since subjects became satiated, variably, at some point between 20 and 40 trials. Once satiated, the model stopped monopolising the Doorian, leaving the device available for manipulation by the observer monkey. In the second phase, the subject was allowed to manipulate the Doorian to search for food. If the observer

was able to open the door by using either method, and retrieve the food reward, the apparatus was re-baited for a total of 20 trials. Each observer who was able to open the Doorian became the demonstrator for the next test subject in the chain, whichever method they employed.

### **Data collection and analysis**

All tests were recorded with a Canon mini-DV video camera. The researcher also dictated the method used and whether the demonstration was watched by the observer, in case it was not clearly visible on film.

The number of lift and slide actions was recorded. The number of food-retrieval demonstrations observed by the subject, regardless of which action was performed, was recorded to assess the percent of all demonstrations observed. Because of the design of the task, coding of lift versus slide was unambiguous and only one coder was necessary; therefore, no inter-observer reliability scores are reported.

Because of the small sample sizes, non-parametric statistics were used to compare the three groups on these measures.

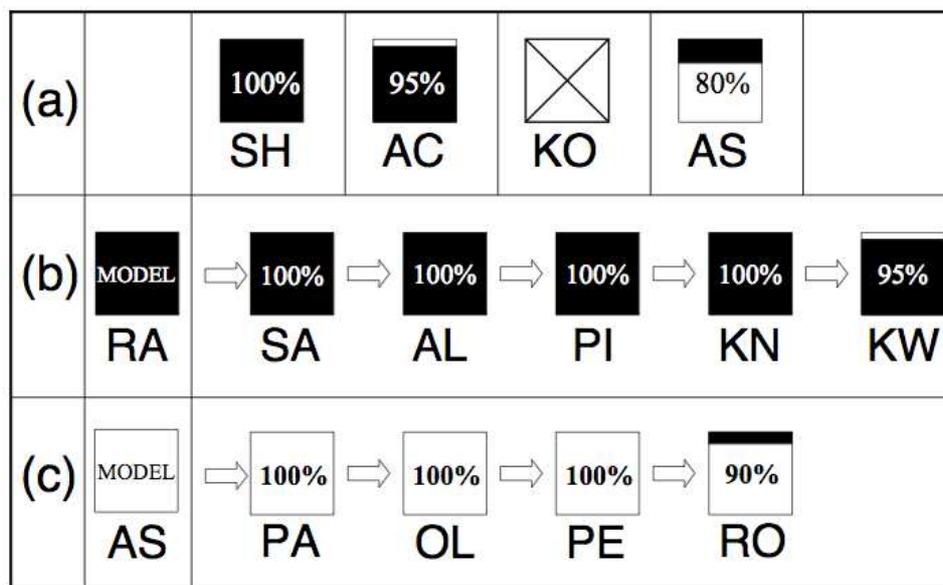


**Figure 2.2.** Subjects accessed the Doorian through the mesh of their enclosure (a). Demonstrators either lifted or slid open the door to retrieve a cereal reward that was located on a tray behind the door. Observers watched in close proximity of the demonstrating monkey (b).

## RESULTS

### Controls

The control tests demonstrated that either method was possible for at least some capuchins to discover. Of the four controls, two performed the lift method with 100% and 95% success respectively and one performed 80% slide during their respective 20 trials. A fourth subject manipulated various places including the door handle on the Doorian, but was unable to open the door and did not extract food rewards (Figure 2.3a).



**Figure 2.3.** Subjects in the Control, Lift, and Slide groups had 20 trials in which to open the door to the Doorian and extract food rewards. Control subjects were presented with the Doorian without the opportunity to observe a model. Lift and Slide subjects did observe a model for their group-specific technique. Arrows indicate the progression in the diffusion chain; each subject followed by an arrow was the model for the next subject in the chain. Each subject's test was analysed for the number of 'slide' and 'lift' actions performed and is represented here as the percent of behaviours performed by group.

## Observers

Subjects were all given between 20 to 40 demonstrations depending on how quickly the respective model became satiated. Subjects observed between 38-100% demonstrations performed by the model, with all subjects witnessing at least 10 trials (Table 2.1). Subjects were considered ‘observing’ when facing the apparatus within arm’s reach of the demonstrator. All but two observers watched 80% or more of the demonstrations. The subject who watched 49% (KN) was initially pushed away by the model (PI), but quickly tolerated after the first seven trials. The second subject who watched 38% (KW) was tolerated by the model, but preferred to forage in the gravel of the test area for part of the demonstration phase.

**Table 2.1.** The percent of model demonstrations observed by the test subjects are presented by group in the order in which subjects appeared within their respective chain.

<b>LIFT GROUP</b>		<b>SLIDE GROUP</b>	
<i>Subject</i>	% trials observed	<i>Subject</i>	% trials observed
<i>Samir (SA)</i>	90%	<i>Paola (PA)</i>	95%
<i>Alila (AL)</i>	80%	<i>Olive (OL)</i>	85%
<i>Pistou (PI)</i>	100%	<i>Petula (PE)</i>	100%
<i>Kinika (KN)</i>	49%	<i>Rosy (RO)</i>	100%
<i>Kiwi (KW)</i>	38%		

The number of food retrievals using either lift or slide was tallied for each of the 20 trials. A ‘slide’ score was then calculated for the subject between 0 and 1 based on

the number of actions performed. A score of 1 represented 20 slides (100% slides) whereas a score of 0 represented 20 lifts). In the single case of no food retrieval, and therefore no method bias, a score of 0.5, was given. A two-tailed Mann-Whitney test showed that the two chains initiated with either lift or slide methods (i.e. excluding the initial models) were significantly different in their slide score (median Lift chain = 0, median Slide chain = 1;  $Z = -2.61$ ,  $n_1 = 5$ ,  $n_2 = 4$ ,  $p = 0.01$ )

The first four lift-group observers performed 100% lift, while the last subject in the chain performed 90% lift (Figure 2.3b, with slide actions at trials 15 and 17 in a total of 20 trials). The first three slide-group subjects performed 100% slide, while the last subject in the chain performed 95% slide (Figure 2.3c), with one lift at trial 7, in a total of 20 trials. Although some corruption emerged for the last monkey in each chain, these were isolated incidents followed by responses that continued to replicate the actions of the prior monkey. It should be emphasised that chains were not terminated at this point because of these results, but because these were the maximum number of subjects available and assigned to the experimental design.

During the observer testing phase, only one subject in each test group (RO and AL) did not immediately open the apparatus; instead, they spent 8 and 24 seconds respectively feeling the front panel before acting on the door. During the control testing phase, the unsuccessful subject (KO) manipulated the Doorian, touching the handle, door, and various other parts of the device several times throughout the 15 minutes, but never opened the door.

## ***DISCUSSION***

This study demonstrates that capuchin monkeys are capable of learning a foraging technique from a conspecific demonstrator and that this process will repeat over several ‘cultural generations’ of group members. To our knowledge, this kind of finding has not previously been shown experimentally in monkeys, and adds to a small body of experiments demonstrating socially learned diffusion effects in a variety of vertebrates (Curio et al. 1978; Lefebvre 1986; Laland & Plotkin 1990; Laland & Williams 1997; Reader & Laland 2000). However, these earlier studies contrasted only a single experimental group with controls, and thus concern only a single behaviour pattern such as pecking through a paper cover to gain food (Lefebvre 1986). In such experimental designs, effects may reflect only the facilitation or targeting of existing elements of behaviour. For example, if we had used only a slide model compared with non-observing controls, a greater occurrence of ‘slide’ in the first group might be because they had discovered through observation that food was in the box and ‘slide’ came naturally to them as a means to obtain it, whilst controls remained ignorant of this opportunity. By contrast, the two-action aspect of our design shows, crucially, that some kind of copying process was at work, to provide the necessary differentiation between the replications that occurred along each chain of individuals seeded with the alternative methods.

To our knowledge, ours is the first two-action transmission chain study to demonstrate such an effect in monkeys, and indeed in any non-human species other than the chimpanzees studied by Horner et al. (2006). Moreover, the tendency of

the two individuals who discovered (possibly by accident) the alternative method to nevertheless stay faithful to the method they had observed hints at the kind of conformity to group-mates' methods described in recent chimpanzee experiments (Whiten et al. 2005). Because this concerns only two individuals this must remain a tentative interpretation at this point, but deserves more attention in future studies. Nevertheless, the fidelity of transmission we documented remains remarkable given the potential for corruption, and since one might expect that a monkey attempting to lift could all too easily accidentally discover slide, or vice versa (in both cases its hand is on the same handle).

Our study can draw limited conclusions about the social learning mechanism (or mechanisms) at work and was not designed to do so, other than controlling for processes as elementary as stimulus enhancement, by ensuring that the same handle was used to open the door by either lifting or sliding. Ruling out stimulus enhancement means that more sophisticated processes are implicated, with some capacity for copying of either actions (lift versus slide - 'imitation'), or the results of such actions (door rising, versus door sliding - 'emulation': Tomasello & Call 1997). That three of the four controls were able to solve the task by either lifting or sliding suggests that these basic capacities were available to all subjects, but channelled into one form or the other by social learning. In any case, further experiments will be needed to discriminate these, such as 'ghost' conditions in which observers see only the door move (Tennie et al. 2006; Hopper et al. 2007). Given that previous studies with capuchin monkeys have shown little evidence for imitation, we provided the capuchins with relatively straightforward tasks, which

we anticipated might be easily assimilated by them (as well as easily discriminable by the experimenter coding the tests). Further research could expand upon this to investigate more complex manipulations or sequential tasks in order to gain further insight into capuchins' copying abilities.

Whatever the precise mechanism, our two-action transmission chain study has demonstrated a capacity in capuchin monkeys for serial transmission of alternative behaviour patterns. Why we recorded so much greater copying fidelity than the majority of earlier studies with capuchins and other monkeys is not known but we suspect at least two factors may have been important. First, we took great care to modify the task in a number of respects (see Methods) so that it was well suited to the behavioural capacities of the study species; and second, we took great care to perform compatibility checks for each pair of individuals in the experimental chains. The latter may raise an alternative concern that we engineered greater tolerance than would exist for natural opportunities for cultural transmission in this species. Although the generally tolerant nature of capuchins (Ottoni et al. 2005) would appear to make this unlikely, it would be beneficial to supplement our diffusion chain study with one based on the freedom of 'open diffusion' to further examine the role of dominance.

Our study was restricted by subject availability to chains of the lengths achieved, so stands in need of further replication and, ideally, extension to longer chains as well as more naturalistic 'open diffusion' experiments in which whole groups are exposed to expert models (Bonnie et al. 2007). Nevertheless, the transmission

effects we documented are statistically robust. They are consistent with field ethologists' interpretations of their observational data, which suggest that capuchins in the wild sustain socially-transmitted traditions.

Lastly, we note that our 'compatibility checks' were essential to the success of the study. Without social tolerance between test pairs, the observer either had no opportunity or interest in maintaining a close enough distance to observe the model's actions. Future research should take into account the observer's motivations as well as possible deterrents for social learning opportunities. The next chapter investigates motivational effects for copying fidelity in capuchin monkeys.

## **CHAPTER 3:   CONDITIONAL COPYING FIDELITY IN CAPUCHIN MONKEYS**

The data in this chapter are in a paper revised and resubmitted for publication as:

**Dindo, M.**, de Waal, F. B. M., Thierry, B., and Whiten, A. Conditional Copying Fidelity in Capuchin Monkeys (*Cebus apella*).

## **CHAPTER 3: CONDITIONAL COPYING FIDELITY IN CAPUCHIN MONKEYS**

### ***INTRODUCTION***

Local, group-specific traditions have been reported in an increasing variety of animal species, including fish (Warner 1988) rats (Aisner & Terkel 1992; Terkel 1996), birds (Hinde & Fisher 1951; Lefebvre 1986; Lefebvre & Giraldeau 1994) and primates (Leca et al. 2007a; Perry et al. 2003; van Schaik et al. 2003; Whiten et al. 1999). Such reports have become particularly numerous in recent years, as long term field studies have matured (see Laland & Galef, in press, Whiten & van Schaik 2007 for reviews). Capuchin monkeys, the subjects of the present paper, have provided particularly intriguing recent evidence, with Perry et al. (2003) describing the rise, diffusion and loss of social conventions that vary between groups, and Frigaszy et al. (2004), Ottoni & Mannu (2001) and Moura (2007) describing localized patterns of nut-hammering and other forms of tool use that bear a striking resemblance to some of the cultural variations documented for chimpanzees (Whiten et al. 1999).

However, it is difficult to demonstrate convincingly in the wild that such variations are truly socially learned in the rigorous fashion possible in controlled experiments with captive animals. In monkeys, such experiments have produced a surprising plethora of negative results that appear in conflict with the conclusions of the field primatologists: reviewing numerous experimental findings, Visalberghi and Frigaszy (1990, 2002) concluded that the answer to their question “Do monkeys

ape?” was an essentially negative one for monkeys in general and for the capuchin monkeys they study in particular.

In recent years, however, some more positive evidence for capuchins’ social learning has emerged in ‘two-action’ experimental designs, in which observers are exposed to either of two different techniques, typically used to gain access to a food reward. In this approach, the extent to which observers preferentially employ the technique of whichever model they see can be rigorously measured. Dawson and Foss (1965) first used this approach to test the copying abilities of budgerigars (*Melopsittacus undulatus*). Two-action experiments have provided evidence of capuchin monkeys matching the model they see in the case of opening an ‘artificial fruit’ (Custance et al. 1999; Dindo et al. 2008), obtaining juice from a dispenser (Fragaszy et al. 2004) and using a tool to extract food from a container (Fredman & Whiten 2008). The two-action approach has similarly provided some evidence for copying in other monkey species (*Colobus guereza kikuyuensis*, Price & Caldwell 2007; *Callithrix jacchus*, Voelkl & Huber 2000).

We suggest this body of work shifts our understanding forwards, from asking simply “*Can* species ‘x’ copy?” to investigating “*When* does species ‘x’ copy?” In other words, the puzzling mixture of negative and positive findings on social learning in the literature may reflect not mysterious methodological variations among experimenters, but a learning system that is inherently conditional. Laland (2004) has recently distinguished a variety of ways in which animals may employ different ‘social learning strategies’, adaptive to local circumstances. These might

result in either positive or negative evidence of social learning according to the context.

Accordingly, we addressed a key question that remains underdeveloped in studies on capuchin traditions. Do brown capuchins focus their attention on the actions of others or do they focus on the location of food rewards when learning a food processing technique? We investigated social learning in capuchin monkeys using two different versions of a similar task, one of which we predicted would provide more evidence of social learning because the ‘two-action’ alternatives were more exclusive of each other in this case. We used a form of the two-action task called the bidirectional control procedure, in which the two alternatives are stripped down to opposing directions of movement in the apparatus. This was developed by Heyes & Dawson (1990) to study whether rats would copy the direction in which a conspecific pushed a pendulum lever to obtain food (see also Heyes et al. 1994). This particular experiment was later shown to be unexpectedly influenced by odour cues from the rat models (Mitchell et al. 1999), but it paved the way for later two-action experiments that demonstrated matching to a model in species including starlings, *Sturnus vulgaris* (Campbell et al. 1999; Fawcett et al. 2002), Japanese quail, *Coturnix japonica* (Akins et al. 1996, 2002), pigeons, *Columba livia* (Klein & Zentall 2003; Nguyen et al. 2005), budgerigars, *Melopsittacus undulatus* (Heyes & Saggerson 2002), gorillas, *Gorilla gorilla* (Stoinski et al. 2001), and common marmosets, *Callithrix jacchus* (Bugnyar & Huber 1997).

In our study, a small door panel could be moved up either the left or right arm of a V-shaped track. In Experiment 1, moving the panel up to either the left or right revealed a piece of food in a recess in the bottom of the V (Fig 3.1a). This task bears some similarity to that used by Klein & Zentall (2003) with pigeons and Hopper et al. (2008) with chimpanzees and children, where a panel could simply be slid either left or right to reveal food. Anticipating that the fidgety manipulations of capuchins might easily lead them to accidentally push both ways in such a task, we designed the V-shaped track, where sliding left or right also required upward movement, thus adding another element of effort to the task.

In Experiment 2, moving the same panel up further to the left revealed food in a recess at the top of that arm of the V, whereas moving it in the other direction revealed food at the top of the right arm. This design meant that, in Experiment 1, a small movement in the opposite direction to that an observer had witnessed could reveal the food. In Experiment 2, however, starting to move the panel up the same arm as the model has done makes it increasingly less likely that the alternative action will be employed. We predicted that this mutual exclusivity of actions in Experiment 2 would be associated with stronger evidence of social learning than the slight difference embodied in Experiment 1.

## ***EXPERIMENT 1:***

### ***METHODS***

#### **Subjects & Housing**

This experiment was conducted at two study sites, the Centre de Primatologie (CdP) in Strasbourg, France, and the Yerkes National Primate Research Center (Yerkes) in Atlanta, GA, USA.

Subjects from the CdP were 6 male and 6 female brown capuchin monkeys ranging in age from 3 to 14 years (median 5; mean 6.2). Subjects were selected from a colony of 20 individuals (6 males, 11 females, and 3 infants) and were housed in a home enclosure measuring 33 m<sup>2</sup> indoors and 45 m<sup>2</sup> outdoors. The outdoor enclosure was divisible into three sections, and all tests were conducted in one 15 m<sup>2</sup> division outside with subjects having full access to that entire area. A visual barrier prevented non-test subjects from viewing test conditions.

Subjects at Yerkes were 1 male and 3 female brown capuchin monkeys from colony A, and 1 male and 3 female brown capuchin monkeys from colony B. Yerkes subjects ranged in age from 3 to 35 years (median 22; mean 17.5). Colony A consisted of 15 monkeys (6 males, 9 females, 0 infants), and colony B consisted of 16 monkeys (4 males, 10 females, 2 infants). Both groups were housed in the same building, and were visually but not acoustically separated from each other. The combined indoor/outdoor home areas measured 25 m<sup>2</sup> (A) and 31 m<sup>2</sup> (B) respectively. Tests were conducted in a mobile chamber (144 x 60 x 60 cm), which

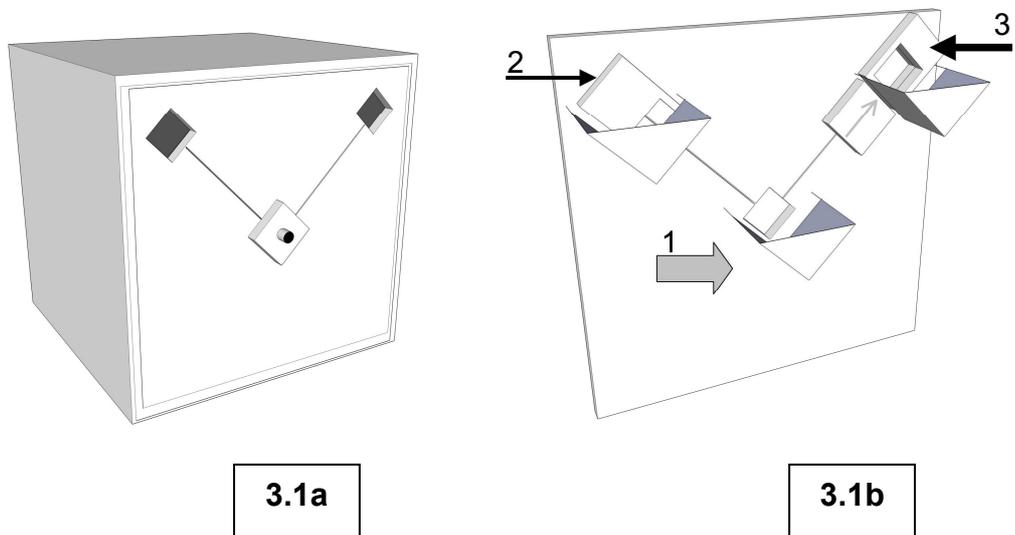
was located directly in front of the monkeys' indoor home area. This allowed for visual separation from future subjects. The separation procedure has been routinely used for several years and is documented in detail in de Waal (2000). The test chamber was divided with a mesh partition into two sections measuring 72 x 60 x 60 cm, allowing one model from each colony (A & B) to serve as a demonstrator to all subjects within his or her respective group without being displaced from the apparatus. Unlike the Yerkes colonies, the CdP subjects were not separated by a mesh partition, which meant that all test pairs had to be socially tolerant to allow observations in close proximity to the model. The limited number of subjects in the CdP colony and issues of social compatibility between certain models and observers, meant that, in addition to two trained monkey models, one control subject and two observer subjects subsequently served as models to future observers. Therefore, the total number of subjects in this experiment was 22, with 7 models, 12 observers, and 5 control subjects.

At both study sites, all tests were performed in less than 30 minutes; therefore a subject's separation from the colony was minimal. No subject was ever food or water deprived.

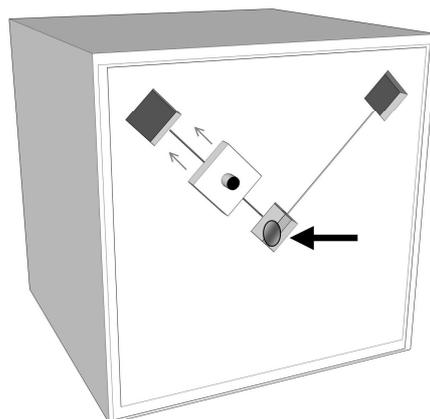
### **Apparatus (a)**

The foraging apparatus was constructed from Lexan and measured 28 x 28 x 28 cm. The front panel of this apparatus had a V-shaped sliding track, with a small handle on a square panel at the bottom centre of the V. The square panel at the bottom of

the V obscured the view of a food cup. The square's round handle allowed subjects to move the panel by sliding it up-left or up-right to retrieve food from the centre cup (Figures 3.1 & 3.2). If the subject let go of the handle, the square panel fell back into the neutral, centre position, and the hole became obscured again. For each trial, one piece of Coco-puffs cereal was placed in the cup behind the panel by the experimenter. The experimenter sat or stood facing the subject, with the subject viewing the front of the panel and the experimenter viewing the back of the panel. Each trial was defined by one food retrieval followed by the return of the door to the original (centre) location.



**Figure 3. 1.** The foraging apparatus is shown here with the door resting in the centre of the V-shaped track **(a)**. The door is covering the centre recess, and the dark shaded squares are covered by panels, which obscure the top left and top right recesses **(b)**. In Experiment 1, only the centre cup is baited (back view, arrow 1), and pins prevent the door from pushing the panels (arrows 2 and 3). In Experiment 2, the pins are removed, allowing the door to push either panel upwards and reveal food. Arrow 2 shows the panel in the closed position, and arrow 3 shows the panel being pushed open by the door.



**Figure 3.2.** In Experiment 1, a square door, which moves along a V-shaped track, can be pushed either left or right to reveal food behind the door. This figure shows the “Left Center” (LC) method for moving the square left and revealing food in the centre recess (noted by a black arrow). The shaded squares at the top left and top right of the V- track are inaccessible recesses and do not contain food in Experiment 1.



**Figure 3.3.** CdP subjects had full access to one section of their home area, and accessed the apparatus through chain link mesh (a). Yerkes subjects were separated from their group into a test chamber with access to the apparatus through circular arm holes (b).

CdP subjects accessed the apparatus through the 2.5 cm holes of the chain-link fence that surrounded their home enclosure (Figure 3.3a). Yerkes subjects accessed the apparatus through 2.5 cm round holes in the Lexan test chamber (Figure 3.3b). In both cases, subjects were able to extend their entire arm or arms through the respective barrier holes.

## **Procedure**

### **Controls**

In order to establish if the apparatus was suitable for capuchin monkeys, i.e. could they collect food from it without difficulty, and also to assess any side-bias of individual monkeys, 5 control subjects were presented with the apparatus without any prior exposure to the apparatus nor any human or conspecific model to demonstrate the left or right slide technique. Control subjects had 15 minutes, or 20 trials, in which to retrieve food from the centre location only.

### **Model training and selection**

#### **CdP models**

Two high-ranking males were selected as models for the left (LC) and right (RC) methods for uncovering food. High-ranking models were selected in order to avoid displacement at the apparatus by observer subjects.

Training consisted of three sessions of 20 trials each on three separate days. The experimenter demonstrated for the model twice, and then held the door open for the model. Once the model reached for the cereal piece, the door was released, requiring the model to hold it open while extracting the food from the hole.

Models were considered proficient for demonstration sessions after three sessions in which the model exclusively used the trained method. Due to rank and social compatibility issues, these two models were only compatible with subjects close in rank. Therefore, after their first session as a model, they had to be replaced by slightly lower-ranking models. Dindo *et al.* (2008) address the issue of model-observer compatibility in greater detail. The first observer subject in the RC group became the model for the second observer, and that second observer, in turn, became the model for the third observer subject in that group. In the LC group, a control subject was trained in the same manner as the original models on the 'left' method. This model served as the model for the second and third observers.

### **Yerkes models**

One monkey from each Yerkes group was trained as a model for the LC and RC methods. The LC model was the alpha-female of group A, and the RC model was the beta-male of group B. Given problems with one of the high ranking male models in the CdP group, the sex of the Yerkes model was less of a concern than selecting a model who was both high ranking and tolerant to group-members watching in close proximity. Both models were trained in the same way as the CdP

models, with three days of 20 trials each. Because a mesh partition could be placed between models and observers, these two models were able to act as demonstrators to all three observers in their respective groups.

### **Demonstration sessions and observer tests**

Each test consisted of two parts: (1) demonstration session and (2) observer test. At both study sites, the model demonstrated his or her method (LC or RC) to a naïve observer monkey for 40 trials. Each demonstration trial consisted of the model opening the door by sliding up left or up right and collecting one piece of cereal from the cup located behind the sliding door. Once the model let the door fall back into the centre location of the V, the experimenter re-baited the cup with one piece of cereal. Only one method was demonstrated by the model although both methods were always possible.

At the CdP the subject had the opportunity to watch all 40 trials while standing next to the model. The subject also had the opportunity to explore the 15 m<sup>2</sup> enclosure instead of watching the demonstrations; therefore 40 trials were presented to ensure that at least 20 trials would be observed. At Yerkes, subjects were presented with the first 20 trials from behind the mesh divider (<60 cm from the model; see Figure 3.3b). After 20 trials, the observer moved to the other side of the mesh partition (alongside the demonstrator). This was done to ensure that they would have at least 20 trials to watch without displacement of (or by) the model and to provide the same level of proximity to the model as the CdP subjects had.

After the demonstration sessions (40 trials total), the box was taken away from the model and presented to the observer subject. At the CdP, this involved moving the demonstrator to the adjacent home enclosure area. At Yerkes, the model and observer were once again separated by the mesh partition.

For the observer tests, subjects exchanged places with the model so that they were presented with the apparatus in the same location as where they witnessed the demonstration sessions. Subjects were given 20 trials in which to collect food, and both methods were always possible. The experimenter showed the subject a Cocopuff reward before placing the food in the collection cup. The cup was re-baited if a subject slid the door, collected the food, and then returned the door to the neutral position. If a subject were unable to open the device, the test ended after 15 minutes.

### **Data collection and analysis**

All tests were recorded using a digital video camera. The first author dictated the method used, and whether or not the observer watched the demonstration. A subject was considered to be ‘watching’ when he or she was facing the apparatus and model. Due to the experimenter’s proximity to the monkeys, eye gaze was also monitored as a distinguishable sign of ‘watching’.

Tapes were coded (1) for the number of trials out of 40 in which the subject was considered watching and (2) for the number of left slides or right slides performed during the total 20 test trials (Table 3.1). The latter has the advantage that coding was unambiguous for all cases where food was obtained. Inter-observer reliability in coding was analysed using Cohen's kappa. Kappa for the agreement of trials watched or not watched was 0.945, indicating strong agreement.

## ***RESULTS***

### **Controls**

All five control subjects interacted with the foraging apparatus by touching the front, top and sides of the box and by touching the handle to the door behind which food was obscured. Two subjects, an adult male and an adult female, never discovered the upward-slide movements necessary for retrieving food despite manipulating the door of the apparatus. One adult female collected food using the LC method for 17 out of 20 total trials (85% left). Another adult female and a juvenile male used the RC method for 20 and 15 trials out of 20 respectively (100% and 75% right).

### **Demonstration sessions**

Each test subject was presented with one demonstration session consisting of 40 trials in which the model demonstrated either the LC or RC method for obtaining food from the foraging apparatus. Models exclusively demonstrated either the LC

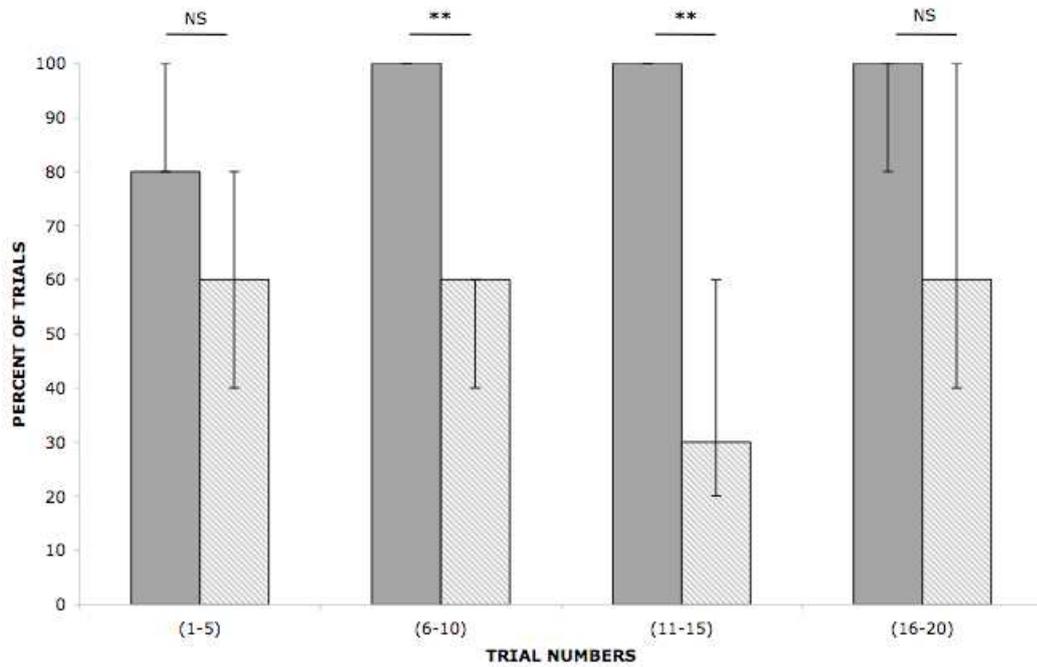
or the RC for all 40 trials. Subjects in the LC group observed between 72% and 100% of the 40 trials (median 86%,  $n = 6$ ). Subjects in the RC group observed between 77% and 100% of the 40 (median 89%,  $n = 6$ ) trials observing the demonstrations (Table 3.1). There was no significant difference between the LC and RC subjects in the time spent observing the model (Mann-Whitney Test, two tailed,  $U=13$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.462$ ).

### **Test sessions**

After observing the demonstration session, each subject was presented with the foraging apparatus and was allowed to manipulate the device using either method for a total of 20 trials. Each subject's performance was coded "L" or "R" for the method used in each trial. A 'left-bias' score was calculated for the number of left actions out of 20 that each subject performed using the equation,  $N = L/(L+R)$ . A score of 0 represented 0 out of 20 left slides (20 out of 20 right slides), and a score of 1 represented 20 out of 20 left slides (0 out of 20 right slides). A low score thus represented a right-bias, a high score represented a left-bias, and a score of 0.5 represented no bias (10 right and 10 left). The median score for the six LC subjects was 0.9 (range 0.7 - 1), and the six RC group subjects had a median left-bias score of 0.1 (range 0 - 0.3) (Table 3.1). A two-tailed Mann-Whitney Test showed a significant difference between the method scores of subjects in the LC versus RC groups ( $U=0$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.004$ ). Further analysis determined that Experiment 1 subjects showed significant differences within the first 5 trials (Mann-Whitney

$U=3$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.03$ ), but not for the first trial alone (Binomial test:  $p = 0.146$ ).

In order to assess the overall copying trends in both LC and RC conditions, each trial was also coded as ‘matching’ or ‘non-matching’ to reflect the number of trials out of 20 in which a subject’s method corresponded with the method of the model. The median percent of matched behaviours for the 12 subjects (i.e. both groups) was broken down into 5 trial increments (1 to 5, 6 to 10, 11 to 15, and 16 to 20). This breakdown shows that a high copying fidelity was consistent throughout the 20 trials, with very little range in inter-quartile values by increment (Figure 3.4). Only 3 of the 12 subjects did not use the modelled method in the first trial (Table 3.1); however, these subjects continued to show a strong bias for the method they had observed and did not continue with the alternative method they had discovered, suggesting that the bias was not due to trial-and-error learning.



**Figure 3.4.** Median and inter-quartile ranges for 'matched' behaviours in Experiment 1 (grey bars: Centre condition) and 2 (striped bars: Sides condition) for trials 1-5, 6-10, 11-15, and 16-20. Significant differences of  $p < 0.005$  are marked with two stars.

**Table 3.1.** This table shows the individual results by subject for each group in Experiments 1 and 2. The rate of observation is shown as a percentage of the total 40 demonstrations they observed the model. The left-bias score represents the amount of left actions performed during the subject's 20 trials, with a 0.00 representing no left actions and 1.00 representing all left actions. The 'per cent trials matched' column shows the degree of fidelity to the model's method, and the last column specifies at which trial the subject first matched the behaviour of the model and at which trial the subject used the opposite method than the model [shown in brackets]. An 'x' is put in the place of a trial number when subjects never matched or mismatched the group method.

### **Experiment 1**

left group				
subject	per cent trials observed (%)	left-bias score (0-1)	per cent trials matched' (%)	trial number of 1st match
<i>Lulu (LU)</i>	94	1	100	1 [x]
<i>Winnie (WN)</i>	72	1	100	1 [x]
<i>Winter (WT)</i>	77.5	0.75	75	1 [5]
<i>Raven (RA)</i>	100	0.9	90	2 [1]
<i>Alila (AL)</i>	76.7	0.95	95	1 [5]
<i>Kinika (KI)</i>	100	0.7	70	2 [1]
right group				
subject	per cent trials observed (%)	left-bias score (0-1)	per cent trials matched' (%)	trial number of 1st match
<i>Georgia (GE)</i>	77.5	0.25	75	4 [1]
<i>Snarf (SN)</i>	95	0	100	1 [x]
<i>Mango (MG)</i>	100	0.1	90	1 [4]
<i>Popeye (PO)</i>	83	0.3	70	1 [12]
<i>Paola (PA)</i>	100	0.05	95	1 [4]
<i>Olive (OL)</i>	80	0	100	1 [x]

### **Experiment 2**

left group				
subject	per cent trials observed (%)	left-bias score (0-1)	per cent trials matched' (%)	trial number of 1st match
<i>Lancey (LA)</i>	50	0	0	X [1]
<i>Nicole (NI)</i>	85	0.4	40	2 [1]
<i>Wilma (WL)</i>	94.5	0.45	45	4 [1]
<i>Wookie (WO)</i>	75	0.9	90	2 [1]
<i>Lucas (LC)</i>	100	1	100	1 [x]
<i>Ike (IK)</i>	57	0.95	95	1 [6]
right group				
subject	per cent trials observed (%)	left-bias score (0-1)	per cent trials matched' (%)	trial number of 1st match
<i>Bias (BI)</i>	60	0.65	35	3 [1]
<i>Bravo (BR)</i>	70	0.3	70	2 [1]
<i>Goya (GY)</i>	80	1	0	X [1]
<i>Bailey (BA)</i>	90	0.55	45	1 [2]
<i>Star (ST)</i>	100	0.25	75	1 [9]
<i>Gretal (GR)</i>	100	0.65	35	1 [4]

## ***EXPERIMENT 2:***

### ***METHODS***

#### **Subjects & Housing**

Experiment 2 was conducted entirely at the Yerkes National Primate Research Center. Subjects were 3 male and 4 female brown capuchin monkeys from colony A (Nuts group) and 2 male and 5 female monkeys from colony B (Bolts group). The subjects ranged between 3 and 35 years in age (median 8; mean 12.9). The models were the same Yerkes individuals that served as models in Experiment 1, however the observers were new subjects that were completely naïve to the experimental conditions.

Tests were conducted in the same mobile test chamber as in experiment 1 and the same separation procedure was employed.

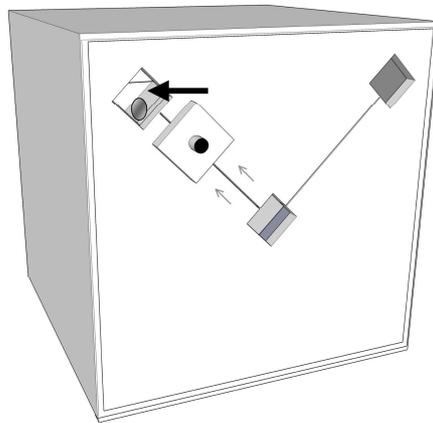
#### **Apparatus (b)**

The same foraging box (see *apparatus (a)*) had two additional locations for obtaining food: top-left end (TL) and top-right end (TR) of the V-track (Figure 3.5).

In experiment 2, the centre square panel at the bottom of the V could be pushed up-left or up-right to retrieve food from cups in the top ends of the V. Just as in experiment 1, subjects could still slide the centre panel left or right at any time, however no food was revealed in the centre square. Instead, food was located in

both the top-left (TL) and top-right (TR) cups (Figure 3.5). When the centre panel was moved left, it revealed food by pushing away a panel in front of the TL cup. When the subject moved the sliding panel right, it revealed food in the TR cup. In this experiment, the movement made by the subject was directly linked to where the food would become available.

One piece of cereal was placed in each TL and TR cup prior to every trial, but only one food retrieval was permitted per trial. Each trial was defined by one food retrieval followed by the return of the door to the neutral (centre) location. No food was placed in the centre hole, and all subjects in Experiment 2 were naïve to the conditions of Experiment 1.



**Figure 3.5.** In Experiment 2, the top “Left Side” (LS) and top “Right Side” (RS) recesses contain food and the centre recess is empty. The apparatus is shown here when the square door is pushed from the centre position to the left, thus pushing the panel that covers the top left recess (as noted by a black arrow).

## **Procedure**

### **Model training and selection**

The LC and RC models from experiment 1 became the left-side (LS) and right-side (RS) models for Experiment 2. Training involved two experimenter demonstrations, after which the model was able to extract food from the top-left (TL) or top-right (TR) location depending on which method he or she was shown. The model was considered proficient when he or she used only the LS or only the RS method for three sessions of 20 trials (on separate days).

### **Demonstration sessions and observer tests**

The conditions for demonstration sessions and observer tests were the same as in Experiment 1, as were the data collection and coding processes.

## ***RESULTS***

### **Demonstration sessions**

Each test subject was presented with one demonstration session consisting of 40 trials in which the model demonstrated either the LS or RS method for obtaining food from the foraging apparatus. Subjects in the LS group observed between 50% and 100% of the 40 trials (median 80%,  $n = 6$ ). Subjects in the RS group observed between 60% and 100% of the 40 trials (median 85%,  $n = 6$ ) observing the demonstrations (Table 3.1). There was no significant difference between the LS and RS subjects in the time spent observing the model (Mann-Whitney Test, two tailed,

$U=14.5$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.519$ ). No significant difference was found between observation rates of Experiment 1 and 2 subjects (Mann-Whitney, two tailed,  $U=54$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.327$ ).

## **Test sessions**

As in Experiment 1, each subject's performance was coded "L" or "R" for the method used and a 'left-bias' score was calculated for the number of left actions out of 20 that each subject performed using the equation  $N = L/(L+R)$ . The median score for the six LS subjects was 0.7 (range 0 - 1) and the six RS group subjects had a median left-bias score of 0.6 (range 0.25 - 1) (Figure 3.4). It was predicted that subjects would show a bias towards the method observed, therefore a two-tailed Mann-Whitney test was used to analyze the left-bias results between LS and RS. Unlike Experiment 1, subjects in Experiment 2 did not show a significant bias during the 20 total trials towards the method they observed ( $U=16$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.818$ ). Experiment 2 subjects did not even show significant differences in the first 5 trials (Mann-Whitney  $U=12$ ,  $n_1=6$ ,  $n_2=6$ ,  $p = 0.485$ ) or in the first trial (Binomial test:  $p = 0.774$ ).

In order to assess the overall copying trends in both LS and RS conditions, subject trials in both LS and RS groups were scored as 'matching' or 'non-matching' by trial for all 20 trials of their respective test. The percent of trials that 'matched' the behaviour of the model were again broken down by trials 1 to 5, 6 to 10, 11 to 15, and 16 to 20 in order to distinguish when fidelity to the modelled method was

strongest. The median and inter-quartile ranges for all 12 subjects were calculated for these intervals and reported alongside Experiment 1 results (Figure 3.4). Subjects showed no significant difference in copying behaviour in the first trial of Experiment 1 (Mann-Whitney Test, two-tailed,  $U=48$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.105$ ), nor was there a significant difference in the number of matched behaviours in the first 5 trials between Experiments 1 and 2 (Mann-Whitney Test, two-tailed,  $U=46$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.121$ ). Significant differences in the level of copying (i.e. median matched behaviours) become apparent when comparing the trials 6-10, and 11-15, but not for the last trials 16-20 (Mann-Whitney, two-tailed (6-10),  $U=17$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.001$ ; Mann-Whitney, two-tailed (11-15),  $U=18$ ,  $n_1=12$ ,  $n_2=12$ ,  $P=0.001$ ; Mann-Whitney, two-tailed (16-20),  $U=46$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.101$ ).

Figure 3.4 shows the clear trend for copying in Experiment 1 relative to Experiment 2, contrary to our original prediction. This difference in copying might be explicable in part by variations in copying fidelity early in the first few trials, i.e. at which trial the first matching, and non-matching responses occurred (see Table 3.1). However there is no significant difference between Experiment 1 and Experiment 2 in the first trial number in which matching or non-matching occurred (1<sup>st</sup> matched trial: Mann-Whitney, two-tailed,  $U=45$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.08$ ; 1<sup>st</sup> unmatched trial: Mann-Whitney, two-tailed,  $U=41$ ,  $n_1=12$ ,  $n_2=12$ ,  $p = 0.07$ ; Table 3.1 x-values were given the value 20).

## ***DISCUSSION***

Following the rationale explained in our introduction, we had predicted that fidelity of social learning would be greater in Experiment 2 than Experiment 1. However, we found the reverse. Only in Experiment 1 was there evidence of social learning. Indeed, the fidelity in Experiment 1 was strong, extending through the whole sequence of 20 trials in both the Left Centre (LC) and Right Centre (RC) conditions. Although we had anticipated that this effect might be weak compared to Experiment 2, the results are in fact consistent with those reported recently by Hopper et al. (2008) for chimpanzees, where fidelity to the direction of push by a conspecific model was as high as 99%, even though the two alternative actions tested differed on only a single dimension (push left versus right). As noted in our introduction, we designed our two-action task in the shape of a 'V' such that the alternative options differ in more than one dimension, so that initiating one is inherently less likely to occasion the other inadvertently. Accordingly, against the background of Hopper et al.'s results, our own is less surprising, except that it concerns capuchins, a species for which prior research has shown little evidence of faithful copying (Visalberghi & Fragaszy, 2002).

More generally, the results of Experiment 1 are thus important in that they extend the growing evidence that monkeys may, at least in certain contexts, copy with more fidelity than previously thought (Bonnie & de Waal 2007; Dindo et al. 2008; Fredman & Whiten 2008; Price & Caldwell 2007; Rigamonti et al 2005; Voelkl & Huber 2007). Whether this copying involves bodily imitation is another matter, and beyond the scope of our study. The copying we documented might have

involved copying the bodily actions of the model (bodily imitation) or the movements of the panel (emulation or object movement re-enactment) or some mixture of these; further experiments such as ‘ghost’ manipulations, in which the panel moves without a model pushing it (Hopper et al. 2008), will be needed to differentiate such mechanisms.

By contrast with Experiment 1, Experiment 2 revealed only a weak and non-significant initial trend consistent with copying; the monkeys in this Experiment explored both food locations through the 20 trials. One possible explanation we need to consider for this variation in copying fidelity between experiments 1 and 2 is that less attention was paid to the model in the second experiment. Resende and Ottoni (2002) reported that their capuchin monkey subjects did not copy the actions of a trained model in a foraging task, but that it was unclear how many of the demonstrations were observed; perhaps relatively few, because of social intolerance maintaining a distance between subjects and models. Rigamonti et al. (2005) reported that macaques showed less copying fidelity than their child-subject counterparts, with the macaques watching an average of only 60% of trials whereas the children watched over 80%. In another social learning study by the same collaborators, observations by pig-tailed macaques are described as “limited and sporadic” (Custance et al. 2006, p. 311). It was therefore important we document attention in our two experiments. However, we found that the median percentage observation time was similar in both experiments (86 and 89% in Experiment 1, 80 and 85% in Experiment 2). These high levels of attention cannot explain the lack of matching behaviour in Experiment 2. Instead, what appeared to happen in

Experiment 2 was that once monkeys explored both directions of movement, and once they thus discovered that food might be available in either location at the ends of the ‘V’, they maintained a steady tendency to examine both, across the 20 trials.

Was it then the case that the monkeys anticipated that the second location might hold food, in Experiment 2? Evidence for that possibility would be that they switched between the matching response and a non-matching one earlier in Experiment 2 than in Experiment 1. However, that was not the case (Table 1): in Experiment 2, 7 monkeys already tried the non-matching response in the first 5 trials, but as many as seven also did so in Experiment 1. In Experiment 2, 11/12 monkeys explored the non-matching option, but so did 8/12 in Experiment 1. Thus it appears that despite capuchin monkeys’ capacity and motivation for social learning revealed in Experiment 1, this species also maintains a motivation to take the risk of occasionally exploring alternatives, a strategy that may well be adaptive under natural conditions. Given that in Experiment 2, this led to discovery of the two possible food locations, we conclude that these monkeys were pursuing an adaptive strategy, in continuing to check both locations rather than stick to the direction of push used by the model.

However, this leads us back to Experiment 1, to question why the monkeys did not also push in both directions, given that here, too, they had discovered doing this provided equivalent rewards. We conclude that capuchins’ copy conditionally, and our experiment revealed the rules ‘when alternative options do not gain more, or a different, reward, copy what others are doing’ (Experiment 1) and ‘when alternative

options yield rewards at different locations (Experiment 2), keep checking both, irrespective of whichever others prefer'. These can be considered adaptive social learning rules, or strategies, of the kind that Laland (2004) urged researchers to search for. Such rules embody a degree of rationality, insofar as although monkeys could have pushed randomly and gained equivalent rewards in Experiment 1, they acted as if reasoning that nothing would be gained by doing so, and instead conformed with what the model did. An interesting question that remains, is whether some tendency to conform might emerge in the Experiment 2 context if the monkeys repeatedly saw a model push on only one side, in between their own attempts. This would require a different population of monkeys for testing.

In conclusion, what our results show most importantly is that monkeys' social learning can be highly context dependent. It is possible that this may help explain some past controversies over whether primates do or do not imitate. Our results bring the monkey findings into a closer conjunction with recent studies with apes and human children that have demonstrated marked context sensitivity in the occurrence of imitation (Buttelmann et al. 2008; Gergely et al. 2002; Horner & Whiten 2005; Schweir et al. 2006). It seems that now our principal research question should no longer be, "*Do* monkeys copy the actions of others?" but instead "*When* do monkeys copy, or not, and *why*?".

The next chapter aims to address social facilitation, a form of social learning that is often assumed to be influential in the learning process for capuchins, but is rarely tested for specifically.

## CHAPTER 4: SOCIAL FACILITATION OF EXPLORATORY FORAGING BEHAVIOUR IN CAPUCHIN MONKEYS

The data in this chapter are in a paper are in press:

**Dindo, M.**, Whiten, A., and de Waal, F. B. M. (in press). Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology*.

## **CHAPTER 4: SOCIAL FACILITATION OF EXPLORATORY FORAGING BEHAVIOUR IN CAPUCHIN MONKEYS**

### ***INTRODUCTION***

Historically, the study of social learning and culture in animals has concerned itself with cognitively complex mechanisms of social learning, with particular emphasis on imitation. This has been particularly true in primatology (Tomasello and Call 1997; Whiten 2000). However, recent advances in the study of cultural diffusion and behavioural innovation in animals are beginning to shed light on a more basic aspect of cultural propagation, that of individual differences in motivational states (Kendal et al. 2005; Huber et al. 2001; Laland & Reader 1999; but see Reader & Laland 2001 for review). Zajonc (1965) suggested that an individual's motivational state might be inhibited by the "mere presence" of another individual. Social presence alone has been shown to have an effect on the behaviour of other individuals, but not only in inhibiting behaviours; in some cases, the mere presence of a conspecific can increase an individual's motivational state and therefore also enhance its interest in engaging in a behaviour (Addessi & Visalberghi 2001; Galloway et al. 2005; Thorpe 1963; Voelkl et al. 2006). This phenomenon is commonly referred to as *social facilitation* and is considered to be an important social mechanism for group-living species, including humans, because of its potential contributions to such significant outcomes as group cohesion, behavioural coordination, foraging efficiency, and predator avoidance (Boinski & Garber 2000; Caro & Hauser 1992; Chalmeau & Gallo 1993; Frigaszy et al. 1994; Coussi-Korbel & Frigaszy 1995).

Ueno (2005) found that infant and juvenile Japanese macaques (*Macaca fuscata*) engage in synchronous feeding behaviour when other group members are feeding within 1m of them. This kind of synchronous behaviour is thought to provide ideal observational learning opportunities for acquiring information about palatability, preference and processing of novel foods. This may be important for Japanese macaques, who exhibit group-specific traditions such as wheat or potato washing, and stone handling (Huffman and Quiatt 1986; Huffman 1996; Kawai 1965), as well as for a number of other species that increase and coordinate feeding in the presence of other feeding conspecifics (fish, Pitcher & Parrish 1993, Laland & Williams 1997, Reader et al. 2003; monkeys, Galloway et al. 2005; chickens, Tolman 1964; Keeling & Hurnik 1993; dogs, James, 1953, Ross & Ross 1949; pigs, Hsia & Wood-Gush 1984; and hyenas, Yoerg 1991).

With regards to cultural learning, however, the effects of social facilitation are largely ignored in the primate literature in favour of a more distinctive and cognitively complex form of social learning, namely imitation. It has been argued that along with language and the ability to teach, the ability to imitate others is at the heart of human cultural complexity. Evidence for imitation and complex culture in apes has strengthened this view that imitation is the ‘holy grail’ of cultural learning (Matheson & Fragaszy 1998; van Schaik 2003; Whiten et al. 1999; Whiten et al. 2005). While the significance of imitation cannot be doubted, it also remains unclear what alternate forms of social learning contribute to, or possibly even inhibit, the development of group-specific behaviours, particularly with

regards to cultural variation in populations of monkeys. Monkey species such as Japanese macaques and white-faced capuchins (*Cebus capucinus*) exhibit culturally distinct behaviours across wild populations (Leca et al. 2007a; Nahallage and Huffman 2007) yet experimental evidence has suggested that they, and other monkey species, rarely imitate conspecifics the way apes and humans may do (Adams-Curtis & Fragaszy 1995; Fragaszy & Visalberghi 2004; Visalberghi & Fragaszy 2002). Although more recent examples of imitation in marmosets and capuchins are emerging, these examples are much less frequent than those in apes and suggest less complexity in copying (Bugnyar & Huber 1997; Dindo et al. 2008; Fredman & Whiten 2008; Voelkl & Huber 2007). For this reason, studying social learning in monkeys should take account of the “collective outcome of interacting physical, social and individual factors” (Fragaszy & Visalberghi 2004, p. 24).

It seems that along with our growing understanding about the kinds of copying that allow certain behaviours to spread throughout a group (e.g. imitation, emulation, and object movement re-enactment), we must also begin to explore the social contexts that support opportunities in which social learning can occur. Social facilitation remains remarkably under-represented in the literature despite its strong potential for supporting the transmission of behaviour through group-cohesion (i.e. increasing opportunities for learning), and behavioural coordination (i.e. synchrony that leads to matching or copying of behavioural activities). King (1994) suggested that synchrony of feeding will result in individuals consuming the same foods because of the close distribution of food patches. Similarly, Galef (1993) argued that if social facilitation influences an individual’s motivation to consume familiar

food in the presence of another feeding conspecific, then this presence will be even more significant to whether or not an individual is willing to accept a novel food. While this may be in part due to a reduction in neophobia to the novel food item, it may also be a result of an increase in motivation to eat (Ferrari et al. 2005; Harlow & Yudin 1933; Visalberghi & Addessi 2000).

The present study of brown capuchin monkeys (*Cebus apella*) aimed to study differences in individual motivation for learning a new foraging task in the presence or absence of a feeding conspecific. Dindo and de Waal (2007) found that capuchin monkeys increase their collection and consumption of a low-valued food when in the presence of a feeding conspecific, regardless of what quality of food the conspecific is eating. Furthermore, when food is present, but the conspecific cannot access or eat the food, capuchins will consume their food at rates similar to when they are alone, rates that are significantly lower when compared with the joint feeding condition. Other studies in capuchin monkeys (Addessi & Visalberghi 2001; Galloway et al. 2005) have found similar effects of social facilitation of food consumption, suggesting that capuchins are highly sensitive to the presence of feeding conspecifics, and that their own motivational state may be significantly enhanced by the mere presence of feeding individuals. A recent study of white-faced capuchins found they are socially motivated to engage in fur-rubbing, a behaviour that appears to promote group cohesion and behavioural coordination (Meunier et al. 2007).

Given the strong evidence for social facilitation in capuchins for behaviours already in their behavioural repertoire, we were interested to see if this enhancement of their motivational state would translate to an increased motivation for exploratory behaviour and potential discovery of a new foraging technique. To test this, we designed an apparatus that could be manually manipulated to release visible food from behind a barrier. This task required several directional pushes, and therefore required an individual to spend time prodding the apparatus. We presented subjects with this apparatus either (1) in the absence of a conspecific, or (2) in the presence of a feeding conspecific who had food, but did not have to work for the food. We predicted that subjects would increase their exploratory foraging behaviour and therefore learn to extract food from the apparatus faster in the social feeding condition than in the alone condition.

## ***METHODS***

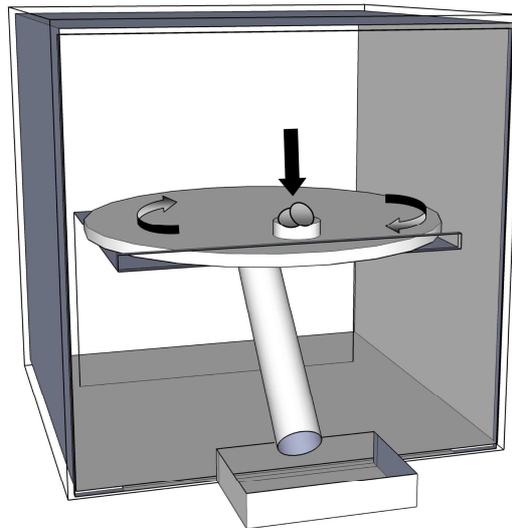
### **Subjects & Housing**

Subjects included 24 brown capuchin monkeys housed at the Yerkes National Primate Center in Atlanta, GA, USA. The capuchins ranged in age from 2 – 40 years old (median 7 years) and belonged to two separate colonies of 15 (A) and 15 (B) monkeys (Table 4.1). The indoor and outdoor home enclosures for each colony measured 25m<sup>2</sup> (A) and 31m<sup>2</sup> (B) in total. Subjects had access to lab chow and water ad libitum and were never food or water deprived. The experimental conditions, foods presented, and subjects included in this study were all approved by the Institutional Animal Care and Use Committee (IACUC) of Emory

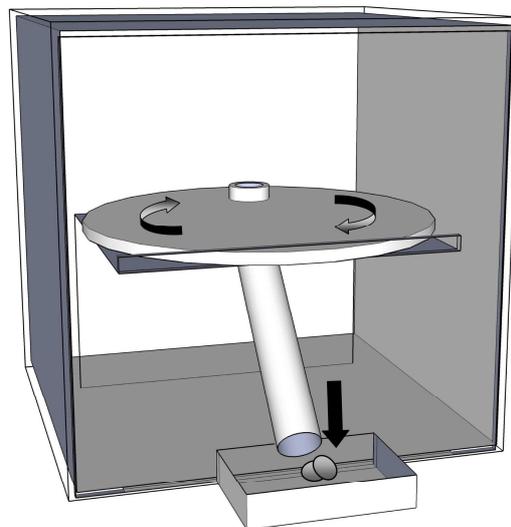
University prior to the start of the study, which was conducted from May 21 to June 25, 2007.

## **Apparatus**

The apparatus used in this study was made of clear Lexan and measured 28 x 28 x 28 cm. The front panel (28 x 28 cm) had a 13 cm horizontal incision located 13 cm above a small food cup. Protruding from the incision was a clear Lexan wheel that measured 18 cm in diameter and had a 2 cm diameter hole (at the 6 o'clock position for the monkey's perspective) in which food rewards were placed (Figure 4.1a). Below the hole was a support panel; food would not fall through this until the wheel was rotated to where the hole lined up with a chute (at the 12 o'clock position), which released the food into the small food cup (Figure 4.1b). Brightly coloured Trix® cereal was used as a food reward so that it was clearly visible through the front panel. The wheel could be rotated by pushing left or right on the protruding piece on the front panel. The back of the box was open, so that the experimenter could bait the hole with food rewards and rotate the wheel back to the 'start' position. The start position is defined by having food presented where the subject could see the food baited in the hole at the 6 o'clock position (Figure 4.1a).



4.1a

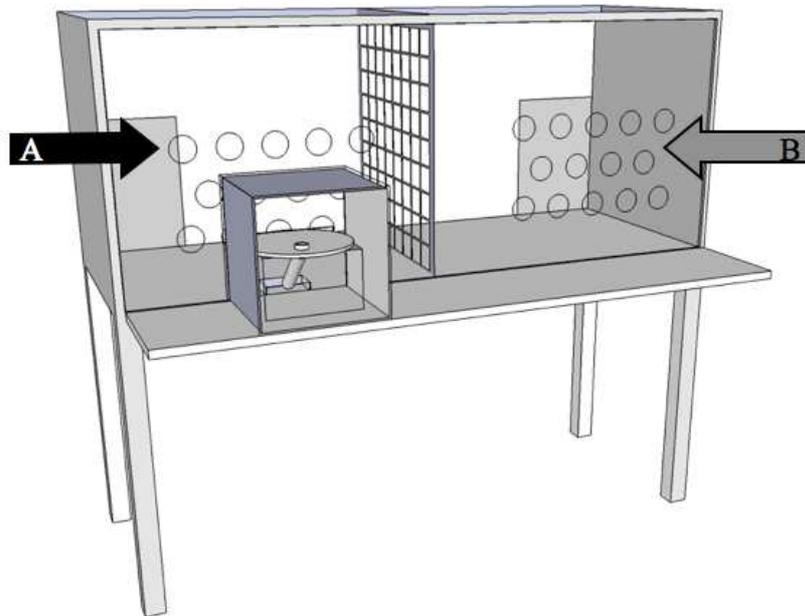


4.1b

**Figure 4.1.** The figures (a & b) show the apparatus as it was presented to the subjects. A small surface of the wheel extended out through the front panel, allowing it to be rotated when pushed either left or right. The black arrow in **Figure 4.1a** shows the food behind the clear front panel in the 6 o'clock start position. The side arrows indicate that the wheel can be rotated to line up with the chute at the 12 o'clock position. Once the food is rotated to the 12 o'clock position, it lines up with a hole and falls down the chute into the presentation cup (as indicated by the black arrow in **Figure 4.1b**).

## Procedure

Test subjects were separated from their group by a familiar and routine procedure that lasted no more than 30 minutes. Tests were conducted indoors in front of each respective group's home enclosure in a test chamber measuring 144 x 60 x 60 cm (Figure 4.2). A mesh partition was inserted into the test chamber to create two compartments of 72 x 60 x 60 cm. All subjects were tested in the left compartment. The back of the test chamber was opaque to prevent group members from viewing the test condition and apparatus. The front of the test chamber was made of clear Lexan panelling with 2.5 cm armholes through which the monkeys could manipulate the apparatus and collect food. All subjects were well habituated to being in the test chamber for testing, both alone as well as with another test partner. Therefore, any potential stress from separation was considered negligible.



**Figure 4.2.** The test chamber is shown here, divided into two sections by a mesh partition. In both the 'alone' and 'social' conditions, the subject was presented with the apparatus in section A (black arrow). In the 'alone' condition, section B (grey arrow) remained empty, while in the 'social' condition, a feeding monkey was in section B.

### **Alone and Social Conditions**

Twelve subjects from each colony were randomly assigned to either the *alone* or *social* condition, so that each condition had 12 subjects, with 6 subjects from each colony. A weather disruption prematurely ended one test in the social condition, thus this subject's data were not included here and overall subject numbers were reduced to 23.

In the alone condition, one test subject was alone on the left side of the test chamber, while the right side remained empty. The experimenter presented the subject with the apparatus by placing it on a tray in front of the armholes of the test chamber. The experimenter immediately lifted a piece of cereal above the apparatus until the subject looked at the food, and then placed the cereal into the holder on the wheel, which was positioned at 6 o'clock relative to the subject. The subject then had 15 minutes in which to retrieve food from the apparatus by turning the wheel in either direction. If the subject was successful at pushing the wheel 180 degrees (to the 12 o'clock position), the hole lined up with a chute and food fell into the food cup for collection. The experimenter would then rotate the wheel back to the start position (6 o'clock), returning the hole to the front of the apparatus with a new piece of cereal in view for the subject. This constituted the beginning of the next trial and the test ended after 20 trials (20 food retrievals). If the subject was unable to rotate the wheel and collect food, the experimenter continued to bait the hole with food every 1 minute for 5 minutes (i.e. a total of 5 pieces in the hole). After that, and if necessary, the experimenter picked up one of the five pieces, showed it to the subject, and placed it back onto the pile every minute for a further

10 minutes, to show that food was still being presented for collection. All tests ended after 20 trials or after 15 minutes without success.

The same protocol that was used in the alone condition was applied to the social condition, but a conspecific monkey was present in the right compartment of the test chamber. The monkey on the right side of the test chamber was presented with a cup of Trix® cereal and peanut butter. Peanut butter was used because the monkeys consumed this food slower than the cereal, thus ensuring that the partner would be eating for the majority of the 15-minute test and not soliciting food from the test subject. The conspecific monkey was a monkey from the alone condition who had successfully extracted food. That individual was not able to reach the apparatus through the mesh partition or assist in moving the wheel in any way. No monkeys were presented with the opportunity to watch a conspecific retrieve food prior to testing in the Alone or Social conditions. All subjects were naïve to apparatus prior to the test.

### **Non-learner post-testing**

In the event that an individual was unable to learn how to manipulate the apparatus for food, the test ended after 15 minutes. Within a month of completing each of the subjects' tests, the non-learners were tested for a second time, but this time after having the opportunity to watch a subject from their social group that had been successful at manipulating the apparatus. Non-learners were allowed into the left side of the test chamber while a group-member demonstrated 40 trials in his or her presence. After the demonstrations, the demonstrator moved over to the right side

of the test chamber and was given Trix® cereal and peanut butter as was done in the social condition. The non-learner subject then had 15 minutes or until 20 trials were completed to interact with the apparatus.

## **Data Collection and Analysis**

All tests were videotaped using a Canon mini-DV recorder. The experimenter placed the first piece of cereal into the holder and said, ‘start of the test’. This marked the start of the test and was considered the 0-second timestamp for coding that test.

Tapes were coded by the first author for the time in seconds between the 0-second mark and successful food collection (i.e. when food was collected from the cup) by recording the time in seconds for each trial. Since the latency times were continuous data points, we first tested for normal distribution and then used parametric statistics for analysis. Independent sample t-tests were used to compare means and reported with two-tailed p-values.

## ***RESULTS***

The overall latency (Table 4.1: ‘Total Test’) of each test was measured as the number of seconds it took from the start (presentation of the apparatus at 0 seconds) to the end of the test (completion of 20 trials). In the event that a subject was unable to manipulate the device for food, a latency of 900 seconds was recorded, since the tests were 900 seconds in duration.

**Table 4.1.** Individual results. Results by subject and experimental condition, along with each subject's success as a learner, or non-learner. The first success, total test, and total trials are all shown in seconds, with the non-learners' results after the observation condition. Any fields marked with an 'x' represent those who failed to complete any trials.

Subject	Sex	Age	Condition	First Success (1st trial)	Total Test (start to finish)	Total Trials (1-20 Trials)
<i>Georgia (GE)</i>	F	22	Alone	Learner	15	277
<i>Winnie (WN)</i>	F	23	Alone	Learner	61	530
<i>Bias (BI)</i>	F	20	Alone	Learner	98	638
<i>Lucas (LC)</i>	M	7	Alone	Learner	513	731
<i>Ike (IK)</i>	M	33	Alone	Learner	502	791
<i>Lancey (LA)</i>	F	5	Alone	Learner	655	959
<i>Snarf (SN)</i>	M	3	Alone	Learner	769	1100
<i>Star (ST)</i>	F	35	Social	Learner	19	201
<i>Benny (BE)</i>	M	3	Social	Learner	30	236
<i>Nancy (NN)</i>	F	22	Social	Learner	79	284
<i>Nate (NT)</i>	M	3	Social	Learner	24	387
<i>Mason (MS)</i>	M	9	Social	Learner	226	539
<i>Sammie (SM)</i>	F	11	Social	Learner	74	633
<i>Nicole (NI)</i>	F	7	Social	Learner	249	690
<i>Wilma (WL)</i>	F	9	Social	Non-Learner	62	407
<i>Goya (GY)</i>	F	14	Alone	Non-Learner	45	281
<i>Gretal (GR)</i>	F	3	Social	Non-Learner	x	x
<i>Scarlett (SL)</i>	F	2	Social	Non-Learner	x	x
<i>Luther (LH)</i>	M	2	Social	Non-Learner	x	x
<i>Lark (LR)</i>	F	5	Alone	Non-Learner	x	x
<i>Winter (WT)</i>	F	3	Alone	Non-Learner	x	x
<i>Wookie (WO)</i>	M	3	Alone	Non-Learner	x	x
<i>Mango (MG)</i>	F	40	Alone	Non-Learner	x	x

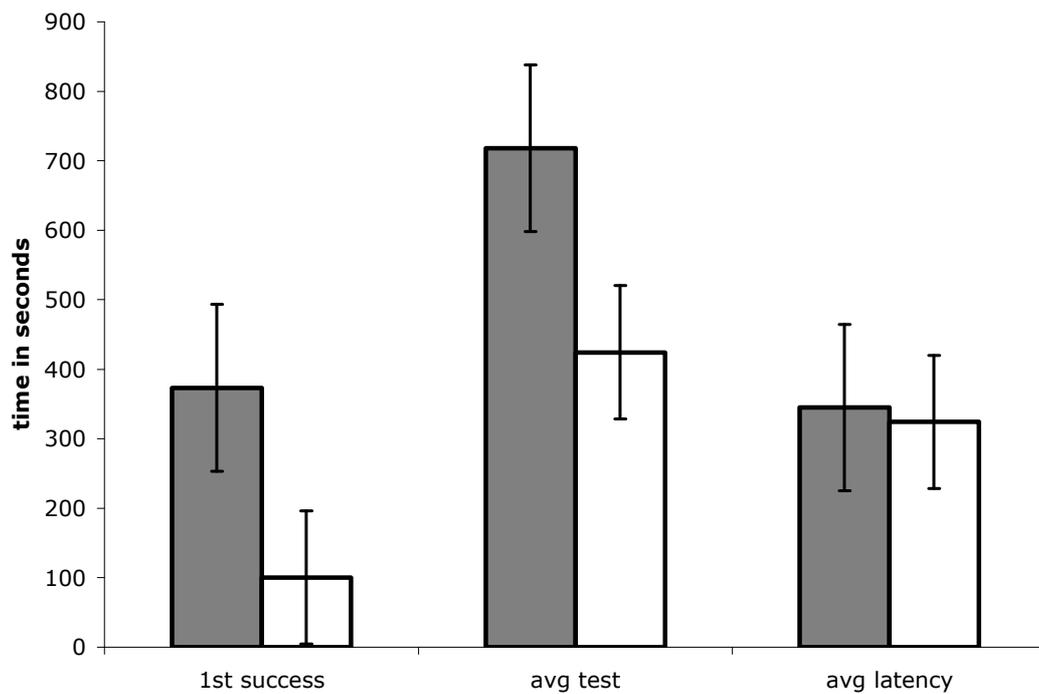
Comparing the overall latencies of each condition, we found no significant difference between the alone and social subjects' performances ( $t(21) = 1.26, p = 0.220, N_A = 12, N_S = 11$ ). However, this analysis lumps social learners and non-learners. We next conducted separate tests for learners and non-learners. In the alone condition, 7 out of 12 subjects were considered 'learners' because they discovered how to rotate the wheel and successfully collect food for all 20 trials. In the social condition, 7 out of 11 subjects were considered 'learners' by the same criterion. All social, 9 subjects were thus non-learners (Table 4.1).

## **Learners**

Clearly, learners were no more common in the social than the alone condition. However, when we compared the 'learners' from the alone condition ( $N_A = 7$ ) with the 'learners' from the social condition ( $N_S = 7$ ), we found a significant difference in the rates of learning between the two conditions, with subjects in the social condition reaching the first successful trial over three times faster on average than those in the alone condition ( $t(12) = 2.23, p = 0.046$ ). Subjects in the alone condition had an average latency of 373 seconds (SD 309) to the first successful trial, while subjects in the social condition had an average latency of only 100 seconds (SD 97) to the first successful trial.

Additionally, the overall rate of completing the tests (start to finish) was significantly faster in the social condition than in the alone condition ( $t(12) = 2.31, p = 0.04$ ). Alone subjects averaged 718 seconds (SD 273) from start to finish,

whereas social subjects had an average rate of 424 seconds (SD 197) from start to finish (Figure 4.3). However, subjects in the social condition did not subsequently perform the task any faster or more efficiently, as is indicated by the similar rates of completing the last 19 trials (Table 4.1: ‘Total Trials’). Subjects in the alone condition spent an average of 345 seconds (SD 117) manipulating the apparatus for food, and subjects in the social condition spent an average of 324 seconds (SD 141).



**Figure 4.3.** The average rates in seconds for (1) first successful food retrieval, (2) total test time and (3) latency between trials are presented here in grey for the ‘alone’ condition, and white for the ‘social’ condition along with standard error bars.

## **Non-learners**

It was possible to determine if a subject was observing the demonstrator by the eye gaze and body position of the individual, and in most cases, the subject and demonstrator were in physical contact during an observation. All of the nine non-learners watched at least 50% of the 40 demonstrations.

Of those who were deemed ‘non-learners’, only three were over 5 years old (Table 4.1). Two were ‘alone’ subjects, and a third was a ‘social’ subject. The first, a 14-year old female, was the lowest ranking member of her social group. The second, a 9-year old female, was moderately ranked within her group and was generally considered to be a good test subject. The third was a 40-year old female, who was mildly arthritic. In their test after watching a proficient demonstrator, the first two of these monkeys had latencies of 62 and 45 seconds respectively for their first successful trial (c.f. the mean of 100 seconds for ‘social’ subjects that were successful in the original tests), and overall testing latencies of 407 and 281 seconds from start to finish. The third adult non-learner touched the wheel repeatedly, but did not move it and collect food even after having observed a demonstration.

Four of the non-learners were juvenile females between the ages of 2 and 5-years old, and two more were juvenile males, aged 2 and 3. None of these juvenile non-learners gained food despite touching and moving the wheel throughout the test sessions.

## ***DISCUSSION***

Our results show that capuchin monkeys who were in the presence of a feeding conspecific were successful in a novel foraging task over three times faster than monkeys who were alone with the apparatus. The results were significant for both the first successful food collection and for the overall time it took to complete the test (Table 4.1: ‘Total Test’), suggesting that the capuchins’ motivation to explore the foraging apparatus was intensified by the presence and behaviour of a familiar, feeding conspecific. However, the actual time it took to perform each trial (‘Total Trials’), did not differ much at all, suggesting that the monkeys were not faster or more efficient in their performance, rather they were more motivated to discover the foraging technique in the social condition. Previous social learning experiments with capuchin monkeys have suggested social facilitation as a likely mechanism at work when capuchin monkeys acquire behaviours after observing a conspecific (see Frigaszy & Visalberghi 2001). They suggest that an increased motivation may be responsible for the subject replicating the same results a social model demonstrated. More recent studies have shown that capuchins and other monkeys are capable of more complex copying than previously thought (Dindo et al. 2008; Fredman & Whiten 2008; Voelkl & Huber 2007) and direct testing of social facilitation as a specific process has been lacking. Our results suggest social facilitation may more generally play an important role in speeding the learning process. Social facilitation may provide the necessary change in motivational state that then leads to an increased willingness to watch others and engage in the same behaviour. As Frigaszy and Visalberghi have noted, social learning in monkeys is “always the

collective outcome...of richly interconnected processes” (2004, p. 24), in which social facilitation may well play a significant role in the learning experience.

Aside from the kind, or kinds, of mechanisms involved in the learning process, another interacting element is the individual’s own life history. This includes, age, sex, and social status, as well as physical abilities. Of the nine non-learners, the six juveniles under the age of 5 years were unable to acquire the foraging technique even after watching a demonstrator performing the task. Juveniles are often assumed to be the most likely innovators of novel behaviours, as well as those for whom social learning is likely to be most important (Kendal et al. 2005; Laland & Reader 1999; Reader & Laland 2001), but in the context of this study there was no evidence of this. Matsuzawa’s theory of learning by “master apprenticeship” (Matsuzawa et al. 2001) may offer one possible explanation here, insofar as it may require a much longer period of observation before young individuals are able to acquire the skills necessary to adopt the behaviour in question. Another explanation could be that some of the juveniles lacked the coordination and/or dexterity to carry out the task based on their age and sex.

The remaining three non-learners were all adult females. In the case of the oldest, 40 year old monkey, her motivation to manipulate the device was evident, but her inability to fully rotate the wheel makes this unquantifiable. It is however safe to say that her age and dexterity were potential limiting factors in her inability to perform the task. The second non-learner was a moderately ranked female in the social condition. The group member in the adjacent section of the test chamber was

her higher-ranking mother. It has been reported in monkeys that low-status monkeys will intentionally inhibit their behaviour in the presence of higher ranking individuals (Drea & Wallen 1999). This is a potential explanation for her initial lack of response to the test in the social condition, but not in the social learning condition. However, our study was not designed to take personal relationships into account. Finally, the third non-learner was the lowest ranking monkey in her group, and although she was presented in the alone condition, her inhibited motivation within the group may have carried over to the test condition. After the non-learners were presented with the opportunity to watch another group-member turn the wheel for food, the two successful adult females were able to complete their first rotation of the wheel and collect food at 62 and 45 seconds, respectively. These rates are within the range seen for those who were in the ‘social’ condition and are well below the 100-second average for that condition, suggesting limited supplementary evidence for social learning.

The findings of this study address an area of social learning research in monkeys that has previously been neglected. When we chose to focus our study on the social influence of feeding conspecifics (as opposed to non-feeding ones), we were aware that previous studies with capuchins (*Cebus apella*), as well as Geoldi’s monkeys (*Callimico goeldii*), have found that rates of food consumption and acceptance of novel foods increase in the presence of other feeding conspecifics (Addessi & Visalberghi 2001; Addessi et al. 2007; Dindo & de Waal 2007; Voelkl et al. 2006). Ferrari et al. (2005) also found that as much as hearing the sound of other macaques eating activated motor programs related to eating, suggesting that there is marked

sensitivity in monkeys to the activities of others. The subjects of this study, capuchin monkeys, are extremely active individuals who engage in social interactions throughout their days. For these reasons, we believed that a social *feeding* condition would provide a more ecologically sound comparison for investigating a potential motivating force for exploratory foraging in these monkeys. Future research should also tease apart the effects of foraging versus non-foraging social facilitation effects, but in our study it was not considered ethical to present a non-feeding partner subject with nothing to do while watching the subject actively collect food for up to 15 minutes.

We focused on social facilitation specifically here because we believe that negative reports for imitation in monkeys often attributed social facilitation as the underlying mechanism by default, as opposed to any direct experimental testing. Voelkl and Huber (2000) found that mere presence had a social effect on exploratory behaviour in marmosets, therefore leading the subjects to discover a method for opening a film canister without the aid of demonstrations. Voelkl and Huber later went on to conduct a more controlled experiment in which they found these monkeys were able to imitate the movements they observed (Voelkl & Huber 2007). We do not argue that the imitative abilities of monkeys are the same as those of the great apes or human children. However in light of recent evidence for copying, we suggest that what was once thought to be merely social facilitation, is in fact the collective outcome of much more. As we showed, social facilitation can speed the process of individual exploration and discovery. In fully social contexts it is also likely to

further support group cohesion, and thereby increase opportunities for observational learning and synchronization of behaviour between groupmates (Cambefort 1981).

While this study showed the potential influence a group-mate can have on the learning experience of a capuchin monkey, it did not take into consideration the relationship between the subject and conspecific partner (e.g. rank, relatedness). The next chapter explores the effect of a conspecific's identity on observer preference in capuchins.

**CHAPTER 5: OBSERVER PREFERENCE DURING  
OBSERVATION OF FORAGING TASKS  
IN CAPUCHIN MONKEYS**

## **CHAPTER 5: OBSERVER PREFERENCE DURING OBSERVATION OF FORAGING TASKS IN CAPUCHIN MONKEYS**

### ***INTRODUCTION***

The view that monkeys are incapable of imitative learning has been challenged in the last decade (Fragaszy & Visalberghi 2004; Visalberghi & Frigaszy 1990, 2002), with increasing reports that monkeys copy movements they observe, which are already in their behavioural repertoire (Bugnyar & Huber, 1997; Dindo et al. 2008; Ferrari et al. 2006; Fredman & Whiten 2008; Voelkl & Huber, 2000, 2007; but see Subiaul 2007 for review). Recently, Dindo et al. (*submitted*, Chapter 2) have found that copying among capuchin monkeys is context dependent, consistent with similar findings in chimpanzees, children, and dogs (Buttleman et al. 2007; Gergely et al. 2002; Horner & Whiten 2005; Range et al. 2007). This context dependency should not be too surprising given that the behaviour of capuchin monkeys has been shown to be sensitive to the presence of conspecifics under varying social conditions. For example, Brosnan and de Waal (2003) found that capuchin monkeys will accept cucumber as a food reward in a simple exchange task, but will refuse that same reward if their partner receives a much more desirable grape. The authors attributed the monkeys' refusal as an aversion to social inequity, suggesting that the monkeys were averse to working for less 'pay' than their social partner. When the 'work' (exchange task) element was removed from the experimental paradigm, Dindo & de Waal (2007) found that the same capuchin monkeys readily collected cucumber presented to them, even when their

partner received the more desirable food, grapes. Additionally, Dindo & de Waal (2007) found that capuchins increased their rate of consumption of cucumber pieces when their partner was also eating, but not when their partner's food was merely visible yet inaccessible to the partner, suggesting a social facilitation effect of a feeding conspecific on food consumption. Despite such findings, social context is often under- or altogether unreported in the social learning literature, with relatively few studies providing information about the identity, age, sex, rank, or affiliation between subjects that may, in part, explain the differing results reported for copying complexity and fidelity in monkeys (de Waal & Bonnie, in press; Laland 1993; Coussi-Korbel & Fragaszy 1995; Range & Huber 2007).

One of the first to acknowledge that individual personalities and life histories may play a role in social learning was Imanishi (1957) in his study of Japanese macaques. Kawai (1965) went on to suggest that juvenile females were the most likely among group members to acquire the technique of potato washing. Huffman (1982, 1984) and others (Huffman & Quiatt 1986; Watanabe 1994) have proposed that the spread of potato washing behaviour began with juvenile females related to the female who invented the technique. While Galef (1990, 1992) argued that the slow rate of spread of the behaviour was not consistent with social learning, Huffman and others have counter-argued that the spread was relatively slow due to the strict matrilineal hierarchy found in Japanese macaques, with limited opportunities for social learning reflecting a lack of social tolerance between unrelated females and male group members (Huffman 1996; de Waal 2001). Coussi-Korbel and Fragaszy (1995) referred to such effects as 'directed-social

learning' and proposed that social learning opportunities would vary by species depending on the level of social tolerance exhibited. Socially acquired information would therefore spread unevenly in more despotic species, such as the Japanese macaques. Similarly, Cambefort (1981) conducted studies involving the discovery of hidden food items in vervets and baboons. Cambefort reported species differences in the spread of the foraging behaviours, with baboons exhibiting directed social learning. According to Cambefort, baboon juveniles first acquired the behaviour of harvesting the novel items followed by adults, whereas in vervets, the adults and juveniles both learned at equal rates from the first few that discovered the food. Coussi-Korbel and Fragaszy (1995) argued that in the case of the baboons, individual relationships and group social structure meant that certain individuals would not maintain the same level of saliency to all members of their group. Therefore, directed social learning took place in the baboon group but not in the vervet group where all members paid attention to the initiators of the foraging behaviour.

Differences in learning motivations have also been found, as in wild populations of chimpanzees. Lonsdorf (2006) reported that bouts of termite-fishing were more often observed by juvenile females than juvenile males, with specific attention being given to mothers. Biro et al. (2003) also found that juvenile chimpanzees spent more time observing their mothers, and more time in close proximity to nut-crackers than did older individuals. In capuchin monkeys, Ottoni and colleagues (2005) showed similar trends for juveniles to be tolerated in close proximity to nut-crackers, but in their case, found that capuchins actively, and non-randomly, chose

to observe more proficient nut-crackers. These species differences in observer preferences potentially result from differences in social organization between chimpanzees and capuchin monkeys (Day et al. 2003, 2005)

Given the suggestions about social context-sensitivity in these studies, the purpose of the present study was to create an experimental test of observer preference with regard to social context. Dindo et al. (2008) concluded that the high level of social tolerance and closeness in rank of their capuchin subjects was likely to have had a strong effect on the faithful social learning of their foraging task. In the present study, we therefore presented subjects from two colonies of capuchin monkeys with both a high-ranking model, the alpha female of their respective group, and a low-ranking adult female from the group. Coussi-Korbel and Fragaszy (1995) predicted that more socially tolerant species, such as capuchins, would exhibit more flexibility in their motivation to watch other group-members. However, they also predicted that extreme differences in rank (and therefore in the degree of affiliation) would affect the opportunity for observation to occur between high- and low-ranking individuals. We based our experimental design in part on a Range and Huber (2007) study in which marmosets were presented with the opportunity to watch a conspecific through a 'peep-hole'. If the subject was motivated to watch the test partner, they would approach the hole that allowed them to view that individual on the other side of an opaque panel. In our study, we taught a high-ranking and a low-ranking female a different method for extracting food from a foraging box. Subjects were then presented with the opportunity to watch either model performing their respective foraging method by looking through a peep-hole

on their left or on their right. In Dindo et al. (2008, Chapter 2), social compatibility was an important factor influencing whether or not a capuchin test subject would be motivated to come close enough to observe the demonstrator. Social compatibility was viewed as social tolerance for close proximity (within arm's reach) between the observer and model, and individuals that were most socially compatible shared similar rank classes (i.e. high, medium, low). Since relative rank between demonstrators and observers influences the learning process, we predicted that capuchin subjects would show an observer preference for the model with a rank similar to their own.

## ***METHODS***

### **Subjects & Housing**

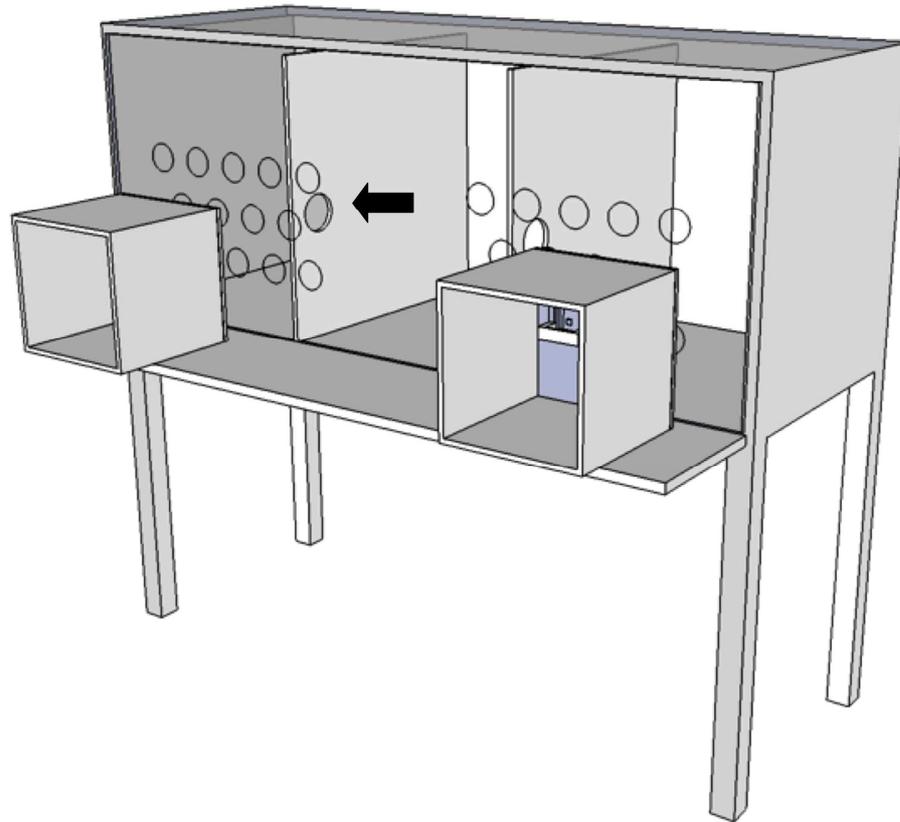
The subjects for this study were members of two social groups of capuchin monkeys at the Yerkes National Primate Research Center in Atlanta, Georgia. Each colony numbered 15. This study was conducted from 6-27 August, 2007.

A total of 26 capuchin monkeys served as subjects for this study. The highest and lowest ranking females from each group were selected as demonstrators for their group for a total of 4 model subjects ranging in age from 23 to 33 years (median 24). Eleven observer subjects from colony A consisted of 5 males and 6 females ranging in age from 3 to 33 years (median 5). Eleven observer subjects from colony B included 4 males and 7 females ranging in age from 3 to 40 years (median 9).

Both colonies were housed in the same building, visually but not acoustically separated from each other, with indoor and outdoor enclosures measuring 25m<sup>2</sup> (Colony A) and 31m<sup>2</sup> (Colony B). Subjects had ad libitum access to monkey chow and water, and all testing occurred before the daily feeding of fresh produce and bread.

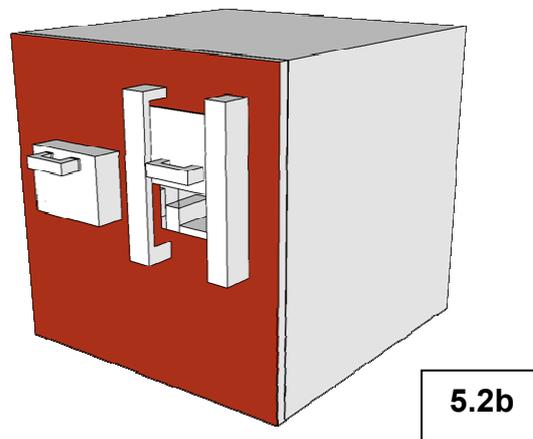
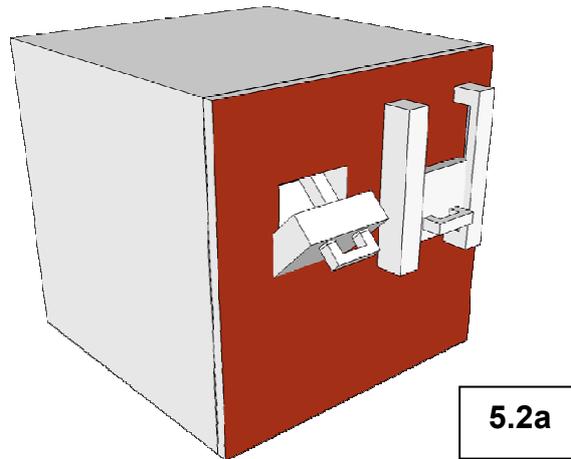
### **Apparatus & Test Chamber**

Tests were conducted in a mobile chamber (156 x 64 x 58 cm), which was located directly in front of the subjects' respective home area. Two opaque partitions, each with a 4 cm diameter viewing hole, separated the chamber into three sections of 52 x 64 x 58 cm (Figure 5.1).



**Figure 5.1.** The test chamber. Two identical boxes are as presented in front of the left and right model sections. The black arrow points to one of the two peep-holes available to the subject from the centre section.

The foraging box measured 28 x 28 x 28 cm. The front panel of the box had two doors with horizontal handle bars. The door on the left could be pulled outward to reveal a cup with food in it (Figure 5.2a). The door on the right could be lifted by sliding the handle bar upward to reveal a food cup with the same food reward as the left cup (Figure 5.2b). The back panel of the box remained open so that the experimenter holding the box could bait the cups from behind the front panel (Figure 5.3).



**Figure 5.2.** The foraging box. **(a)** the left (pull) method open to reveal a cereal piece, **(b)** the right (lift) method open to reveal a cereal piece.



**Figure 5.3.** Experimental procedure. The observation condition of the test is shown here with Experimenters 2 (KL, left) and Experimenters 1 (MD, right) presenting the two models with the boxes. The subject (centre) is observing the left model through the peep-hole. (Both experimenters stood for tests; here, Experimenters 1 has lowered her head so as not to obstruct the photograph).

Two identical versions of this box were presented simultaneously to the high-ranking and low-ranking female models. In colony A, the *pull* method was demonstrated by the *low*-ranking model (LO), whereas the *lift* method was demonstrated by the *high*-ranking model (HI). In colony B, the *pull* method was demonstrated by HI and the *lift* method was demonstrated by LO. This was done to ensure that, if one method were more salient than the other, this would not be confused with a bias for HI or LO, as the methods were not associated with rank. The method was however linked with a side of the test chamber. The left, pull

method was associated with the *right* side of the test chamber, as this allowed the subject to view it more closely, just as the right, lift method was viewed from the *left* side of the test chamber for the same reason (Figure 5.4a & b). To account for potential side biases in attention, we conducted baseline tests without the boxes present, as is noted in the procedure section below.

Since the test condition presented two boxes simultaneously, it was necessary to have two experimenters for this study. Experimenter 1 was Marietta Dindo (noted by initials MD) and Experimenter 2 was Kristi Leimgruber (noted by initials KL).



**Figure 5.4.** The subject's views of the boxes. (a) the lift method and (b) the pull method as seen through the respective peep-holes.

## **Procedure**

### **Model selection and training**

Weekly 30-minute ‘food scans’ were collected by KL, in which subjects’ order of access to a food tray was recorded. This method of ranking the order to the food trays was analyzed to assess the relative rank of group members (high, medium, or low ranking). This method has been used at the Living Links Capuchin Lab for over ten years and is generally a good indicator of group rankings (see de Waal 1997). Additionally, a ‘perceived-rank questionnaire’ was also given to three researchers within the capuchin laboratory to confirm the ranks derived from the food scan data. Two individuals were considered higher ranking in the food scans than they were perceived to be by the researchers studying them. These two monkeys were overweight and tended to rush to the food trays and then run away, essentially ‘cutting in line’ of higher-ranked individuals. Since all ‘perceived-rank questionnaires’ showed only these two individuals as lower-ranking, their scores were re-assigned to the lower ranked tier and noted with an asterisk in Table 5.1.

One high- and one low-ranking female from each colony served as models for their respective groups. The models were temporarily separated from their group and individually trained in the test chamber by the first author to use one of the two possible methods. Training sessions consisted of the model collecting food 20 times by only using the trained method. All four models were able to perform the trained method consistently in the first session, but two more sessions on subsequent days were given in order to insure their ability to model the behaviour

with fidelity for the trained method since both methods were always available. On the fourth day of training, MD and KL performed a practice test, where both models were presented with their respective box at the same time in the test chamber. This was done to ensure that they would not be distracted by the model at the opposite end of the test chamber.

### **Baseline observer preference**

In order to determine if subjects had a preference for looking at one side more, or at one model over the other, each monkey was first given a 5-minute baseline preference test. Subjects were moved to the test chamber, and situated between two models, one high ranking and one low-ranking, from their social group. The foraging box was not present during this baseline phase, but each model was given a block of wood, a novel object to the subject, to control for interest in a novel object

Data were recorded from video, and for each subject, the amount of time/number of looks made towards each model, with 'look' operationally defined as a subject peering through one of the two observation holes in the opaque panel. The observation holes were similar in size to the monkeys' faces, making it apparent during coding when a subject was looking, because the subject would press his or her face up to the hole.

### **Observer preference tests**

Immediately after the control period, the two experimenters (MD and KL) returned to the test area and began the test phase. Both experimenters were similar in age, general appearances, and both were very familiar to all subjects and models. In case any of the subjects had a bias towards or against one of the experimenters, the experimenters switched sides half way through every test, so that a method or model was not associated with any potential bias for an experimenter.

Tests began with MD and KL presenting the box to both models (Figure 5.3). The experimenters coordinated their movements so that each demonstration occurred at nearly the exact same time. Each trial consisted of both models demonstrating their respective method once to collect a piece of cereal from the box. The boxes were then pulled away by the experimenters. Once the experimenters each stepped back, they then moved forward again for the next trial. After 20 trials, the experimenters switched sides (but not boxes) and proceeded with 20 more trials.

### **Method preference tests**

After the demonstrations, the models were let out of the test chamber and back into their group enclosure. The subject remained in the test chamber and the partition panels were removed, giving the subject full access to all three sections of the test chamber.

The first experimenter presented the subject with the box on the left side of the test chamber for 20 trials. The second experimenter then presented the subject with 20 more trials on the right side of the test chamber. This was done in case a side was associated with the previous model. The order in which the experimenters first presented the box in the test condition alternated each day of testing so that 11 subjects were presented with MD first and 11 subjects were presented with KL first. Each trial consisted of the experimenter stepping forward with the box in hand, and presenting it to the subject in front of the test chamber. Subjects were only allowed to collect food once, therefore only one method, pull or lift, could be used per trial. The results of Dindo et al. (*submitted*, Chapter 3) suggested that capuchin monkeys may perceive an opportunity for maximizing their food collection when they are aware that a second piece of food is present. Since subjects in this study had the opportunity to watch both methods and gain knowledge about foods available, the experimenters took a step back from the test chamber, thus moving the box out of reach, allowing the subject to consume the food before approaching again for the next trial.

### **Data collection**

All tests were recorded using a Canon mini-DV recorder. The first author coded all tests for the 'looks' through the left and right observation holes by the subject during baseline and the whether or not 'looks' occurred left and/or right during each of the 40 observer preference trials, as well as the method performed during the method preference tests. A second coder who was familiar with the monkeys,

but did not take part in running the experiments, coded three tapes at random, i.e. 400 observation trials and 220 test trials for inter-observer reliability in coding. Kappa for the agreement of watching per trial was 0.82 and for the method used was 1.0.

## ***RESULTS***

### **Baseline observer preference**

In the 5-minute baseline condition in which the low- and high-ranking models on either side of the subject had a novel object (wooden block), only two high-ranking monkeys, the alpha male and the beta female of colony B (BI & BR), showed a significant preference in the number of looks towards one of the models, in both cases the high-ranking model (BI:  $p < 0.01$ , B4:  $p < 0.03$ , two-tailed binomial; Table 5.1).

### **Observer preference tests**

There was no overall preference for watching one of the models among the 22 subjects ( $p=1.17$ , two-tailed binomial test). However, 11 of the 22 subjects did show a significant preference for which model they observed (see Table 5.1), with 10 out of the 11 preferring to watch the model of the 'Pull' method ( $p < 0.02$ , two-tailed binomial test). These monkeys did not show a preference for watching the high or low ranked models, as 5 watched a low-ranking model and 6 watched a high-ranking model. Of the 5 who watched the low-ranking models, all 5 were

related to the model, but only 2 of the 6 who watched the high-ranking models were related to the model; therefore there was significance in the degree of relatedness between models and observers ( $p = 0.05$ , Fisher exact test).

There was no significant relationship between the rank of the observer and the rank of the preferred model, with only 8 out of the 11 subjects being similarly ranked to the model they observed ( $p = 0.23$ , two-tailed binomial test). There was also no relationship between the sex of the subject and preferring a model; 2 out of 8 males had a model preference ( $p = 0.29$ , two-tailed binomial test) and 9 out of 14 females had a model preference ( $p = 0.09$ , Fisher exact test). Furthermore, there was no significant relationship between age and preferring a model as 5 of the 11 subjects with a preference were youngsters under the age of 5, and 6 were adults over the age of 5, and the same was true for the 11 subjects without a model preference that 5 were youngsters and 6 were adults ( $p = 0.67$ , Fisher exact test). Finally, we looked at the lift-bias score for the first 20 trials and last 20 trials of each subject to distinguish an effect of experimenter, and found that there was no effect of which experimenter (MD or KL) presented the box (Mann-Whitney U,  $U = 252$ ,  $z = -0.22$ ,  $p = 0.83$ ).

**Table 5.1.** Subject information. Data are presented for each individual with regards to sex, age, rank, observations made, and methods performed. The first letter of subject codes indicates are based on matriline, e.g. LH and LC are related along the L-matriline. Asterisk ( \* ) note when the subject was related to the non-preferred model, x marks subjects with no significant model preference

Subject	Colony	Lift-Bias Score	Sex	Age	Rank	Preferred Model		Rank-Relation to Preferred Model	Relatedness to Preferred Model	Relatedness to a Model	Preferred Method Observed	Preferred Method Used
						Observed	Relatedness to Preferred Model					
<i>Ike (IK)</i>	A	0.00	M	33	HIGH	X	X	X	NO	NO	X	PULL
<i>Lancey (LA)</i>	A	0.98	F	5	LOW	LOW	SAME	YES	YES	YES	PULL	LIFT
<i>Lark (LR)</i>	A	0.00	F	5	LOW	LOW	SAME	YES	YES	YES	PULL	PULL
<i>Lucas (LC)</i>	A	0.03	M	7	HIGH	X	X	X	YES	YES	X	PULL
<i>Luther (LH)</i>	A	0.13	M	2	HIGH	LOW	DIFFERENT	YES	YES	YES	PULL	PULL
<i>Nate (NT)</i>	A	0.00	M	3	HIGH	X	X	X	YES	YES	X	PULL
<i>Nicole (NI)</i>	A	0.38	F	7	LOW	X	X	X	YES	YES	X	PULL
<i>Wilma (WL)</i>	A	0.00	F	9	LOW	X	X	X	NO	NO	X	PULL
<i>Winnie (WN)</i>	A	0.03	F	23	HIGH	LOW	DIFFERENT	NO	NO	NO	PULL	PULL
<i>Winter (WT)</i>	A	0.85	F	3	LOW	X	X	X	NO	NO	X	LIFT
<i>Wookie (WO)</i>	A	0.00	M	3	HIGH	X	X	X	NO	NO	X	PULL
<i>Benny (BE)</i>	B	0.03	M	3	HIGH	X	X	X	NO	NO	X	PULL
<i>Bias (BI)</i>	B	0.00	F	20	HIGH	HIGH	SAME	NO	NO	NO	PULL	PULL
<i>Bravo (BR)</i>	B	0.00	M	13	HIGH	HIGH	SAME	NO	NO	NO	PULL	PULL
<i>Goya (GY)</i>	B	0.00	F	14	LOW	HIGH	DIFFERENT	NO*	YES	YES	PULL	PULL
<i>Gretal (GR)</i>	B	0.98	F	3	LOW	LOW	SAME	YES	YES	YES	LIFT	LIFT
<i>Mango (MG)</i>	B	0.00	F	40	LOW	HIGH	DIFFERENT	NO	NO	NO	PULL	PULL
<i>Mason (MS)</i>	B	1.00	M	9	HIGH	X	X	X	NO	NO	X	LIFT
<i>Sammie (SM)</i>	B	0.00	F	11	HIGH	HIGH	SAME	YES	YES	YES	PULL	PULL
<i>Scarlett (SL)</i>	B	0.00	F	2	HIGH	HIGH	SAME	YES	YES	YES	PULL	PULL
<i>Snarf (SN)</i>	B	0.88	M	3	HIGH	X	X	X	YES	YES	X	LIFT
<i>Bailey (BA)</i>	B	0.13	F	7	LOW	X	X	X	NO	NO	X	PULL

## Method preference tests

Immediately after the demonstration session, subjects were presented with the box in the absence of the models. Subjects had 40 trials in which to collect food from the device using either lift door or pull door. There was no significant difference in which methods were observed between the two colonies (A vs B: two-tailed Mann-Whitney U,  $U=60$ ,  $p=0.97$ ,  $N_A=11$ ,  $N_B=11$ ). A lift-bias score was calculated by counting the number of lifts performed and dividing it by the total number of trials (i.e. 2 lifts out of 40 would be a lift-bias score of 0.05). In both colonies, the lift-bias score for each subject revealed that the pull method was employed significantly more than the lift method with 17 out of 22 individuals using it for 62.5% - 100% of the 40 trials (two-tailed Mann-Whitney U,  $U = 67.0$ ,  $z=4.1$ ,  $p < 0.001$ ).

While there was a main effect of method on looking preference, there was no effect of rank on observer preference for a model. Ten of the 11 subjects that showed a significant preference in the observation phase preferred to watch the high- or low-ranking model that performed the pull method. Nine of those 10 individuals used the pull method themselves during the method preference tests (two-tailed binomial test,  $p < 0.02$ ). Seven of those 9 pulled for all 40 trials (100% pull), and the remaining two pulled for 87.5% and 97.5% of their trials, respectively. The one subject (LA) who observed significantly more pulls but performed lift, lifted for 97.5% of her test trials. The one subject (GR) that watched the lift method significantly more during the observer preference test used the lift method for

97.5% of her trials. Thus, 10 out of the 11 subjects who specifically watched a model, also matched the method they saw demonstrated during the method preference tests (two-tailed binomial test,  $p < 0.01$ ).

## ***DISCUSSION***

The model preference results indicate that individual preference and motivation for observing others are quite variable among capuchins, with no overall significant preference for a foraging model among the 22 subjects tested. All subjects except one chose to observe both models, but only half of the 22 subjects in this study showed a significant preference in which model they observed more. Coussi-Korbel & Fragaszy (1995) predicted that greater degrees of social tolerance would provide more opportunities for social learning to take place. The behaviour of the capuchins, a socially-tolerant species, in this study was consistent with this principle: they chose to watch both the low- and high-ranking models regardless of their own rank. Among those with viewing preferences, there was a significant preference for watching a related model over a non-related model. It is possible that the relative rank within the group did not carry over to the test condition when the relationship between the subject and models became dyadic or even triadic. It is also possible that rank does not play a strong role in an observer's selection of a model. Ottoni and colleagues (2005) suggest that capuchin monkeys prefer to watch the most proficient nut-crackers, basing their choice not on relatedness or rank order, but on an active assessment of the model's proficiency. In the case of our study, both models were given the same amount of training, and both completed the foraging trials at the same time with the same end result of collecting

one piece of cereal. We therefore considered both models to be equally proficient demonstrators and can assume that this was not an influential factor in the current study.

Of the 11 subjects who showed significant viewing preferences, instead of any overall trend to watch the high- or low-ranked model, a significant preference was seen for watching the pull method (10 out of 11). These method preference results contribute to the mounting evidence that capuchin monkeys are sensitive to the motions involved in the behaviours they observe (Custance et al. 1999; Dindo et al. 2008, *submitted*; Fredman & Whiten 2008; Humle & Snowdon 2008; Voelkl & Huber 2000, 2007). Of the 10 who showed a preference for watching the pull method, 9 preferred to perform that same method during the test condition. Furthermore, 17 of the 22 subjects preferred to perform the pull method, suggesting that this method was potentially a more distinguishable and therefore a more salient method to learn. These findings can be related to Range and Huber's (2007) study where monkeys watched individuals more who engaged in manipulative behaviour rather than simple searching behaviour, perhaps suggesting that the kinds of motion involved in a behaviour may influence the learning process more than previously thought.

From the results of this experiment we failed to find a relationship between relative rank and observer preference. It was not anticipated during the design of this study that subjects would be so able to watch both models in a trial; however, the small section of the test chamber (52 cm wide) allowed subjects to quickly alternate

between the two peep-holes. Additionally, the opaque panelling may have provided the subject with a sense of security knowing that the models could not reach through the partition except at the holes. In this sense, there was no apparent cost involved in observing one model over the other, since there was no potential for direct aggression or food sharing opportunities. This artificial context does not reflect conditions that would occur in the wild, where all group members are free to observe whatever and whomever they choose. In this context it may be possible to better investigate the kinds of opportunities naturally available to capuchins for social learning, as well as the processes by which behaviours are transmitted throughout a group. This is the subject of the next chapter.

## **CHAPTER 6: IN-GROUP CONFORMITY SUSTAINS DIFFERENT FORAGING TRADITIONS IN CAPUCHIN MONKEYS**

The data in this chapter have been submitted for publication as:

**Dindo, M.**, de Waal, F. B. M., and Whiten, A. In-group conformity sustains different foraging traditions in capuchin monkeys.

## **CHAPTER 6: IN-GROUP CONFORMITY SUSTAINS DIFFERENT FORAGING TRADITIONS IN CAPUCHIN MONKEYS**

### ***INTRODUCTION***

The study of culture in animals has its origin in field reports from primatology decades ago, on the ‘proto-cultural’ behaviour of Japanese macaques on Koshima Island (Imanishi 1957; Kawai 1965). In a provisioned troop, a juvenile female, Imo, began taking potatoes presented on the sandy beach, and submerged the potatoes under water before eating. The gradual spread of this behaviour, which became known as potato-washing, was documented for decades to reveal a very slow spread that began among related females, and eventually spread to many other family groups within the troop (Watanabe 1994, 2001). This particular case was later questioned as ‘cultural’ because the spread appeared too slow to be explained by observationally based social learning (Galef 1990, 1992). However, such critiques did not take into consideration the particularly despotic nature of macaque social structure (Chapais 1992; de Waal 1996; Flack et al. 2006). Opportunities for social learning in this species were limited by the level of social tolerance exhibited between ‘potato-washers’ and naïve observers (Coussi-Korbel & Fragaszy 1995).

Despite the rich behavioural data available from Koshima Island, thus we still know little about the ways in which traditions and other culturally acquired behaviours spread in wild populations of monkeys. This contrasts with apes, in which we see evidence for group-specific foraging behaviours, as well as a substantial repertoire

of tool-use behaviours and social conventions, which some argue may shed light on the cumulative nature of human cultural origins (Whiten et al. 1999; van Schaik et al. 2003). These putative examples of wild ape culture have a much clearer connection to decades of captive work demonstrating the observational learning skills of apes, in particular chimpanzees (Call et al. 2005; Custance 1998; Horner & Whiten 2005; Horner et al. 2006; Tomasello et al. 1993b; Whiten et al. 2004) In a landmark paper, Visalberghi and Fragaszy (1990) argued that monkeys, by contrast, ‘do not ape’: in other words, the observational learning skills of monkeys do not lead to copying of behaviours. Fragaszy & Visalberghi (2004, p. 24) went on to more specifically state that monkeys “do not learn *from* each other”, rather they “learn *with* each other”. While the numerous examples these authors presented support the claim that monkeys appear to be weak social learners, this left an enormous disconnect in explaining the newly emerging reports from the field that presented evidence that capuchin monkeys maintain social conventions and other group specific traditions that are highly suggestive of social transmission (Moura and Lee 2004; Perry et al 2003; Panger et al. 2002). How was it possible to spread and maintain these very specific traditions in the absence of imitation or other forms of complex behavioural coordination?

With new advances in experimental approaches, including the application of the two-action task paradigm (Dawson & Foss 1965), we are now beginning to see more convincing evidence that monkeys may copy other group members in more sophisticated ways than previously suggested. This kind of task is designed with two different methods of solution possible, but only one is usually demonstrated to

each monkey subject (Bugnyar & Huber 1997; Price & Caldwell 2007; Custance et al. 1999; Fredman and Whiten 2008; Dindo et al. 2008; Voelkl & Huber 2000, 2007).

While evidence is mounting in support of copying in monkeys, this ability is often limited by social or physical context and individual motivation (Dindo et al. *submitted*; Subiaul et al. 2004). The latter, individual motivation, can be the most difficult to discern as it relates to multiple aspects of an individual's relationships within a group such as age, rank, relatedness and overall affiliation with others. This phenomenon has been referred to as *Bonding- and Identification-Based Observational Learning* (BIOL) by de Waal (2001); an intrinsically rewarding aspect to acting like others, suggested to play a large role in an individual's adoption of group-specific behaviours. Under this model, as with the social tolerance model suggested by Coussi-Korbel and Frigaszy (1995), it is predicted that in species, such as brown capuchin monkeys, with high levels of social tolerance (i.e. maintaining close physical proximity without aggression), we would expect to see learning opportunities among those with the strongest social affiliations.

Dindo et al. (2008) found high levels of copying fidelity in capuchin monkeys using a two-action task, an artificial 'Dorian Fruit'. This foraging box presented monkeys with a door that could either be (1) slid to the side or (2) lifted to reveal a piece of food. In the study, Dindo and colleagues found that monkeys adopted the method they observed demonstrated to them, and maintained that behavioural

tradition along a ‘transmission chain’ of individuals in the absence of the originally trained model (i.e. the experimental ‘innovator’ of the foraging tradition). This particular experiment controlled for social ties between the model and observer at each step along the chain, checking for social tolerance in joint feeding opportunities prior to the test condition.

This study revealed a condition in which monkeys accurately copied the foraging activities of a conspecific, but it did not demonstrate how the behaviour spreads in the group context in which all group members have potentially equal access to the foraging apparatus. This ‘open group’ scenario provides a more ecologically valid picture of the spread of social behaviours as it may occur in the wild. Here we report the first open diffusion experiment in capuchin monkeys, in which the alpha male of each of two groups of capuchins was trained to open the ‘Doorian’ foraging device, using either the slide or lift method, and then was reunited with his group to demonstrate this artificial ‘foraging innovation’. We investigated the potential spread of this new behaviour in each group.

## ***METHODS***

### **Subjects and Housing**

This study was conducted at the Living Links Capuchin Laboratory at the Yerkes National Primate Research Center in Atlanta, GA, USA, from May 25 to June 13, 2008. All individuals in two groups of capuchin monkeys (*Cebus apella*) served as subjects (N=27) and all were naïve to the test apparatus.

Group A consisted of 15 individuals: 3 adult males, 8 adult females and 4 juveniles, ranging in age from 3 to 34 years (median = 8 years). Colony B consisted of 12 individuals: 1 adult male, 5 adult females and 6 juveniles, ranging in age from 2 to 41 years (median = 6 years). The alpha male from each colony served as the model for his respective group, with the remaining members serving as observer subjects. Therefore, the total number of observer subjects for group A was 14, for group B, 11. Both groups were housed in the same building, visually and were visually but not acoustically separated, with combined indoor and outdoor enclosures measuring 25 and 31 m<sup>2</sup>, respectively.

Subjects had access to all areas of their home enclosures during testing, with the exception of Day 7 of the Open Diffusion condition, where specific high-ranking individuals were separated inside for the entire testing hour. Subjects were never food or water deprived. Tests commenced approximately 1 hour after the afternoon feeding inside.

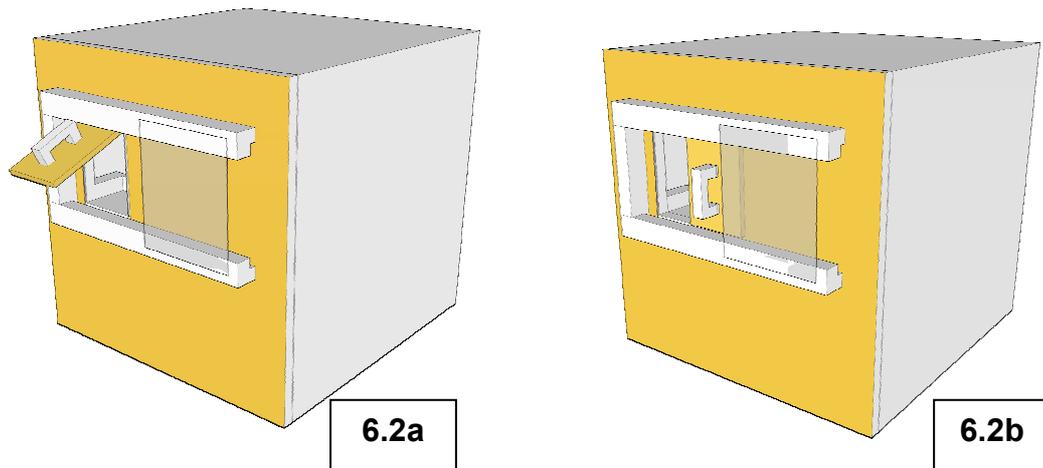
## **Apparatus**

The same foraging apparatus used by Dindo et al. (2008) was employed in this study. The apparatus was constructed from Lexan and measured 28 x 28 x 28 cm. The front of the apparatus faced the mesh enclosure, and was accessible to the monkeys, while the back of the apparatus faced the experimenter, who sat behind it (Figure 6.1). The back of the apparatus was open to allow the experimenter to

place food on a hidden tray. The tray could be accessed by a subject from the front of the apparatus by either (1) lifting or (2) sliding an opaque door (Figure 6.2). Each trial consisted of a subject opening the door by either method and food being collected from the tray. In the lift condition, the door returned to the start position by gravity once it was released. In the slide condition, the experimenter returned the door to the closed position by pushing a pin at the back of the door. Pieces of cereal were used as food rewards. It was always possible to use either or both methods for opening the door throughout this study.



**Figure 6.1.** Test setup. The experimenter sat behind the foraging apparatus, re-baiting the food tray with cereal for every trial (a). Subjects accessed the apparatus through the mesh of their outdoor enclosure (b).



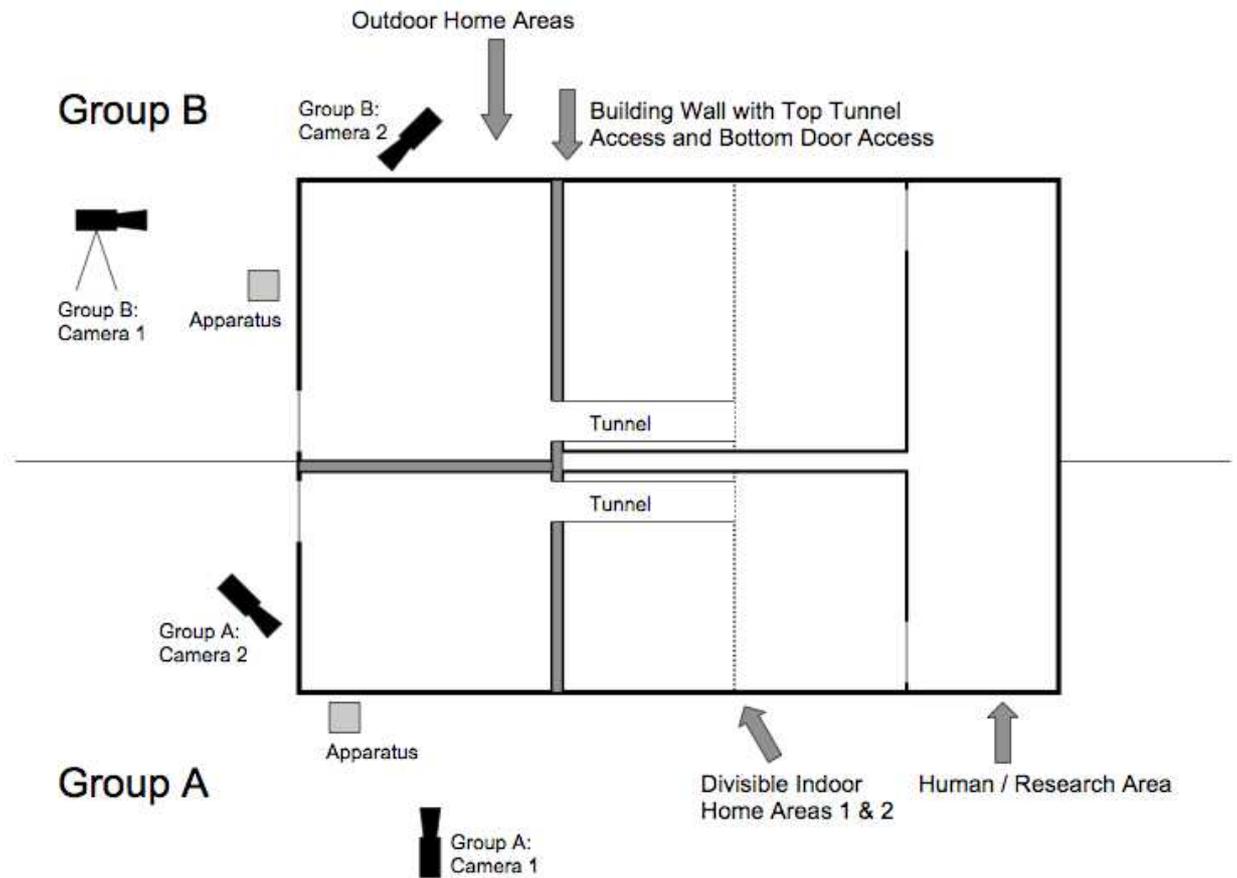
**Figure 6.2.** Foraging apparatus. The ‘Doorian Fruit’ presented two distinct methods for extracting food from the apparatus. The same door could either be lifted (**a**) or slid (**b**) open in order to reveal a food tray.

## Procedure

### Model Training

The alpha males of each group (OZ & MS) were selected as models since their high rank would ensure that they were not displaced by other group members during the Observation Phase.

For three consecutive days, OZ and MS were briefly separated from their groups for training sessions in the outdoor enclosure (where all tests took place). The other group members were kept in the inside area during training sessions. Both males had visual access to their groups via a tunnel running over their respective inside home areas (Figure 6.3). This allowed them to monitor their group-mates and minimized any separation anxiety. Group members did not have visual access to the outside enclosures during these three separate 10-minute sessions.



**Figure 6.3.** Capuchin Lab home enclosures. The Capuchin Lab floor plan shows the outdoor areas for each respective group (A and B), where the two cameras filmed the tests, where the apparatus was located for testing, and the visual barrier to the indoor area.

OZ (lift model) was presented with the apparatus, shown a piece of cereal that was placed on the food tray, and then the experimenter demonstrated the lift method. After the model collected the food piece, the door was dropped back to the neutral, closed position. A new piece was shown and placed on the obscured tray inside the apparatus. OZ opened the door using the lift method and continued to do so for 10

trials in total. One test session of 10 trials was conducted each day for three days and no session lasted longer than 10 minutes.

The same opportunity for training was presented to MS (slide model), but MS chose to stay in the tunnel for the entire 10 minutes on each day of his three sessions. Therefore, MS was subsequently trained in a test chamber (see Chapter 3 for description), where he was already well habituated to being tested. The apparatus was presented to MS, a piece of cereal was shown and placed on the food tray, and then the experimenter slid the door open for him to collect his food. The door was returned to the start position by the experimenter, and the model proceeded with 30 consecutive trials.

Both models were considered proficient models after these training sessions, and so the Observation Phase began on the following day.

### **Baseline Observation Phase**

The Observation Phase consisted of presenting the apparatus along the mesh of the outside enclosure to the trained models, OZ and MS. Each observation session consisted of 50 trials, where, due to the models' alpha-status and ability to monopolize a resource, only the model had the opportunity to manipulate the door. When the model was present, no other monkeys were able to handle the apparatus. Each model demonstrated only his respective trained method. If the model walked away at any point, the apparatus was pulled back, out of the reach of other group

members, until he returned. It took between 9-10 minutes in total to complete all 50 trials for each observation session, and only one session was given per day per group. Each group received a total of five observation sessions before the Open Diffusion Test Phase began.

### **Open Diffusion Test Phase**

One hour before each Open Diffusion Test session, the afternoon food trays were presented inside. Food trays included oranges, bread, and vitamin formula and were given daily in the afternoon. Tests took place after 6 p.m. to avoid the summer heat, as well as to give at least an hour's break between feeding and testing. One Open Diffusion Test session was conducted per day for approximately 1 hour per session.

The apparatus was presented to each group in the same place each day (Figure 6.3). The five Observation Phase sessions meant that the individuals who chose to watch the demonstrations had the opportunity to observe the group specific method before being able to access the apparatus themselves. The apparatus was no longer pulled away, so all monkeys had the opportunity to manipulate the apparatus using either method. Tests continued for one hour so that no one individual was likely to monopolize the apparatus for the entire test session. In total, seven days of testing per group were conducted to provide a generous number of trials, so as to examine the establishment of any sustained traditions.

## **Data Collection and Analyses**

All tests were recorded on video from two locations (Figure 6.3). The first camera was situated behind the experimenter and provided a view of the entire enclosure. The resulting video tapes were coded for the identity of individuals observing each trial, and their proximity to the apparatus within 1 meter. The second camera filmed the front of the apparatus to record the identity of the subject per trial and the method used per trial. The experimenter also dictated the identity of subjects, methods used, and those observing each trial. This information as well as the two tapes per test were used for coding. One test was selected at random and was coded for inter-observer reliability for the method used and identity of the subject. The kappa for agreement was 0.944, indicating a high level of agreement.

## ***RESULTS***

### **Baseline Observation Phase**

In group A, only the highest ranking group members (SN, ST, SL, SM) and the two youngest group members (GN, BK) were able to observe the model within one meter of the apparatus. In group B, a low ranking female that was in estrus was able to sit next to the alpha male as he modelled on all five days (LL). The remainder of observers within one meter of the apparatus were other high ranking males (NT, LH, LC, WO) and one juvenile female (WN).

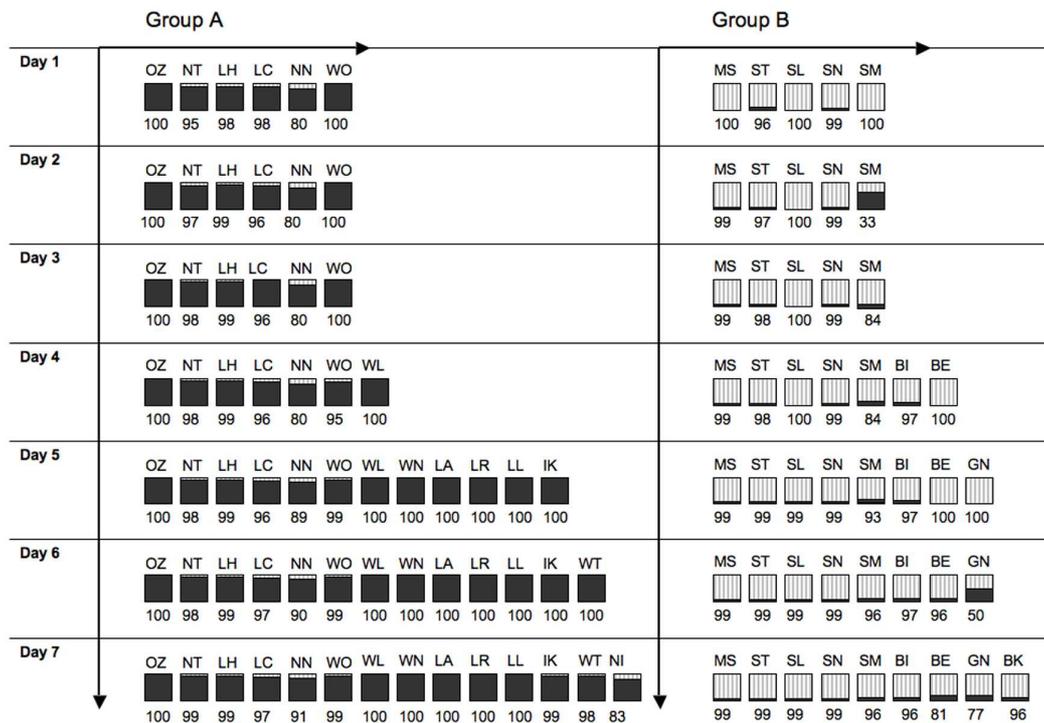
Since only one piece of cereal was presented in the apparatus per trial, there were no opportunities for scrounging food away from the alpha males.

## Open Diffusion Test Phase

In the lift-modelled group (A), 13 out of the 14 observer subjects collected food from the apparatus ( $p = 0.002$ , two-tailed Binomial test). All 13 of these subjects also used the lift method for the majority of their trials (83.11 – 100% lift;  $p = 0.0002$ , binomial test; see Table 6.1.). The one subject who never accessed the apparatus was one of the lowest ranked females in the group.

In the slide-modelled group (B), 8 out of the 11 observer subjects collected food from the apparatus and all used the model's slide method ( $p = 0.23$ , two-tailed Binomial test). All 8 of these subjects also used the slide method for the majority of their trials (76.83 – 99.52% slide;  $p = 0.008$ , binomial test; see Table 6.1.). Three of the lowest ranking females in this group never attempted to collect food from the apparatus.

To test whether groups A and B differed in their method preference, a method preference score was calculated for each subject that successfully collected food from the apparatus. Method preference scores were calculated by: the number of slide actions divided by the total number of actions (i.e. 'number of lift + number slide actions'). A score of 0 represented 0% slide and 1 represented 100% slide actions performed (Table 6.1.). Groups A and B showed a significant difference in their preferences for the method that was seeded into their group by the trained models ( $U = 0.00$ ,  $z = -3.80$ ,  $p < 0.0001$ ,  $n_A = 13$ ,  $n_B = 8$ , two-tailed Mann-Whitney Test; Median preference score: A = 0.01, B = 0.96: see Figure 6.4).



**Figure 6.4.** Group diffusion chart. Each square represents a subject, with the subject's code above and cumulative percent fidelity below. Gray indicates the lift method and striped indicates slide. Left to right arrows indicate the order of acquisition beginning with the models (OZ and MS), and top to bottom arrows indicate the progression of days. The first letter of each code indicates to which matriline an individual belongs, and therefore also indicates relatedness. Note that NT, LH, LC, and WO were absent on day 7, thus there scores represent at total of 6 days.

All subjects that collected food from the apparatus used their group specific method on the very first trial (21 of 21,  $p < 0.0001$ , two-tailed Binomial test). Each of the 21 subjects subsequently maintained 76.83% fidelity or more for the group method, with 17 out of the 21 maintaining 91.30% or higher fidelity for their method. While 4 subjects exhibited 100% fidelity to their method, seventeen of the successful 21 monkeys discovered the alternative action to that seeded in the group, performing it a median of 4 times. Nearly half of these seventeen subjects

discovered the alternative method within the first 20 trials, yet none of the subjects performed more than 25 trials in total of the alternative method out of hundreds of trials (Table 6.1.). After their first discovery of the alternative method, the median fidelity remained as high as 99.03% (range 77.78% to 100%; Table 6.1).

The order of acquisition of the techniques in each group followed relative rank order, from highest to lowest (Spearman's  $\rho = 0.81$ ,  $DF = 19$ ,  $p < 0.001$ ; Table 6.1.). In both groups, only the highest ranked individuals gained access to the apparatus in the first three days, so those individuals (indicated by \* in Table 6.1, and excepting the models) were locked in the front inside home area on day seven to prevent them from manipulating the apparatus and allow lower-ranking individuals access.

Table 6.1. Method acquisition chart. Social information is provided for each subject and presented by group in acquisition order. Asterisks (\*) indicate subjects that were separated from the group on day 7.

Social Group	Subject	Model Group	Sex	Age	Rank	Acquisition Order	Total No. of Trials	Total Lift	Total Slide	Percent Fidelity	Method Score
A	Ozzie (OZ)	Lift	M	20	H	model	859	858	1	99.88%	0.00
A	Nate (NT)	Lift	M	4	H	1*	672	663	9	98.66%	0.01
A	Luther (LH)	Lift	M	3	H	2*	489	486	3	99.39%	0.01
A	Lucas (LC)	Lift	M	8	H	3*	783	762	21	97.32%	0.03
A	Nancy (NN)	Lift	F	23	M1	4	69	63	6	91.30%	0.09
A	Wookie (WO)	Lift	M	4	M1	5*	121	120	1	99.17%	0.01
A	Wilma (WL)	Lift	F	10	M1	6	87	87	0	100.00%	0.00
A	Winnie (WN)	Lift	F	24	M2	7	31	27	4	87.10%	0.13
A	Lancey (LA)	Lift	F	6	L	8	3	3	0	100.00%	0.00
A	Lark (LR)	Lift	F	6	L	9	1	1	0	100.00%	0.00
A	Lulu (LL)	Lift	F	24	L	10	16	16	0	100.00%	0.00
A	Ike (IK)	Lift	M	34	M1	11	102	101	1	99.02%	0.01
A	Winter (WT)	Lift	F	4	M2	12	52	51	1	98.08%	0.02
A	Nicole (NI)	Lift	F	8	L	13	148	123	25	83.11%	0.17
A	Nadia (ND)	Lift	F	7	L	-	-	-	-	-	-
B	Mason (MS)	Slide	M	10	H	model	562	1	561	99.82%	1.00
B	Star (ST)	Slide	F	34	H	1*	822	9	813	98.91%	0.99
B	Scarlett (SL)	Slide	F	3	H	2*	124	1	123	99.19%	0.99
B	Snarf (SN)	Slide	M	4	M1	3*	623	3	620	99.52%	1.00
B	Sammie (SM)	Slide	F	12	M1	4	152	6	146	96.05%	0.96
B	Bias (BI)	Slide	F	21	M2	5	96	4	92	95.83%	0.96
B	Benny (BE)	Slide	M	4	M2	6	111	21	90	81.08%	0.81
B	Gonzo (GN)	Slide	M	2	M1	7	82	19	63	76.83%	0.77
B	Beeker (BK)	Slide	F	2	M1	8	55	2	53	96.36%	0.96
B	Mango (MG)	Slide	F	41	L	-	-	-	-	-	-
B	Bailey (BY)	Slide	F	8	L	-	-	-	-	-	-
B	Gretel (GR)	Slide	F	4	L	-	-	-	-	-	-

## ***DISCUSSION***

In this study different foraging traditions were seeded into two groups of capuchin monkeys and the spread of each behaviour from the first experimental ‘innovator’ (the trained model) was followed. The majority of individuals in both groups not only learned to forage from the apparatus, but also showed the same preference for the method demonstrated to them by the models. This strong evidence for observational learning complements the growing number of reports that monkeys may copy with greater fidelity than previously thought (Bugnyar & Huber 1997; Dindo et al. 2008; Fredman & Whiten 2008; Voelkl & Huber 2000, 2007), and expands upon the few documented attempts to present learning opportunities in an open group context (Price & Caldwell 2007; see Frigaszy et al. 2004, p. 254-5, for an unpublished account). Price & Caldwell’s open diffusion study utilized a video-taped model to show a group of three and a group of four individuals a simple push or pull technique for collecting food from a foraging apparatus. Their study showed that multiple individuals could learn together, but their limited number of subjects did not provide information about how the foraging behaviour spread throughout the natural social structure of that species. Furthermore using video-taped models for the initial demonstrations meant that social tolerance, or the lack thereof, was not a variable affecting the spread of the behaviour, as it was in the present study. Compared with previous studies (e.g. Price & Caldwell 2007), the current study presented a more ecologically sound comparison to wild populations of capuchin monkeys, as it involved two large social groups with subjects varying considerably in age, sex, relatedness and rank (Fragaszy et al. 2004). Additionally,

the limited visibility and proximity to others in the wild was mimicked by utilizing the outdoor enclosures at the Capuchin Laboratory since subjects had a choice to remain inside, away from the demonstrations, or to come closer to observe. This likely assisted lower ranking individuals in their attempts to approach the foraging device when dominant individuals chose to go inside since their attempts could not be monitored by the dominants under these circumstances.

During the first five days of the study, subjects were only allowed to watch the model demonstrate his respective method, lift or slide. This ensured that future subjects had the opportunity to watch before attempting to forage themselves. The baseline observation data showed that the next highest ranking individuals were the only individuals in each group to approach and watch the demonstrator within 1 meter. Thereafter, these same individuals were the first to manipulate the apparatus to collect food, and did so with the same method preference as the model. The order of acquisition suggests that rank played a strong role in the transmission process and in opportunities for learning. Although capuchin monkeys exhibit a more relaxed social structure than other monkey species, such as Japanese macaques, a significant hierarchical trend was associated with the order of acquiring the food collection behaviour. Dominant individuals monopolized the foraging device for the first four days in both groups before lower-ranking individuals began to gain access.

During the first four days of the open diffusion phase, nine of the twelve high-ranking subjects discovered the alternate technique, and subsequently lower-

ranking individuals observed the alternative method in addition to the originally modelled method. Despite these interspersed corruptions to the group norm, all 21 subjects performed the group specific method on the first trial, and 17 of the 21 (81%) later used the alternative method but continued to faithfully prefer the principal group technique. To our knowledge this is the first evidence for this kind of conformity in monkeys.

While there are countless differences between human and animal cultures, the drive to act like others may be one of the most universal similarities between them (de Waal 2001). In attempts to distinguish human from animal culture, some have emphasized imitation as a necessary prerequisite for cultural complexity as it is the most faithful form of copying (Tomasello & Call 1997). The role of imitation may in fact be overestimated, and emulation or object movement re-enactment may be sufficient social learning mechanisms for copying the behaviours of others. We cannot distinguish between these mechanisms in our study. To date, there is limited evidence for copying in capuchins and other monkey species (Caldwell & Whiten 2004; Dindo et al. 2008; Fragaszy and Visalberghi 2004; Fredman & Whiten 2008; Price & Caldwell 2007; Visalberghi & Fragaszy 1990, 2002; Voelkl & Huber 2007), which is why it is particularly surprising to find the level of fidelity to the group method observed in this study. This level of motivation to do as others do, even to conform to the group norm, could offer strong underlying support to sustain group specific traditions in capuchin monkeys in the wild.

## **CHAPTER 7: GENERAL DISCUSSION**

## CHAPTER 7: GENERAL DISCUSSION

*We suggest that socially biased learning is always the collective outcome of physical, social, and individual factors, and that differences across populations and species in social bias in learning reflect variations in all these dimensions.*

*Fragaszy & Visalberghi 2004, p. 24*

The objective of the work within this thesis was to contribute to our understanding of the *physical, social and individual* factors that influence social learning in capuchin monkeys, and determine how these factors collectively result in differences across populations. The quote above accurately describes social learning and behaviour transmission in capuchin monkeys as a whole, but the conclusion was derived from numerous studies that relied on negative evidence.

### ***Physical factors***

With regards to “physical factors”, many experiments on capuchin monkeys were not designed with the capuchin behavioural repertoire in mind. For example, the trap-tube task in Visalberghi and Limongelli’s (1994) study required capuchins to use long sticks that were more than half their own body length in size. Capuchins are known tool-users, but the main evidence for this comes from observations with stone tools (Otoni & Mannu 2001, 2003), or using leaves to wrap around and disarm spiny insects (Perry 2006). The use of sticks and small branches has been reported in the wild for predator-avoidance tactics such as clubbing venomous snakes, and throwing sticks at humans (Boinski 1988, 1998; Boinski et al. 2000),

but not for the kind of extractive foraging as in the trap-tube experiment. The study by Fragaszy and colleagues (1998) involving human reared capuchins also had the same short coming, as it required capuchins to engage in movements that were not normally seen in their repertoire, such as zipping up a zipper. It has been argued by some that imitation requires the copying of a “novel or otherwise improbable act” (Thorpe 1956, p.211). Critics have counter-argued that the tasks provided must be physically suitable for the subjects, as was the criticism of Thorndike’s work (1898, 1911) with animals learning to get out of his experimental boxes (Mills 1899; Haggerty 1909; Warden & Jackson 1935). When Bugnyar and Huber (1997) presented marmosets with a simple task of pushing or pulling a door, their subjects predominantly copied the method they had observed performed. This may appear to be imitation, but it can also be described as “object movement re-enactment”, a form of copying associated with the movements of a task observed. Voelkl and Huber (2000, 2007) presented marmosets with a another relatively simple task of removing a film canister lid and found that the monkeys would replicate the actions performed on the object, i.e. they used their mouth or their hands depending on which method they had seen performed by another group member. The authors referred to this kind of copying as “true imitation” (Voelkl & Huber 2000) because the marmosets not only performed the same the tasks they observed, but they also matched the motor patterns using the same body parts as the model (i.e. mouth vs hand). Regardless of what form of copying was discovered in these monkeys, the experimental designs were much more relevant and salient for the species in question. This approach was taken in this thesis, to provide simple, but distinct

tasks, that were not so physically demanding that the learning process may be inhibited.

### ***Social and individual factors***

With regards to “social and individual factors”, Imanishi (1957) was one of the first to suggest that individual differences (i.e. age, sex, rank, relatedness) are associated with opportunities for observation and interaction during the transmission of group-specific behaviours in Japanese macaques. Similarly, white-faced capuchins in Costa Rica have been shown to exhibit the same foraging methods as individuals with whom they associate most (Panger et al. 2002; Perry & Ordonez 2007).

Surprisingly few studies on social learning in capuchins, as well as other species, report details on the differences between observers and models (e.g. age and sex), or the quality of relations between test pairs, which is thought to influence motivation for observation of others (Coussi-Korbel & Fragaszy 1995; but see Range et al. 2008 for review). It has been hypothesized that high-status individuals may be more influential and therefore more attention is paid to them (Gil-White & Henrich 2001); but it has also been suggested that individuals pay more attention to those whom they affiliate with most (Coussi-Korbel & Fragaszy 1995). Thus reporting on individual status and the quality of relationships between test subjects is crucial. It is also important to report the time or percent of time spent watching models in observational learning experiments, which relatively few studies have done, as this provides an indication of how much information was actually

observed by the subject (Bugnyar & Huber 1997; Day et al. 2003; Miklosi 1999; Moscovice & Snowdon 2006; Range et al. 2008).

Some of the most influential and informative studies on social learning and culture in primates have reported age, sex, and/or individual affiliations as motivating factors for observational learning (Biro et al. 2003; Imanishi 1957; Kawai 1965; Lonsdorf et al. 2004; Lonsdorf 2006; Panger et al. 2002). For example, Lonsdorf (2006) found that among young chimpanzees, females attended to their mother's foraging skills significantly more than their male counterparts, and in turn showed greater matching for maternal foraging techniques. Similarly, Biro and colleagues (2003) found evidence that chimpanzees observed the nut-cracking sessions of other group members so long as the demonstrator was not younger in age than the observer. In capuchin monkeys, Ottoni and colleagues (2005) found that group members preferred to watch the most proficient nut-crackers, reflecting a difference between two species of primates in their preferences for observing nut-cracking. These studies from the field and captivity highlight the importance of assessing model-observer relationships before testing, as this may significantly influence a subject's willingness to observe the experimental model.

Furthermore, individual life-history (e.g. testing experience, socially housed vs pair housed, rearing-history) is an important factor to consider when designing social learning experiments. For example, Fredman & Whiten (2008) chose to pair human-reared capuchins with human models, and mother-raised monkeys with monkey models in their study of learning a tool-use task. The authors argued that

the model should be a salient one, as this may influence an individual's motivation to act like the model (see also de Waal 2001). Both subject groups predominantly achieved the same results they had seen the model perform, but variation was seen in the level of fidelity for using the tool to do so. The hand-raised monkeys were more adept tool-users, whereas the mother-raised monkeys often chose to ignore the stick-tools provided. In addition to accounting for the model-observer relationship, Fredman and Whiten's (2008) study also showed how the life-history of a subject may affect their ability to perform the tasks presented to them.

Specific consideration was taken with regards to the choice of subjects and opportunities for observation in all five of the experiments reported in this thesis. Additionally, the percentage of trials spent watching the model were also carefully reported in Chapters 2-5. This thesis aimed first to address the individual motivation and ability to learn from others (Chapters 2-5), before approaching the more complex issue of how a behaviour is transmitted throughout a social group.

## *Overview of experiments*

### **Chapter 2**

Chapter 1 of this thesis described reports that wild capuchin monkeys exhibit several group-specific behavioural traditions (Panger et al. 2002; Perry et al. 2003; Perry 2006), but how, by contrast, experiments have found little evidence for the social learning assumed necessary to support such traditions (Adams-Curtis & Fragaszy 1995; Fragaszy & Visalberghi 1998; Visalberghi 1987; Visalberghi &

Fragaszy 1990, 2002; Visalberghi & Limongelli 1994). Chapter 2 used a diffusion chain paradigm to investigate whether a novel foraging task could be observationally learned by capuchins and then transmitted along a chain of individuals. A two-action paradigm was used to control for independent learning. Either of two methods (lift or slide) could be used to open the door of a foraging apparatus to retrieve food. Two chains were tested, each beginning with an experimenter-trained model who demonstrated for a partner its group-specific method for opening the foraging apparatus. After the demonstration, if the observer was able to open the apparatus twenty times by either method, it then became the demonstrator for a new subject, thus simulating the spread of a foraging tradition among ‘generations’ of group members. Each method was transmitted along these respective chains with high fidelity, echoing similar results presently available only for chimpanzees and children. These results provided the first clear evidence for faithful diffusion of alternative foraging methods in monkeys, consistent with claims for capuchin traditions in the wild.

The findings in Chapter 2 provided answers to long-standing questions such as, *can a behaviour be transmitted and endure socially beyond the original innovator?* Durability is one of the twelve components of culture addressed in Chapter 1, and is defined as *a pattern that endures beyond demonstrator's presence* (Table 1.2). Field studies of white-faced capuchins have yet to provide support for traditions enduring beyond the original innovator because it is often impossible to assess who the originator of the behaviour was. Perry and colleagues (2003) were mindful to call the reported group-specific behaviours in their study ‘social conventions’ instead of

‘traditions’ as they did not have compelling generational data available. While the diffusion chain paradigm can only simulate generational transmission, it lends support for the establishment of *traditions* in capuchins, as it is defined in Table 1.2 as *a pattern that endures across generations*.

Lastly, Chapter 2 investigated whether or not capuchin monkeys could faithfully replicate the foraging method of a conspecific. While this study controlled for stimulus and local enhancement, it could not specifically address what form of copying was taking place. The capuchins lifted or slid the door of the apparatus with fidelity to the method they had observed. The movements required to lift or slide were very distinct, and therefore there was no ambiguity as to which method was being pursued by the subjects, however these actions were not necessarily imitation as defined as ‘novel or altogether improbable’ acts since some of the control subjects were able to individually learn the task (Table 1.2; Thorpe 1956, p. 211). It is possible that the kind of learning that took place in Chapter 2 was ‘object movement re-enactment’ (Table 1.1). However, a more conservative description would be to simply refer to this as ‘copying’ in capuchins, since it cannot be determined from this study. Table 1.2 specifically refers to imitation as a component of culture, because imitation is considered the most faithful form of copying. Faithful replication of a behaviour is necessary in order for it to spread and endure throughout a group and persist for generations. If the behaviour is not copied with fidelity, then it will likely not endure for very long. Nevertheless, Chapter 2 showed that capuchins copied the foraging method they observed with fidelity, and that behaviour did endure along several generational transmissions. I

will argue here that imitation, specifically, is not a necessary component of culture, rather it is more simply the ability to faithfully copy and maintain a behaviour that supports the development of culture. The subsequent chapters of this thesis aimed to investigate *when* capuchins would faithfully copy, and more importantly *why* they would be motivated to copy other group members.

### **Chapter 3**

In the last two decades, it became largely accepted that monkeys show little, if any, copying fidelity (Fragaszy & Visalberghi 2004; Visalberghi & Fragaszy 1990, 2002). However, some recent studies have begun to challenge this notion (Bugnyar & Huber 1997; Fredman & Whiten 2008; Voelkl & Huber 2000, 2007). Chapter 3 aimed to explore reasons for such contrary findings. A foraging apparatus was designed so that in each of two experiments with capuchin monkeys, a model would demonstrate one of two alternative methods to obtain food. The apparatus had a V-shaped track on which a panel could be slid up left or right from the centre to reveal food. In Experiment 1, food was located in a cup directly behind the centre panel. In Experiment 2, sliding the panel left or right revealed food either in left or right ends of the V-track. Since the sliding movement led directly to the food's location, we predicted capuchins would show greater copying fidelity in Experiment 2. Instead, subjects were significantly more faithful to the model's method in Experiment 1. These results suggest that capuchins can copy movements they observe, but instead prioritize exploratory behaviour when alternative foraging locations are accessible.

As was seen in Chapter 2, capuchins were capable of matching the movements performed with the door of the Doorian Fruit. Since the location of the task was the same (local enhancement), and the same door could be moved by either of two methods (stimulus enhancement), we had compelling evidence that capuchins learned about the movements others made during foraging tasks. In Chapter 3, the same panel at the centre of a V-track could be moved left or right to reveal food (1) in the centre location or (2) *either* in the left top corner or the right top corner of the V-track. Subjects in Experiment 1 adopted the directional pushing of the panel that they observed the model perform, but in Experiment 2 they did not. Since the movement required in Experiments 1 and 2 were the same, and even the same apparatus was used, it appears the capuchins made a choice as to *when* to copy the foraging method of a group-member. This ‘choice’ also affected the *standardization* of the foraging method used in each group. Table 1.2 defines standardization as *a pattern that is consistent and stylized*. In Experiment 2, the method was not consistent, and subjects did not faithfully adhere to the model’s method. This may in part explain why *standardization* in monkeys is in question in Table 1.2 (Kroeber 1928; Subiaul 2007), because it relates directly to whether or not an individual matches the behaviour of others.

Laland (2004) has proposed that animals may employ different ‘social learning strategies’ that are adaptive to local circumstances. These might result in either positive or negative evidence of social learning according to the context. For example, it would be maladaptive for an individual to copy others if the information were in some ways ‘out-dated’ and a better strategy existed (Boyd & Richerson

2005; Galef & Laland 2005). Recent studies suggest that ‘selective’ copying allows individuals to switch between individual learning and social learning depending on the perceived circumstances (Buttelmann et al. 2008; Gergely et al. 2002; Horner & Whiten 2005; Schweir et al. 2006). This would certainly explain why capuchins chose to explore the alternative method more in Experiment 2 than in Experiment 1, because it was possibly perceived that rewards were maximized this way. A limitation of captive experiments is that there was also no cost involved for a subject to explore both options. Boyd and Richerson (1985) suggested that individual learning would decrease when the costs associated with it increased.

The results of Chapter 3 led to the next question for Chapter 4: *what motivates a capuchin to engage in individual learning?* Since it is difficult to project ‘costly’ conditions on well-provisioned, captive capuchins with ample enrichment, Chapter 4 approached the question of individual motivation from a social perspective.

## **Chapter 4**

Much research on capuchin social learning has focused on the most complex cognitive functions such as imitation. When compelling evidence for such processes is not forthcoming, simpler processes are often assumed but rarely directly tested for. Chapter 4 aimed to specifically test for the phenomenon of social facilitation, whereby the presence of a conspecific is hypothesized to affect the motivation and behaviour of the subject, elevating the likelihood of exploration and discovery in relation to the task at hand. Using a novel foraging task sufficiently

challenging that only just over half the subjects successfully gained food from it, performance was compared between capuchin monkeys tested either alone, or in a ‘together’ condition where an actively feeding conspecific was in an adjacent chamber. Although similar numbers of subjects in these conditions were eventually successful during the 20 trials presented, the latency to successful solution of the task was over three times faster for monkeys in the together condition. These monkeys also gained the whole set of 20 rewards faster. The minority of monkeys that failed to learn (9/23) were then exposed to a proficient model. Only those older than 5 years provided evidence of learning from this. Accordingly, robust evidence was found for the social facilitation the study was designed to test for, and limited supplementary evidence for social learning in the older individuals who had not learned individually.

Chapter 4 addressed the question *what motivates exploratory foraging, and how may that lead to innovation or individual learning?* Studies of social facilitation in capuchins have focused on food choice and maintaining group cohesion, but have not directly tested for motivational effects for individual learning (Addessi & Visalberghi 2001; Galloway et al. 2005; Meunier et al. 2008). If capuchins “do not learn *from* each other”, rather they “learn *with* each other” (Fragaszy & Visalberghi 2004, p. 24), then it is imperative to address social facilitation specifically and not simply attribute it in the absence of imitation. The results of Chapter 4 showed that capuchins were on average three times faster at discovering how to collect food from the experimental apparatus when they were paired with a feeding conspecific than when they were alone, suggesting that the presence of another monkey can in

fact enhance motivation for exploratory behaviour. Nevertheless, half the subjects in the study, both from the alone and together conditions, were unable to solve the task at all. In some of these cases social learning appeared to be necessary in order for the behaviour to be acquired.

The research objective of Chapter 4 was mainly to determine how, if at all, social facilitation by itself could explain individual learning, or “learning *with* each other”, in capuchin monkeys. These results suggest that while social presence has a strong effect on motivation, opportunities for observation are critical in some circumstances.

If social presence is such a strong motivator, then to what extent does the identity of a nearby conspecific matter? Chapter 5 investigated observer preference during foraging activities, to see whether individuals preferred to watch high or low ranking models depending on their own rank within the group.

## **Chapter 5**

Chapters 2 and 3 addressed the long-standing interest in the copying abilities of monkeys. While some have argued that imitation is essential for faithful copying (Tomasello et al. 1993a,b), this perspective assumes a certain degree of attentiveness by the observer. How can a study otherwise show (or not show) copying if it has not also shown that observational learning has taken place? Chapter 5 explored this question, by investigating whether capuchin monkeys show

preferential attention to some demonstrators, over others, and specifically asked *does a model's rank affect an individual's motivation for observing them?*

In this study, capuchins from two social groups were presented with the opportunity to observe high- and/or low- status adult females during experimental foraging tests. Subjects were moved from their home closure to a test chamber that was partitioned by two opaque panels into three compartments. The subject was located in the centre compartment, with a low-ranking demonstrator and a high-ranking demonstrator on either side. A peep-hole in each opaque partition allowed the subject to see a model by looking through the hole. Each model was trained on one of the two different methods, lift or pull, for retrieving food from a foraging apparatus. This experiment involved two social groups of capuchins, and subjects were only tested with models from their own group. Thus, there were 4 models in total: one low-status female trained to lift and one high-status female trained to pull in Group A; one low-status female trained to pull and one high-status female trained to lift in Group B. This assured that rank was not correlated with the method performed.

During the 40-trial test sessions, subjects could choose which model they would watch (high versus low) in each trial. It was predicted that subjects would show a bias for observing the model with whom it was closer in rank, and therefore presumably showed greater amounts of affiliation with. The results showed that only half the subjects showed a preference, and that preference was not linked to status. It was more likely that relatedness played a larger role in determining

whether or not a subject showed a preference for a model, and a correlation was found for relatedness and observer preference. After the observer preference tests, subjects were presented with the foraging apparatus to see if they showed a preference for one of the two tasks. The majority of subjects (17/22) showed a preference for the pull method, suggesting that this method may have been more salient to the monkeys in this study.

Although rank is associated with learning opportunities in Japanese macaques (Huffman & Quiatt 1986; Leca et al. 2007a), macaques are also much more despotic in their social structure than capuchin monkeys (Chapais 1992; de Waal 1996; Flack et al. 2006) As Coussi-Korbel & Fragaszy predicted (1995) species with high levels of social tolerance should have more opportunities for social learning. Ottoni and colleagues (2005) have also suggested that capuchins' preference is not related to a demonstrator's identity, rather with the proficiency with which the demonstrator performs the task. This may explain why no significant effect for observer preference was found overall in Chapter 5, and why subjects preferred to use the possibly more conducive pull method more.

Another factor is simply the design of the study. The test chamber was small enough so that the subject could easily alternate between watching both models. In some ways these results are similar to the results of the second experiment in Chapter 3, where capuchins used both methods available; why choose if you can have both? Additionally, why choose if there is no cost involved? The opaque partitions allowed the subject to watch a higher-ranking individual in very close

proximity without the risk of physical aggression, which would be a very strong motivation in the group context for *not* watching a high-ranking demonstrator up close. In order to fully evaluate how the observer-demonstrator relationship affects the transmission of information, a more ecologically valid test scenario was necessary. Thus the final study in this thesis aimed to examine the open diffusion of novel foraging behaviours in two large social groups of capuchin monkeys.

## **Chapter 6**

Chapters 2 – 5 investigated whether capuchins can copy, when they copy, and what motivates them to engage in the behaviours they observe. Chapter 6 expanded upon these findings to see how learning takes place at the group level. How do novel behaviours spread throughout a group to become a tradition? Experimental studies to date do not support the conclusion that capuchins, and other monkeys, are capable of the social learning capacities required to support the traditions or potentially cultural behaviours observed in the field (Visalberghi & Fragaszy 1990, 2002). Chapter 6 presented a new experimental approach with capuchin monkeys, in which the alpha male of each of two groups of captive capuchins was trained to open an artificial foraging device in a unique, but equally difficult way. Following training, the alpha males were reunited with their groups, and allowed to demonstrate the foraging technique in the presence of their group mates. In each group a majority of monkeys, 8/11 and 13/14, subsequently mastered the task. Seventeen of the 21 successful monkeys discovered the alternative action to that seeded in the group, performing it a median of 4 times. Nevertheless, all 21 monkeys primarily adopted the alternative technique seeded in their group. These

results demonstrated a striking effect of social conformity in learned behavioural techniques, consistent with field reports of capuchin traditions and convergent on the only other primate species in which such cultural phenomenon has been reported, namely chimpanzees and humans (Asch 1956, Whiten et al. 2005).

The final research chapter of this thesis presents the ‘collective outcome’ of the previous research chapters, in that the design of the study (1) utilized an apparatus that was within the physical repertoire of the monkey subjects, (2) used high ranking models that would not be displaced during the observer phase of testing, (3) provided hour long sessions so that no individual could monopolize the apparatus for the entire test, and (4) examined the social spread within the ‘normal’ day-to-day living quarters of two large groups of capuchin monkeys. By giving the monkeys the choice to move from the indoor and outdoor enclosures, the transmission was not dictated by the experimenter, instead it was a reflection of the social affiliations within each group.

The most notable finding in this study was an effect of conformity. Conformity, like imitation, has been subject to several interpretations. In the most basic form, it involves following the majority, which has been demonstrated in fish (Day et al. 2001), rats (Galef & Whiskin 2008), and birds (Lachlan et al. 2004). The kind of conformity found here is of a more robust nature, in that conformity overrides familiarity with alternative methods. The majority of subjects in this study discovered the alternative method at some point, but they continued to employ the predominant group method that had initially been demonstrated by the trained

models. This effect has not previously been shown in any monkey species, and is perhaps due to the two-action task and open-diffusion paradigm of the study, which has only previously been used with two small groups of colobus monkeys (Price & Caldwell 2007). In this study (Chapter 6), subjects essentially ‘took turns’ at the apparatus, since no one individual, aside from the models, was able to monopolize the apparatus, thus possibly reinforcing the group method through opportunities for observation.

### ***Conclusions***

Each chapter of this thesis focused on aspects of social influence or social learning that may support behaviour transmission and culture in capuchin monkeys. Together these findings present some of the first solid evidence for copying, transmitting and sustaining traditions, and conformity to group norms, which are considered hallmarks of culture (Kroeber 1928; Galef 1992; McGrew 1998; Tomasello & Call 1997; Whiten & van Schaik 2007).

I believe the strength of these experiments came from shifting the research interest away from imitative learning specifically, instead focusing on what may lead to matching-matching or faithful copying of others. Future research should take this into account, by asking *when* and *why* do monkeys copy?

## References

- Adams-Curtis, L., & Fragaszy, D. M. (1995). Influence of a skilled model on the behavior of conspecific observers in tufted capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *37*, 65-71.
- Addressi, E., Chiarotti, F., Visalberghi, E., & Anzenberger, G. (2007). Response to novel food and the role of social influences in common marmosets (*Callithrix jacchus*) and Goeldi's monkeys (*Callimico goeldii*). *American Journal of Primatology*, *69*(11), 1210-1222.
- Addressi, E., & Visalberghi, E. (2001). Social facilitation of eating novel foods in tufted capuchin monkeys (*Cebus apella*): input provided, responses affected, and cognitive implications. *Animal Cognition*, *4*, 297-303.
- Aisner, R., & Terkel, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. *Animal Behaviour*, *44*, 327-336.
- Akins, C. K., Klein, E. D., & Zentall, T. R. (2002). Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Animal Learning & Behavior*, *30*(3), 275-281.
- Akins, C. K., & Zentall, T. R. (1996). Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *Journal of Comparative Psychology*, *110*(3), 316-320.
- Asch, S. E. (1956). Studies of independence and conformity: A minority of one against a unanimous majority. *Psychological Monographs*, *70*, 1-70.
- Baldwin, J. M., (1895) Consciousness and evolution. *Science*, *2*, 219-223.
- Baldwin, J. M., (1902). *Development and Evolution*. New York: Macmillan.
- Bartlett, F. (1932). *Remembering*. Oxford: Macmillan.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, *6*(4), 213-223.
- Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica*, *54*, 86.

- Boinski, S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology*, 14(2), 177-179.
- Boinski, S. (2000). Social manipulation within and between troops mediates primate group movement. In S. Boinski & P. A. Garber (Eds.), *On the Move. How and Why Animals Travel in Groups* (pp. 421-469). Chicago: The University of Chicago Press.
- Boinski, S., & Garber, P. A. (2000). New directions for group movement. In S. Boinski & P. A. Garber (Eds.), *On the Move. How and Why Animals Travel in Groups*. Chicago: The University of Chicago Press.
- Boinski, S., Quatrone, R. P., Sughrue, K., Selvaggi, L., Henry, M., Stickler, C. M., et al. (2003). Do brown capuchins socially learn foraging skills? In *The biology of traditions: models and evidence* (pp. 365-390). New York: Cambridge University Press.
- Boinski, S., Quatrone, R. P., & Swartz, H. (2000). Substrate and tool use by brown capuchins in Suriname: Ecological contexts and cognitive bases. *American Anthropologist*, 102(4), 741-761.
- Bonnie, K. E., & de Waal, F. B. M. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, 47(1), 27-34.
- Bonnie, K. E., & de Waal, F. B. M. (2007). Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Animal Cognition*, 10(3), 283-292.
- Bonnie, K., Horner, V., Whiten, A. & de Waal, F. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B: Biological Sciences*, 274, 367-372.
- 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.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.

- Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, 425(6955), 297-299.
- Brown, C. & Laland, K. N. (2006). Social learning in fishes. In *Fish Cognition and Behavior* (ed. C. Brown, K. N. Laland & J. Krause), pp. 186-202. Oxford: Blackwell.
- Bugnyar, T., & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour*, 54, 817-831.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, 10(4), F31-F38.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2008). Rational tool use and tool choice in human infants and great apes. *Child Development*, 79(3), 609-626.
- 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.
- Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition*, 8(3), 151-163.
- Cambefort, J. P. (1981). A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. *Folia Primatologica*, 36, 243-263.
- 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.
- Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology*, 67, 151-174.
- Chalmeau, R., & Gallo, A. (1993). Social constraints determine what is learned in the chimpanzee. *Behavioural Processes*, 28, 173-180.
- Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In A. Harcourt & F. d. Waal (Eds.), *Coalitions and alliances in humans and other animals*. New York: Oxford University Press. pp. 29-59

- Clayton, D. A. (1978). Socially facilitated behavior. *Quarterly Review of Biology*, 53, 373-391.
- Coussi-Korbel, S., & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441-1453.
- Curio, E., Ernst, U., & Vieth, W. (1978). Cultural transmission of enemy recognition: one function of mobbing. *Science*, 202(4370), 899-901.
- Custance, D. (1998). Apes ape! *Behavioral and Brain Sciences*, 21(1), 118-119.
- Custance, D., Prato-Previde, E., Spiezio, C., & Rigamonti, M. M. (2006). Social learning in pig-tailed macaques (*Macaca nemestrina*) and adult humans (*Homo sapiens*) on a two-action artificial fruit. *Journal of Comparative Psychology*, 120(3), 303-313.
- 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), 13-23.
- Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H. (2004). Public information: from noisy neighbors to cultural evolution. *Science* 305, 487-491.
- Darwin, C. (1871). *The descent of man*. London: Murray.
- 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, 559-571.
- Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. (2001). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, 62, 917-925.
- de Waal, F. B. M. (1996a). *Good natured: the origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press.
- de Waal, F. B. M. (1996b). Macaque social culture: development and perpetuation of affiliative networks. *Journal of Comparative Psychology*, 110, 147-154.
- de Waal, F. B. M. (1997). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology*, 111(4), 370-378.

- de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, 60, 253-261.
- de Waal, F. B. M. (2001). *The ape and the sushi master: cultural reflections by a primatologist*. London: Penguin Press.
- de Waal, F. B. M. (2003). *My family album: thirty years of primate photography*. Berkeley: University of California Press.
- de Waal, F. B. M., & Bonnie, K. E. (in press). In tune with others: the social side of primate culture. In K. N. Laland & B. G. Galef (Eds.), *The Question of Animal Culture*. Cambridge, MA: Harvard University Press.
- de Waal, F. B. M., & Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology*, 43, 339-346.
- Dindo, M. (in press). Social learning and behavior transmission. In G. Koob, R.F. Thompson, & M. Le Moal (Eds.), *Encyclopedia of Behavioral Neuroscience*. Oxford: Elsevier Press.
- Dindo, M., & de Waal, F. B. (2007). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology*, 69(4), 448-456.
- Dindo, M., de Waal, F. B. M., Thierry, B., & Whiten, A. (submitted). Conditional copying fidelity in capuchin monkeys
- 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. M. (in press). Social facilitation of exploratory foraging behavior in capuchin monkeys. *American Journal of Primatology*.
- Drea, C. M., & Wallen, K. (1999). Low-status monkeys "play dumb" when learning in mixed social groups. *Proceedings of the National Academy of Sciences of the United States of America*, 96(22), 12965-12969.
- Fawcett, T. W., Skinner, A. M. J., & Goldsmith, A. R. (2002). A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour*, 64(4), 547-556.
- Ferrari, P. F., Maiolini, C., Addessi, E., Fogassi, L., & Visalberghi, E. (2005). The observation and hearing of eating actions activates motor programs related

- to eating in macaque monkeys. *Behavioural Brain Research*, 161(1), 95-101.
- Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, 4(9), 1501-1508.
- Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439(7075), 426-429.
- Fragaszy, D. M. (2003). Making space for traditions. *Evolutionary Anthropology*, 12(2), 61-70.
- Fragaszy, D. M., Deputte, B. L., Hemery, C., & Johnson, M. H. (1998). *Human-reared capuchins match familiar but not novel actions*. Unpublished manuscript.
- Fragaszy, D. M., Fedigan, L. M., & Visalberghi, E. (2004). *The complete capuchin: the biology of the genus cebus*. New York: Cambridge University Press.
- Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B., & Gomes de Oliveira, M. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, 64, 359-366.
- Fragaszy, D. M., & Perry, S. (2003). *The biology of traditions: models and evidence*. New York: Cambridge University Press.
- Fragaszy, D. M., & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 103, 159-170.
- Fragaszy, D. M., & Visalberghi, E. (1996). Social learning in monkeys: primate "primacy" reconsidered. In C. Heyes & R. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*. San Diego: Academic Press. pp. 65-84.
- Fragaszy, D. M., & Visalberghi, E. (2001). Recognizing a swan: Socially-biased learning. *Psychologia*, 44(1), 82-98.
- Fragaszy, D.M., & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning & Behavior*, 32(1), 24-35.

- Fragaszy, D. M., Vitale, A. F., & Ritchie, B. (1994). Variation among juvenile capuchins in social influences on exploration. *American Journal of Primatology*, 32(4), 249-260.
- Fredman, T., & Whiten, A. (2008). Observational learning from tool using models by human-reared and mother-reared capuchin monkeys (*Cebus apella*). *Animal Cognition*, 11(2), 295-309.
- Galef, B. G. (1988). Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In T. Zentall & B. G. Galef (Eds.), *Social Learning: Psychological and Biological Perspectives*. Hillsdale, NY: Erlbaum.
- Galef, B. G. (1990). Tradition in animals: field observations and laboratory analyses. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and Explanation in the Study of Animal Behavior, Vol. 1: Interpretation, Intentionality, and Communication*. Boulder, CO: Westview Press. pp. 74-95.
- Galef, B. G. (1992). The question of animal culture. *Human Nature*, 3, 157-178.
- Galef, B. G. (1993). Functions of social-learning about food - a causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour*, 46(2), 257-265.
- Galef, B. G. (2003). "Traditional" foraging behaviours of brown and black rats (*Rattus norvegicus* and *Rattus rattus*). In D. M. Fragaszy & S. Perry (Eds.) *The biology of traditions: models and evidence*. Cambridge, UK: Cambridge University Press. pp. 159-186.
- Galef, B. G. & Giraldeau, L. A. (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour* 61, 3-15.
- Galef, B. G. & Heyes, C. H. E. (2004) Special issue on social learning in animals. *Learning & Behavior* 32, 1-140.
- Galef, B. G., Manzig, L. A., & Field, R. M. (1986). Imitation learning in budgerigars: Dawson and Foss (1965) revisited. *Behavioural Processes*, 13(1-2), 191-202.
- Galef, B. G., & Whiskin, E. E. (2008). 'Conformity' in Norway rats? *Animal Behaviour*, 75(6), 2035-2039.

- Galloway, A. T., Addessi, E., Frigaszy, D. M., & Visalberghi, E. (2005). Social facilitation of eating familiar food in tufted capuchins (*Cebus apella*): does it involve behavioral coordination? *International Journal of Primatology*, 26(1), 181-189.
- Gergely, G., Bekkering, H., & Kiraly, I. (2002). Rational imitation in preverbal infants. *Nature*, 415(6873), 755.
- Haggerty, M. E. (1909). Imitation in monkeys. *Comparative Neurology and Psychology*, 19, 337-441.
- Harlow, H. F., & Yudin, H. C. (1933). Social behavior of primates. I. Social facilitation of feeding in the monkey and its relation to attitudes of ascendance and submission. *Journal of Comparative Psychology (1921)*, 16(2), 171-185.
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165-196.
- Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour*, 46(5), 999-1010.
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, 69, 207-231.
- Heyes, C. M. (1996). Genuine Imitation? In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: the Roots of Culture*. London: Academic Press, pp. 371-390.
- Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational-learning in rats using a bidirectional control. *Quarterly Journal Of Experimental Psychology Section B-Comparative And Physiological Psychology*, 42(1), 59-71.
- Heyes, C. M., Jaldow, E., & Dawson, G. R. (1994). Imitation in rats: conditions of occurrence in a bidirectional control paradigm. *Learning and Motivation*, 25, 276-287.
- Heyes, C. M., Ray, E. D., Mitchell, C. J., & Nokes, T. (2000). Stimulus enhancement: Controls for social facilitation and local enhancement. *Learning and Motivation*, 31(2), 83-98.

- Heyes, C. M., & Saggerson, A. (2002). Testing for imitative and non-imitative social learning in the budgerigar using a two-object/two-action test. *Animal Behaviour*, *64*, 851-859.
- Hinde, R. A., & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *British Birds*, *44*, 393-396.
- 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*, 1021-1032.
- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*(3), 164-181.
- Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the USA*, *103*(37), 13878-13883.
- Hsia, L. C., & Wood-Gush, D. G. M. (1984). Social facilitation in the feeding behavior of pigs and the effect of rank. *Applied Animal Ethology*, *11*, 265-270.
- Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, *62*(5), 945-954.
- Huffman, M. A. (1984). Stone-play of *Macaca fuscata* in Arashiyama B troop: transmission of a non-adaptive behavior. *Journal of Human Evolution*, *13*, 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. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*. New York: Academic Press, pp. 267-289.
- Huffman, M. A., & Quiatt, D. (1986). Stone handling by Japanese macaques (*Macaca fuscata*): implications for tool use of stone. *Primates*, *27*, 413-423.

- Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, 58(3), 133-148.
- Humle, T., & Snowdon, C. T. (2008). Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, 75(1), 267-277.
- Hurley, S. & Chater, N. (2005). *Perspectives on imitation: from neuroscience to social science*. Cambridge, MA: MIT Press.
- Imanishi, K. (1957). Social behavior in Japanese monkeys, *Macaca fuscata*. *Psychologia*, 1, 47-54.
- James, W. T. (1953). Social facilitation of eating behavior in puppies after satiation. *Journal of Comparative Physiological Psychology*, 46, 427-428.
- Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, 6, 1-30.
- Keeling, L. J., & Hurnik, J. F. (1993). Chickens show socially facilitated feeding behavior in response to a video image of a conspecific. *Applied Animal Behaviour Science*, 36, 223-231.
- Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of Callitrichid monkeys. *American Journal of Primatology*, 66, 167-188.
- King, B. J. (1994). Evolutionism, essentialism, and an evolutionary perspective on language: moving beyond a human standard. *Language and Communication*, 14, 1-13.
- Klein, E. D., & Zentall, T. R. (2003). Imitation and affordance learning by pigeons (*Columba livia*). *Journal of Comparative Psychology*, 117(4), 414-419.
- Köhler, W. (1927). *The mentality of apes* (Second ed.). London.
- Kroeber, A. L. (1928). Sub-human culture beginnings. *Quarterly Review of Biology*, 3, 325-342.
- Lachlan, R. F., Janik, V. M., & Slater, J. B. (2004). The evolution of conformity-enforcing behaviour in cultural communication systems. *Animal Behaviour*, 68, 561-570.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4-14.

- Laland, K. N., & Galef, B. G. (Eds.). (in press). *The Question of Animal Culture*. Cambridge: Harvard University Press.
- Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology*, *12*, 150-159.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542-547.
- Laland, K. N., Odling-Smee, J., & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, *23*, 131-175.
- Laland, K. N., & Plotkin, H. C. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning & Behavior*, *18*(3), 246-251.
- Laland, K. N., & Plotkin, H. C. (1992). Further experimental analysis of the social learning and transmission of foraging information amongst Norway rats. *Behavioural Processes*, *27*, 53-64.
- Laland, K. N., & Plotkin, H. C. (1993). Social transmission of food preferences among Norway rats by marking of food sites and by gustatory contact. *Animal Learning & Behavior*, *21*(1), 35-41.
- Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour*, *57*, 331-340.
- Laland, K. N., & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, *53*(6), 1161-1169.
- Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, *9*(5), 493-499.
- Leca, J. B., Gunst, N., & Huffman, M. A. (2007a). Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour*, *144*, 251-281.
- Leca, J. B., Gunst, N., Watanabe, K., & Huffman, M. A. (2007b). A new case of fish-eating in Japanese macaques: implications for social constraints on the diffusion of feeding innovation. *American Journal of Primatology*, *69*(7), 821-828.

- Lefebvre, L. (1986). Cultural-diffusion of a novel food-finding behavior in urban pigeons: an experimental field test. *Ethology*, 71(4), 295-304.
- Lefebvre, L., & Giraldeau, L. A. (1994). Cultural transmission in pigeons is affected by the number of tutors and bystanders present. *Animal Behaviour*, 47(2), 331-337.
- Lonsdorf, E. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, 9(1), 36-46.
- Lonsdorf, E., Lynn E. Eberly, A. V., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees *Nature*, 428(6984), 715-716.
- Matheson, M. D., & Fragaszy, D. M. (1998). Imitation is not the "Holy Grail" of comparative cognition. *Behavioral and Brain Sciences*, 21(5), 697-698.
- Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: education by master-apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557-574). Tokyo: Springer.
- McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C. (1998). Culture in nonhuman primates? *Annual Review of Anthropology*, 27, 301-328.
- McGrew, W. C. (2001). The nature of culture: Prospects and pitfalls of cultural primatology. In F. B. M. de Waal (Ed.), *Tree of Origin: What primate behavior can tell us about human social evolution*. Cambridge, MA: Harvard University Press.
- McGrew, W. C. (2004). *The cultured chimpanzee: reflections on cultural primatology*. New York: Cambridge University Press.
- McGrew, W. C., Marchant, L. F., Nakamura, M., & Nishida, T. (2001a). Local customs in wild chimpanzees: The grooming hand-clasp in the Mahale Mountains, Tanzania. *American Journal of Physical Anthropology*, 107-107.

- McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. G. (2001b). Inter-group differences in a social custom of wild chimpanzees: the grooming hand-clasp of the Mahale mountains. *Current Anthropology*, *42*, 148-153.
- Meltzoff, A., & Gopnik, A. (1993). The role of imitation in understanding persons and developing a theory of mind. In S. Baron-Cohen, Tager-Flusberg, H., & Cohen, D. J. (Eds.), *Understanding other minds: Perspectives from autism*. New York : Oxford University Press, pp. 335-366.
- Menzel, E. W., Davenport, R. K., & Rogers, C. M. (1972). Protocultural aspects of chimpanzees' responsiveness to novel objects. *Folia primatologica*, *17*(3), 161-170.
- Meunier, H., Petit, O., & Deneubourg, J. L. (2008). Social facilitation of fur rubbing behavior in white-faced capuchins. *American Journal of Primatology*, *70*, 161–168.
- Miklosi, A. (1999). The ethological analysis of imitation. *Biological Reviews*, *74*(3), 347-374.
- Mills, W. (1899). The nature of animal intelligence and the methods of investigating it. *Psychological Review* *6*(262-274).
- Mitchell, C. J., Heyes, C. M., Gardner, M. R., & Dawson, G. R. (1999). Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour Cues on the Manipulandum. *Quarterly Journal of Experimental Psychology: Section B*, *52*(3), 193-202.
- Morgan, C. L. (1900). *Animal Behaviour*. London: Edward Arnold.
- Moscovice, L. R., & Snowdon, C. T. (2006). The role of social context and individual experience in novel task acquisition in cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, *71*(4), 933-943.
- Moura, A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*, 1909.
- Moura, A. C. A. (2007). Stone banging by wild capuchin monkeys: an unusual auditory display. *Folia Primatologica*, *78*(1), 36-45.
- Nahallage, C. A., & Huffman, M. A. (2007). Age-specific functions of stone handling, a solitary-object play behavior, in Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, *69*(3), 267-281.

- Nakamura, M., & Uehara, S. (2004). Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: Implications for chimpanzee social customs. *Current Anthropology*, 45, 108-114.
- Nguyen, N. H., Klein, E. D., & Zentall, T. R. (2005). Imitation of a two-action sequence by pigeons. *Psychonomic Bulletin & Review*, 12(3), 514-518.
- Nishida, T. (1987). Local traditions and cultural transmission. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate Societies*. Chicago: The University of Chicago Press, pp. 462-474.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T., & Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift für Tierpsychologie*, 67, 284-301.
- Nishida T., Wrangham RW, Goodall J, Uehara S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution*, 12(5):467-480.
- Otoni, E. B., & Mannu, M. (2001). Semi-free ranging tufted capuchin monkeys (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology*, 22, 347.
- Otoni, E. B., & Mannu, M. (2003). Spontaneous use of tools by semifree-ranging capuchin monkeys. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal Social Complexity: Intelligence, culture and individualized societies*. Cambridge, MA: Harvard University Press, pp. 440-443.
- Otoni, E. B., 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.
- Panger, M. A., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., Mackinnon, K. C., et al. (2002). Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 119(1), 52-66.
- Perry, S. (2006). What cultural primatology can tell anthropologists about the evolution of culture. *Annual Review of Anthropology*, 35, 171-190.

- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., et al. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. *Current Anthropology*, 44(2), 241-268.
- Perry, S., & Manson, J. H. (2003). Traditions in monkeys. *Evolutionary Anthropology*, 12, 71-81.
- Perry, S., & Ordonez Jimenez, J. C. (2006). The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In G. Hohmann, M. M. Robbins & C. Boesch (Eds.), *Feeding ecology in apes and other primates: ecological, physical and behavioral aspects* (pp. 203-234). New York: Cambridge University Press.
- Pitcher, T. J., & Parrish, J. K. (1993). Functions of shoaling behaviour in teleosts. In T. J. Pitcher (Ed.), *The Behaviour of Teleost Fishes* (2nd ed.). London: Chapman & Hall, pp. 363-440.
- Prato-Previde, E., & Poli, M. (1996). Social learning in the golden hamster (*Mesocricetus auratus*). *Journal of Comparative Psychology*, 110, 203-208.
- Price, E., & Caldwell, C. A. (2007). Artificially generated cultural variation between two groups of captive monkeys, *Colobus guereza kikuyuensis*. *Behavioural Processes*, 74(1), 13-20.
- Range, F., & Huber, L. (2008). Attention in common marmosets: implications for social-learning experiments. *Animal Behaviour*, 73(6), 1033-1041.
- Range, F., Viranyi, Z., & Huber, L. (2007). Selective imitation in domestic dogs. *Current Biology*, 17(10), 868-872.
- Reader, S. M., Kendal, J. R., & Laland, K. N. (2003). Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, 66, 729-739.
- Reader, S. M., & Laland, K. N. (2000). Diffusion of foraging innovations in the guppy. *Animal Behaviour*, 60, 175-180.
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, 22, 787-805.

- Resende, B. D., & Ottoni, E. B. (2002). Observational learning in the manipulation of a problem-box by tufted capuchin monkeys (*Cebus apella*). *Revista de Etologia (São Paulo)*, 3, 89-94.
- Rigamonti, M. M., Custance, D. M., Previde, E. P., & Spiezio, C. (2005). Testing for localized stimulus enhancement and object movement reenactment in pig-tailed macaques (*Macaca nemestrina*) and young children (*Homo sapiens*). *Journal of Comparative Psychology*, 119(3), 257-272.
- Rilling, J. K., & Insel, T. R. (1999). The primate neocortex in comparative perspective using magnetic resonance imaging. *Journal of Human Evolution*, 37, 191-223.
- Romanes, G. (1884). *Mental Evolution in Animals*. New York: Appleton.
- Rose, L. M., Perry, S., Panger, M. A., Jack, K., Manson, J. H., Gros-Louis, J., et al. (2003). Interspecific interactions between *Cebus capucinus* and other species: data from three Costa Rican sites. *International Journal of Primatology*, 24, 759-795.
- Ross, S., & Ross, J. G. (1949). Social facilitation of feeding behavior in dogs: II. Feeding after satiation. *Journal of Genetic Psychology*, 74, 293-304.
- Schweir, C., van Maanan, C., Carpenter, C. & Tomasello, M. (2006). Rational imitation in 12-month-old infants. *Infancy*, 10, 303-311.
- Shettleworth, S. J. 2001 Animal cognition and animal behaviour. *Animal Behaviour*, 61, 277-286.
- Spence, K. W. (1937). Experimental studies of learning and the higher mental processes in infra-human primates. *Psychological Bulletin*, 34, 806-850.
- Stanley, E. L., Kendal, R. L., Kendal, J. R., Grounds, S. & Laland, K. N. (2008). The effects of group size, rate of turnover and disruption to demonstration on the stability of foraging traditions in fishes. *Animal Behaviour*, 75, 565-572.
- Stoinski, T. S., & Whiten, A. (2003). Social learning by orangutans (*Pongo abelii* and *Pongo pygmaeus*) in a simulated food-processing task. *Journal of Comparative Psychology*, 117(3), 272-282.

- Stoinski, T. S., Wrate, J. L., Ure, N., & Whiten, A. (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology*, 115(3), 272-281.
- Subiaul, F. (2007). The imitation faculty in monkeys: evaluating its features, distribution and evolution. *Journal of Anthropological Sciences*, 85, 35-62.
- Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation in rhesus macaques. *Science*, 305(5682), 407-410.
- Tennie, C., Call, J. & Tomasello, M. (2006). Push or pull: emulation versus imitation in great apes and human children. *Ethology* 112, 1159-1169.
- Terkel, J. (1996). Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In C. M. Heyes & B. G. Galef Jr. (Eds.), *Social learning in animals: The roots of culture*. London: Academic Press, pp. 17-48.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Review Monographs, Suppl.* 2(8).
- Thorndike, E. L. (1911). *Animal Intelligence*. New York, NY: Macmillan.
- Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen.
- Thorpe, W. H. (1963). *Learning and Instinct in Animals* (2nd ed.). London: Methuen.
- Tolman, C. W. (1964). Social facilitation of feeding behavior in the domestic chick. *Animal Behaviour*, 12, 245-251.
- Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In S. T. Parker & K. R. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*. Cambridge: Cambridge University Press, pp. 275-311.
- Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture*. New York: Academic Press, pp. 319-345.
- Tomasello, M. (1999). The human adaptation for culture. *Annual Review Of Anthropology*, 28, 509-529.

- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993a). Cultural Learning. *Behavioral And Brain Sciences*, 16(3), 495-511.
- Tomasello, M., Savagerumbaugh, S., & Kruger, A. C. (1993b). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development*, 64(6), 1688-1705.
- Uehara, S., Nishida, T., Takasaki, H., Kitopeni, R., Kasagula, M. B., Norikoshi, K., et al. (1994). A lone male chimpanzee in the wild: the survivor of a disintegrated unit-group. *Primates*, 35, 275-281.
- Ueno, A. (2005). Development of co-feeding behavior in young wild Japanese macaques (*Macaca fuscata*). *Infant Behavior and Development*, 28, 481-491.
- van Schaik, C. P. (2003). Local traditions in orangutans and chimpanzees: Social learning and social tolerance. In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: models and evidence*. New York: Cambridge University Press, pp. 297-328.
- van Schaik, C. (2006). Why are some animals so smart? *Scientific American*, April, 64-71.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singletin, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science* 299, 102-105.
- Verderane, M. P., Falotico, T., Resende, B. D., Labruna, M. B., Izar, P., & Ottoni, E. B. (2007). Anting in a semifree-ranging group of *Cebus apella*. *International Journal of Primatology*, 28(1), 47-53.
- Visalberghi, E. (1987). Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia Primatologica*, 49, 168-181.
- Visalberghi, E., & Addessi, E. (2000). Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour*, 60, 69-76.

- Visalberghi, E., Fragaszy, D., Fedigan, L., Izawa, K., Robinson, J., Defler, T., et al. (1987). Toward Understanding Behavioral Adaptability in Cebus. *International Journal of Primatology*, 8(5), 404-404.
- Visalberghi, E., & Fragaszy, D. M. (2002). Do monkeys ape? Ten years after. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 471-500). Cambridge, MA: MIT Press.
- Visalberghi, E., Fragaszy, D. M., Izar, P., & Ottoni, E. B. (2005). Terrestriality and tool use. *Science*, 308(5724), 951-951.
- Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 108(1), 15-22.
- Visalberghi, E., & Munkenbeck-Fragaszy, D. (1990). Do monkeys ape? In T. S. Parker & K. R. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (pp. 247-273). Cambridge: Cambridge University Press.
- Visalberghi, E., & Trinca, L. (1989). Tool use in capuchin monkeys: distinguishing between performing and understanding. *Primates*, 30, 511-521.
- Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60(2), 195-202.
- Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLOS One*, 2(7), 1-5.
- Voelkl, B., Schrauf, C., & Huber, L. (2006). Social contact influences the response of infant marmosets towards novel food. *Animal Behaviour*, 72, 365-372.
- Warden, C. J., & Jackson, T. A. (1935). Imitative behavior in the Rhesus monkey. *Pedagogical Seminar*, 46, 103-125.
- Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature*, 335, 719-721.
- Watanabe, K. (1994). Precultural behavior of Japanese macaques: longitudinal studies of the Koshima troops. In R. A. Gardner, B. T. Gardner, A. B. Chiarelli & F. X. Plooij (Eds.), *The Ethological Roots of Culture*. Netherlands: Kluwer Academic Publishers, pp. 81-94.

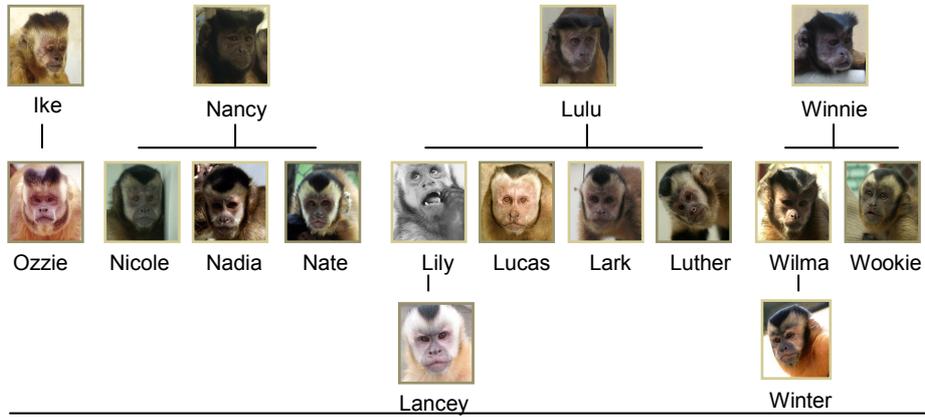
- Watanabe, K. (2001). A review of 50 years of research on the Japanese monkeys of Koshima: status and dominance. In T. Matsuzama (Ed.), *Primate Origins of Human Cognition and Behavior*. Tokyo: Springer, pp. 405-407.
- Westergaard, G. C., Lundquist, A. L., Haynie, M. K., Kuhn, H. E., & Suomi, S. J. (1998). Why some capuchin monkeys (*Cebus apella*) use probing tools (and others do not). *Journal of Comparative Psychology*, *112*(2), 207-211.
- Westergaard, G. C., Wagner, J. L., & Suomi, S. J. (1999). Manipulative tendencies of captive *Cebus albifrons*. *International Journal of Primatology*, *20*(5), 751-759.
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *112*(3), 270-281.
- Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*(3), 477-508.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature* *437*, 52-55.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (1999). Cultures in chimpanzees. *Nature* *399*, 682-685.
- 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*, 239-283.
- Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*(7059), 737-740.
- Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning & Behavior*, *32*(1), 36-52.
- Whiten, A., & Mesoudi, A. (2008). Review. Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1509), 3477-3488.
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. & de Waal, F. B. M. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology* *17*, 1038-1043.

- Whiten, A., & van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 603-620.
- Yoerg, S. I. (1991). Social feeding reverses learned flavor aversions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, 105, 185-189.
- Zajonc, R. B. (1965). Social Facilitation. *Science*, 149, 269-274.
- Zentall, T. R. (2006). Imitation: definitions, evidence, and mechanisms. *Animal Cognition*, 9(4), 335-353.
- Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, 7(6), 343-346.

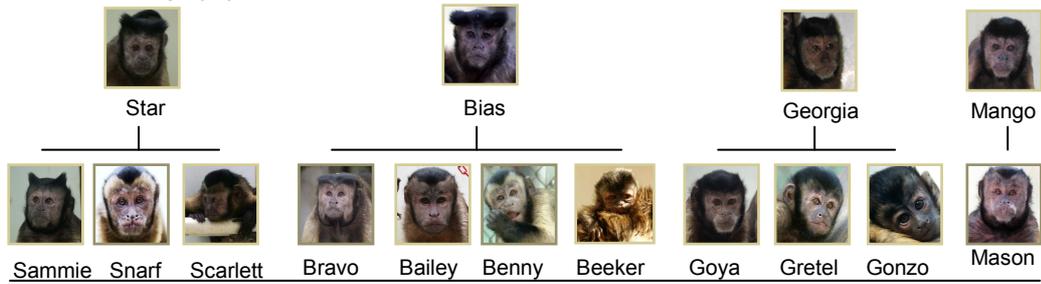
# Appendices

## Appendix A – Family Trees

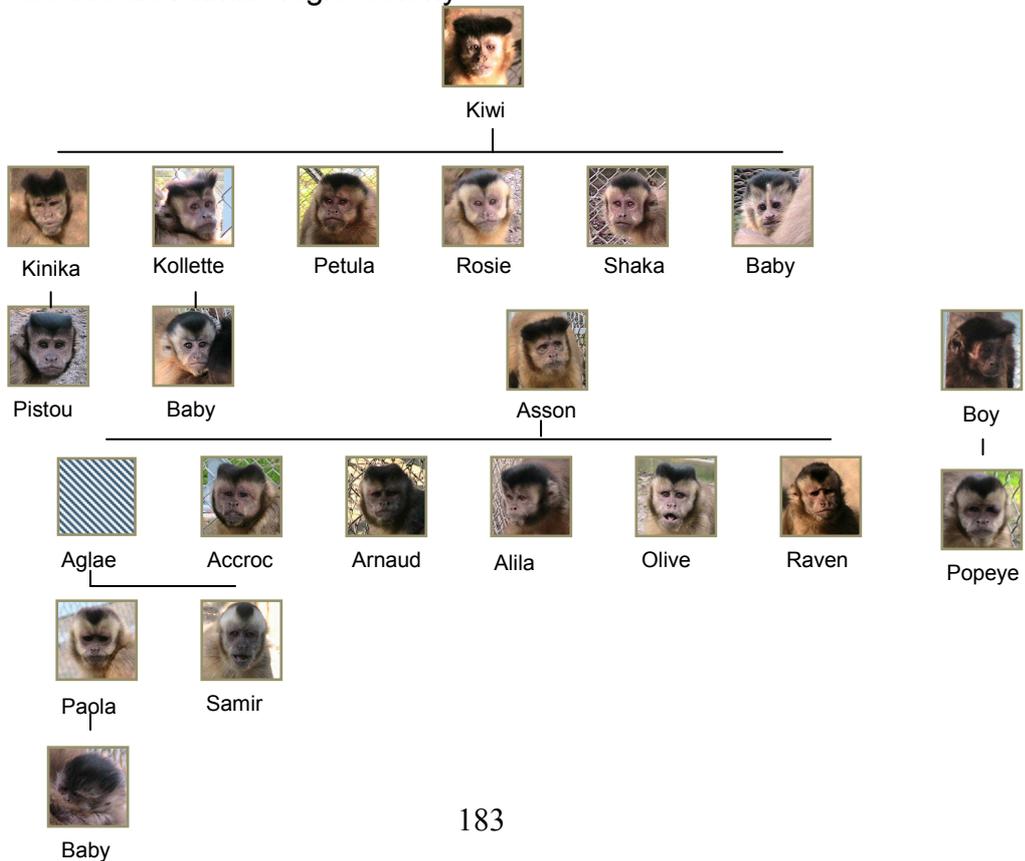
### Nuts Group (A)



### Bolts Group (B)



### Centre de Primatologie Colony



*Appendix B – Study subjects, ranks, and reference codes*

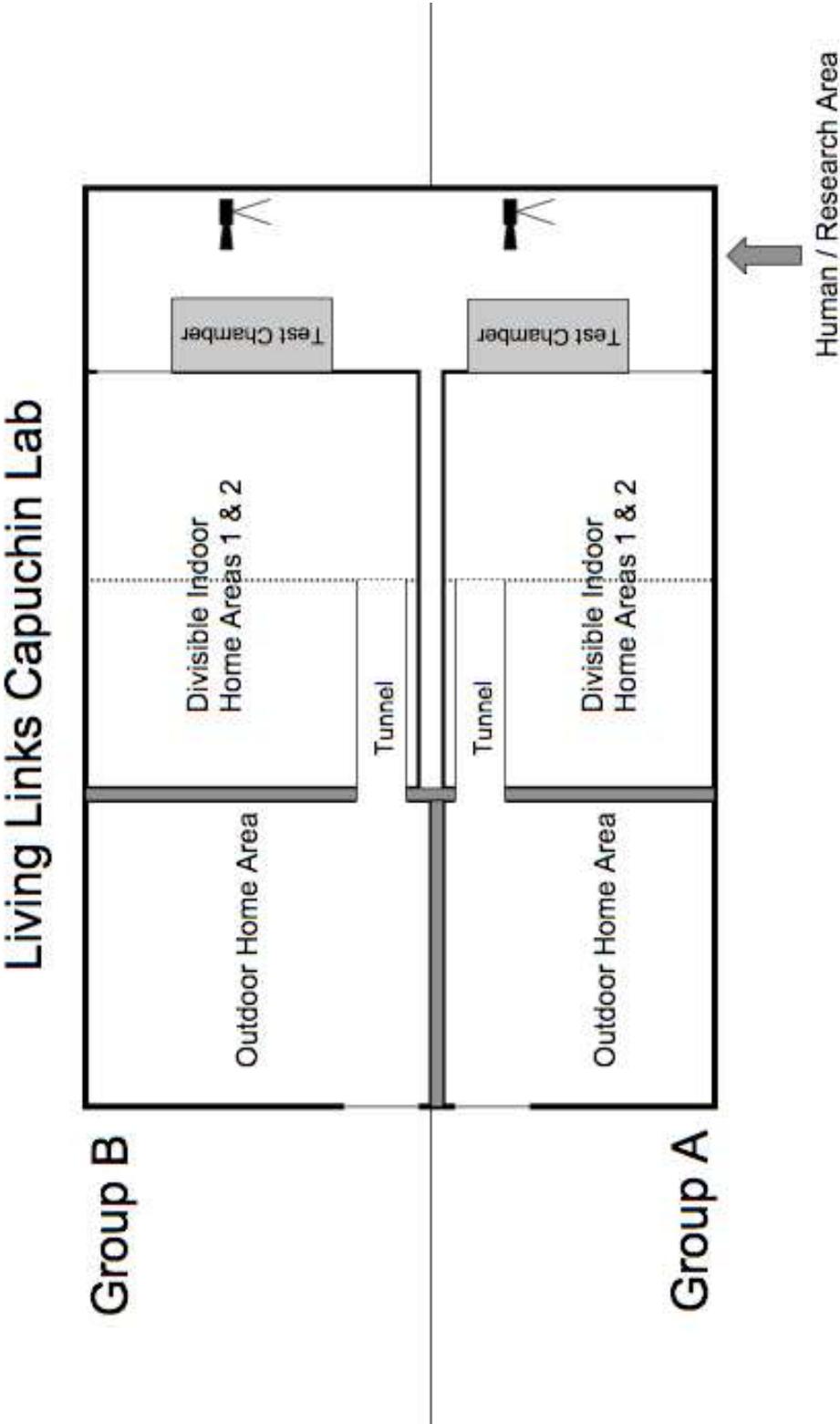
\* Represents monkeys retired to a sanctuary in Jan 2008  
 (-) denotes infants that were too young to be ranked

<b>NUTS GROUP (Colony A)</b>				
Name	Code	D.O.B.	SEX	RANK
Ike	IK	10/16/75	M	H
Lulu	LL	<1984>	F	L
Lance	LA	3/13/02	F	L
Lucas	LC	4/30/00	M	H
Lark	LR	6/23/02	F	L
Luther	LH	1/17/05	M	H
Nancy	NN	<1985>	F	M1
Nicole	NI	12/2/99	F	M2
Nadia	ND	5/16/01	F	L
Nate	NT	8/8/04	M	H
Ozzie	OZ	2/1/88	M	H
Winnie	WN	<1984>	F	M2
Wilma	WL	9/13/97	F	M1
Winter	WT	6/8/04	F	M2
Wookie	WO	6/25/04	M	M1

<b>BOLTS GROUP (Colony B)</b>				
Name	Code	D.O.B.	SEX	RANK 07/08
Bias	BI	<1987>	F	H / M1
Bravo	BR	8/23/93	M	H / *
Bailey	BA	11/9/99	F	H / L
Benny	BE	12/9/03	M	H / M
Beeker	BK	3/30/06	F	(-) / M1
Georgia	GG	<1985>	F	L / *
Gretel	GR	11/30/03	F	L / L
Goya	GY	11/9/92	F	L / *
Gonzo	GN	12/22/05	M	(-) / M1
Mango	MG	<1960s>	F	L / L
Mason	MS	3/9/98	M	H / H
Star	ST	<1970s>	F	H / H
Sammie	SM	7/23/96	F	H / M1
Snarf	SN	3/13/03	M	M1 / M1
Scarlett	SL	10/7/04	F	M1 / H

<b>CdP (Strasbourg)</b>				
<b>Name</b>	<b>Code</b>	<b>D.O.B.</b>	<b>SEX</b>	<b>RANK</b>
Accroc	AC	08/1996	M	H
Alila	AL	08/1999	F	M
Arnaud	AR	07/1998	M	H
Asson	AS	05/1989	F	H
BB (Kiwi)	( - )	05/2006	( - )	( - )
BB (Kolette)	( - )	03/2006	( - )	( - )
BB (Paola)	( - )	10/2006	( - )	( - )
Boy	BY	01/1973	F	L
Kinika	KI	06/1992	F	M
Kiwi	KW	1970's	F	L
Kollette	KO	08/1999	F	H
Olive	OL	09/2000	F	M
Paola	PA	06/2001	F	L
Petula	PE	04/2001	F	M
Pistou	PI	04/2001	M	M
Popeye	PO	05/2001	M	M
Raven	RA	08/2002	M	H
Rosy	RO	05/2002	F	L
Samir	SA	05/2003	M	H
Shaka	SH	07/2003	F	L

*Appendix C – Research site home enclosures*



# Strasbourg CdP Capuchin Housing

